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# A Comparative Analysis of Potential Nitrification and Nitrate Mobility in Forest Ecosystems

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# A COMPARATIVE ANALYSIS OF POTENTIAL NITRIFICATION AND NITRATE MOBILITY IN FOREST ECOSYSTEMS[1]

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*Abstract.* The controls of potential nitrogen mineralization, nitrate production, and nitrate mobilization in a wide range of forest ecosystems were investigated through a combination of field and laboratory experiments. Trenched plot experiments were performed in 17 forests, and laboratory incubation studies of potential ammonium and nitrate production were made on soils from 14 of these sites. The site with the greatest potential for nitrate production in the laboratory was a New Hampshire northern hardwoods forest. Several other sites, including New Hampshire balsam fir, Indiana maple-beech, New Mexico aspen, and Oregon western hemlock forests, also had high potential nitrate production. All of these sites also had rapid nitrate movement to below the rooting zone following trenching in the field.

Of nine processes which could be important in preventing or delaying solution losses of nitrate from disturbed forests, two appeared most important among the forests we examined. Low net nitrogen mineralization (caused by either nitrogen immobilization or low gross nitrogen mineralization) and lags in nitrification (probably caused by either low initial populations of nitrifying bacteria or the allelochemic inhibition of nitrification) were identified as important in several sites and in different regions.

A direct relationship between the amount of nitrogen in annual litterfall and the proportion of forest floor nitrogen mineralized in laboratory incubations was observed, suggesting that refractory organic nitrogen compounds are produced in nitrogen-poor sites. An inverse relationship was found between the amount of nitrogen in litterfall in these and other sites and the carbon:nitrogen ratio of that litterfall, suggesting that the immobilization capacity of litter is increased in nitrogen-poor sites. The presence and length of lags in nitrification were inversely correlated with the mean concentration of mineral nitrogen in mineral soil. These patterns suggest that nitrogen retention within disturbed forest ecosystems can be caused by low nitrogen availability prior to disturbance.

*Key words: disturbance; immobilization; nitrogen cycling; nitrogen mineralization; nutrient loss; resistance.*

## INTRODUCTION

Recognition of the effects of disturbance on element cycling and loss in terrestrial ecosystems has increased in recent years. In part, this emphasis represents the continuation of a long-standing concern among forest scientists over the possibility that forest clearing causes nutrient losses which could affect the long-term productivity of a site (cf. Hesselman 1917*a*, *b* in Stålfelt 1960, Romell 1935, Likens et al. 1978, Leaf 1979). More recently, practical concern has also focused on the effects of disturbance on downstream water quality (Likens and Bormann 1974, Sollins et al. 1981). Element losses following disturbance have also been used to characterize the degree of homeostasis in forest biogeochemical cycles (Bormann and Likens

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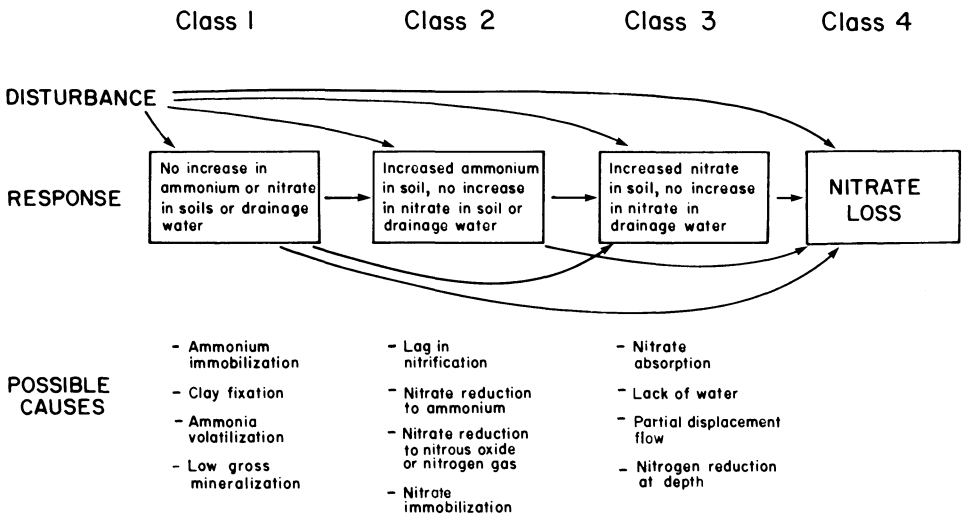


FIG. 1. The possible responses of soil and solution inorganic nitrogen to disturbance, and the processes which could cause each response. All of the responses could be observed sequentially in a single site, or any of the responses could be absent.

1979, Swank and Waide 1980), and they have been suggested as a useful measure of ecosystem-level stability (O'Neill et al. 1977).

Studies of nutrient cycling and loss have emphasized nitrogen for several reasons:

1) Nitrogen is the element most often limiting to forest growth, and substantial losses following disturbance could slow forest regrowth.

2) Following disturbance, losses of nitrogen (especially nitrate) often increase more than do losses of any other nutrient element (Likens et al. 1970, Swank and Douglass 1977, Vitousek et al. 1979).

3) The increased production and loss of nitrate in disturbed forests can cause increased solution losses of cations, since the supply of mobile anions controls cation leaching (Nye and Greenland 1960, Likens et al. 1969, Johnson and Cole 1980).

4) Increased nitrification can either directly (Bremner and Blackmer 1978) or indirectly (Firestone et al. 1979) increase rates of nitrous oxide production and volatilization.

A literature review (Vitousek and Melillo 1979) showed that nitrogen losses from disturbed forests were elevated because of increases in nitrate concentrations in drainage water, but that the magnitude of increases varied from barely detectable at many sites to very high nitrate losses at a few sites. The most extreme nitrate losses were observed in sites where herbicides were applied to inhibit vegetation regrowth, but high losses have also been observed in several sites in New Hampshire and southern Sweden that were commercially clearcut and not herbicide treated (Pierce et al. 1972, Wiklander 1981).

This variability in nitrogen losses from disturbed forests raises two questions. First, why does any forest ecosystem have the potential to lose large amounts of nutrients following disturbance? Second, what processes within disturbed forests could prevent or delay such losses?

We believe that the potential for nitrogen losses following disturbance exists because of the large amounts of nitrogen circulated annually within undisturbed or aggrading forests. Nitrogen uptake in such forests equals or slightly exceeds net nitrogen mineralization, and both uptake and mineralization are generally 10–100 times greater than annual losses (Rosswall 1976, Stone et al. 1979). A destructive disturbance reduces, at least temporarily, the ability of plants to take up mineralized nitrogen. At the same time, removal of the canopy can increase nitrogen mineralization by increasing soil temperature and moisture (Marks and Bormann 1972, Stone 1973, Harcombe 1977), by increasing the frequency and intensity of wetting and drying cycles in the forest floor (Campbell et al. 1972), by increasing the availability of substrate for mineralization (Rice 1979, Johnson and Edward 1979), and by decreasing resource competition between heterotrophs and mycorrhizae (Gadgil and Gadgil 1978). Together, these processes cause nitrogen mineralization in excess of the requirements of regrowing vegetation. The amount of this excess mineralized nitrogen varies among sites depending on: (1) the extent to which plant nitrogen uptake is decreased by disturbance, (2) the rate of nitrogen mineralization prior to disturbance, and (3) the amount of increase in the rate of mineralization caused by disturbance (Vitousek 1981).

If all of this excess mineralized nitrogen were to be lost, nitrogen losses would always be greatly elevated in disturbed relative to control forests. Nine other processes can prevent solution losses of mineral nitrogen

from disturbed systems even in the absence of plant uptake of nitrogen, however. These processes are summarized in Fig. 1 and reviewed in more detail in Vitousek and Melillo (1979). Two of these processes (ammonia volatilization and denitrification) reduce nitrate leaching only by causing gaseous losses of nitrogen. Clay fixation holds nitrogen in a form where it may only slowly be made available to regrowing vegetation (but see Bashkin and Kudeyarov 1977). The remaining processes delay nitrate losses by temporarily holding nitrogen in a form where it is either unavailable (e.g., immobilization) or available (e.g., lags in nitrification) for plant uptake.

Regrowing plants eventually re-establish the intrasystem nitrogen cycle by taking up as much nitrogen as is mineralized. They can also reduce the rate of nitrogen mineralization by shading the soil surface, and this latter effect can be important well before plant nitrogen uptake is back to predisturbance levels (Harcombe 1977, Bormann and Likens 1979).

The overall pattern and control of nitrogen losses in disturbed forests can thus be broken down into three components. Given a disturbance which removes vegetation cover but does not interfere with plant regrowth, the magnitude and timing of nitrogen losses are controlled by: (1) the predisturbance net nitrogen mineralization rate and the extent to which it is accelerated by forest canopy removal, (2) an interaction of the processes which can prevent or delay losses of excess mineralized nitrogen (Fig. 1), and (3) the rate of vegetation regrowth and nitrogen uptake. The first two control the relative resistance to perturbation of the nitrogen cycle in a disturbed forest, whereas the third controls relative resilience. Resistance is defined here as the maximum extent of displacement of a system property (in this case nitrate losses) from a predisturbance level, while resilience is defined as the rate at which a system property recovers or returns to within a definable range of the predisturbance level (Webster et al. 1975, Swank and Waide 1980).

Our goal was a systematic, process-based understanding of the resistance component of nitrogen losses from disturbed forest ecosystems. We believe that while both resistance and resilience contribute to the overall ecosystem response, an analysis of resistance alone can show why many forests do not lose large amounts of nitrate following disturbance. Further, the development of a similar understanding of resilience would allow reasonably accurate predictions of the response of any forest to destructive disturbance.

## Research Approach

Nitrogen mineralization rates and most of the processes in Fig. 1 are relatively well understood in isolation, but their relative importance in controlling nitrogen losses from disturbed forest ecosystems is not well known. The processes can be separated into three groups based on their occurrence at different points in the nitrogen cycle (Fig. 1). Our first goal was to identify those sites with a potential for high solution losses of nitrate following disturbance; our second was to determine (for those sites where nitrate losses were low or much delayed) where in the nitrogen cycle losses were prevented.

Accordingly, we measured changes in inorganic nitrogen concentrations in treeless trenched plots within intact forests (Orlov and Koshelkov 1965, Vitousek 1977). Trenching prevented plant uptake of nutrients and water in a way that could be replicated within a site and repeated across a range of forest ecosystems. We used lysimeter measurements of nitrate concentrations in soil water below the rooting zone in these plots to identify sites which did *not* have the potential for large or rapid nitrate losses following disturbance. We then used the pattern of forest floor and surface mineral soil inorganic nitrogen concentrations to determine where in the nitrogen cycle losses were prevented or delayed in those sites (Fig. 1). Finally, we compared the results of the field measurements with laboratory incubations to identify (where possible) which process caused each response observed.

Trenched plots do not duplicate the conditions in disturbed forests, since revegetation is prevented, roots are killed, and the tree canopy remains intact over the trenched plots. They do allow the identification of sites where nitrate can potentially move below the rooting zone and processes which could be important in retaining nitrogen following a large-scale disturbance.

We emphasized inorganic forms of nitrogen in this study because our focus has been on understanding the mechanisms which prevent or delay losses of nitrate following disturbance. Dissolved and fine particulate organic nitrogen are quantitatively the most important forms of nitrogen in water draining many undisturbed or aggrading forests (Swank and Waide 1980, Sollins et al. 1981). Dissolved organic nitrogen concentrations in drainage water may be increased following disturbance in some forests (Sollins and McCorison 1981), but not to the very high levels of nitrate losses observed in certain disturbed forests (Vitousek and Melillo 1979).

## Study Sites

Seventeen sites located in six states were included in this study (Fig. 2). We selected a range of forests dominated by commercially important species or located on the extremes of environmental gradients, including forests where previous stand or watershed level measurements suggested that we would find a wide range of nitrate losses following disturbance.

Particular emphasis was placed on selecting a range of sites supporting coniferous and deciduous vegetation, since Stone (1973) and others have suggested that nitrogen mineralization and/or nitrification are suppressed in coniferous forest soils. Seven deciduous

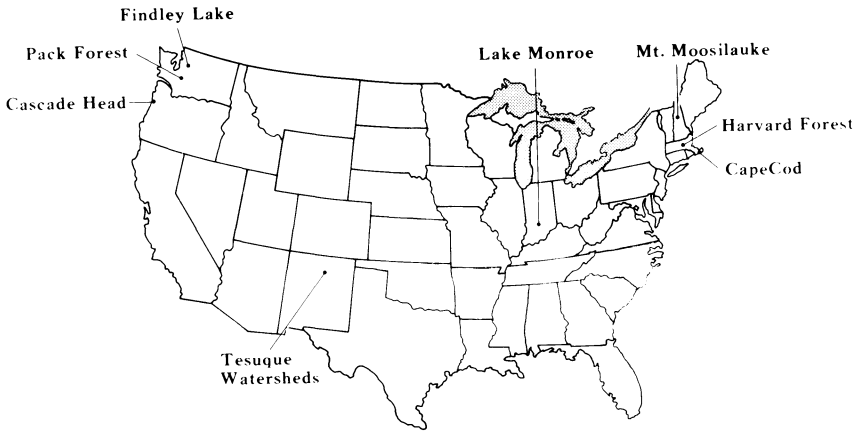


FIG. 2. Locations of the study sites. See Table 1 for general information on each site.

and 10 coniferous sites (including two pine plantations on former hardwood sites) were included in the study. Acid and circumneutral soils were also selected, as nitrification by laboratory cultures is suppressed under acid conditions (Alexander 1976). The sites with extreme climatic conditions included subalpine sites (New Hampshire, New Mexico, Washington), very wet sites (Washington, Oregon), and a very dry site (New Mexico). The locations, climatic properties, and soil types for these sites are summarized in Table 1, and their vegetation and soil characteristics are summarized under Results.

## METHODS

### *Field experiments*

Trenches were dug around 20 1 × 1 m (or larger) plots in each site. Trenched and comparable control plots were located in large areas free of trees, large logs, or boulders. The trenches were dug to a depth of 0.7–1.2 m, the inner edge of each trench was lined with two layers of 0.15 mm thick (6-mil) plastic, and the trenches were then refilled. All vegetation was clipped at the ground surface in each plot, and repeated clipping prevented the establishment of any vegetation in the plots.

Porous cup soil water samplers (lysimeters) were installed in 10 of the trenched and 10 control plots in each site. Each hole was augered to 55–75 cm, which was below almost all of the fine roots and most of the coarse roots. Each cup was firmly placed in silica flour which had been poured into each hole, and each hole was filled with the original soil. The initial samples had rather variable nitrate concentrations, resulting perhaps from soil profile disturbance during installation, but nitrate concentrations stabilized within 2–3 mo.

Lysimeter samples were collected weekly throughout the experiment whenever snow depth allowed access to the lysimeters. After each collection, the tension was reset to 20 kPa with a vacuum pump. Extensive tests during the summer of 1977 showed that ammonium and nitrate concentrations did not change significantly during the maximum of 1 wk that the samples remained within the cups in the field.

To reduce the number of chemical analyses, 10% of the volume of each weekly collection from each lysimeter was used to accumulate a monthly composite sample for that lysimeter. One composite sample per lysimeter per month was analyzed for ammonium and nitrate as described below.

The other 10 trenched plots and an additional 10 control plots were used for sampling forest floor and surface mineral soil (0–15 cm). Mineral soil was sampled periodically with a 2 cm diameter corer, while forest floor was sampled either by collecting a known area or with a 6 cm diameter corer. Forest floor and mineral soil samples were subsampled immediately, and a subsample was weighed and dried to constant mass at 80°C to determine water content. Another 10 g (wet mass) of fresh mineral soil (or 2–3 g of forest floor) from each plot were immediately placed in 100 mL KCl (148 g/L) with phenylmercuric acetate (PMA) at 0.5 mg/kg added as a preservative, mixed, and set aside for 24 h. The samples were then centrifuged for 5 min at 2000 rpm and the supernatant was stored at 4° for chemical analyses.

### *Laboratory experiments*

Samples of forest floor and surface mineral soil from most of the sites were incubated in the laboratory to determine their nitrogen mineralization potential and nitrification potential. Numerous techniques for these measurements have been proposed (Keeney 1980, Powers 1980); we used an aerobic incubation since we wanted to measure both nitrogen mineralization potential and nitrate production under comparable conditions.

Samples for the laboratory measurements were collected from untrenched areas in most of the sites in late summer, 1979, a time when inputs of organic material with a high C:N ratio should have been minimal.

TABLE 1. Climatic and site characteristics of the study areas. See Fig. 2 for locations.

| Location | Site | Soil subgroup | Soil series | Parent material | Aspect | Slope | Elevation (m) | Precipitation (cm) | Mean Jan Temp. (°C) | Mean July Temp. (°C) |
|---|---|---|---|---|---|---|---|---|---|---|
| Indiana | | | | | | | | | | |
| Lake Monroe | maple | Typic Dystrochrept | Berks | loess, siltstone | N | 50% | 190 | 112 | 1 | 26 |
| Lake Monroe | oak | Typic Dystrochrept | Muskingum | loess, siltstone | ridgetop | 0–10% | 220 | 112 | 1 | 26 |
| Lake Monroe | pine | Typic Hapludalf | Hagerstown | limestone | W | 10% | 225 | 112 | 1 | 26 |
| New England | | | | | | | | | | |
| Cape Cod | oak-pine | Typic Udipsamment | Plymouth | granite-gneiss till | SE | 0–10% | 20 | 102 | 0 | 17 |
| Harvard Forest | red pine | Typic Dystrochrept | Gloucester | granite-mica schist till | S | 0–5% | 360 | 107 | −2 | 20 |
| Harvard Forest | oak-red maple | Typic Dystrochrept | Gloucester | granite-mica schist till | S | 0–5% | 360 | 107 | −2 | 20 |
| Mt. Moosilauke | northern hardwoods | Aquic Fragiorthod | Becket | Littleton mica schist | SE | 10% | 670 | 150 | −9 | 15 |
| Mt. Moosilauke | balsam fir | Typic Cryorthod | none | Littleton mica schist | W | 7% | 1220 | 220 | −9 | 12 |
| New Mexico | | | | | | | | | | |
| Tesuque watersheds | ponderosa pine | Typic Ustorthent | Mirabal | Embudo granite | SW | 12% | 2740 | 45–65 | −5 | 18 |
| Tesuque watersheds | mixed conifer | Typic Udorthent | Hyde | Embudo granite | SW | 10% | 2720 | 45–65 | −5 | 15 |
| Tesuque watersheds | aspen | Typic Cryochrept | Medio | Embudo granite | WSW | 10% | 3110 | 49–75 | −7 | 12 |
| Tesuque watersheds | spruce-fir | Dystric Cryochrept | Nambe | Embudo granite | W | 15% | 3415 | 55–85 | −10 | 10 |
| Pacific Northwest | | | | | | | | | | |
| Cascade Head | coastal hemlock | Typic Haplohumult | Tyee | marine siltstone | ridgetop | 0–10% | 200 | 300 | 5 | 15 |
| Pack Forest | alder | Typic Haplumbrept | none | andesitic colluvium | NW | 15% | 300 | 155 | 2 | 12 |
| Pack Forest | old Douglas-fir | Typic Haplumbrept | Wilkinson | lacustrine silt under colluvium | NE | 5% | 240 | 150 | 2 | 12 |
| Pack Forest | poor-site Douglas-fir | Typic Dystrochrept | Everett | glacial outwash | level | 0% | 220 | 150 | 2 | 12 |
| Findley Lake | Pacific silver fir | Typic Fragiorthod | none | volcanic ash, andesite till | SW | 0–5% | 1150 | 350 | −3 | 11 |

Large samples (several kilograms) of forest floor and mineral soil were collected at 4–5 points in each site and composited. Preliminary incubations demonstrated that the inclusion of the L horizon in the incubations decreased net nitrogen mineralization in some sites, probably because of nitrogen immobilization in the fresher litter. The entire forest floor was used in the sites where the L horizon did not affect mineralization (the New Mexico and Pacific Northwest sites), while only the F and H horizons were used in the other sites. Wood and large roots were removed from the forest floor composites, and mineral soil composites were passed through a 4-mm screen. Sieving, sorting, and mixing were carried out on fresh soils immediately after collection. The water content of the composite samples was adjusted to −10 kPa on laboratory lysim-

eters, and eight subsamples each of the mixed forest floor and mineral soil composites were extracted in KCl (148 g/L) as described above to allow the determination of initial nitrogen concentrations.

Sixty-four 10-g subsamples of mineral soil (or 3 g of forest floor) from the composites were then placed in covered plastic cups, each of which had a small hole in the lid to allow aeration. The cups were incubated in a dark, humid growth chamber at 20°. The water content of the samples was maintained near −10 kPa by monitoring water loss from the cups gravimetrically, and adding distilled water as necessary to replenish the initial levels. Eight cups/wk of each horizon were removed from the growth chamber and extracted in KCl (148 g/L) as described above.

### *Chemical methods for nitrogen analyses*

Ammonium and nitrate were determined using Technicon AutoAnalyzer II instruments (Technicon Instrument Systems 1976). Samples from the field experiments were preserved with phenylmercuric acetate (PMA) at 0.5 mg/kg and shipped to analytical laboratories at Indiana University and the University of New Mexico. Analyses for the laboratory experiments were carried out on similar instruments in all five of our institutions. Samples from the field experiments were exchanged among all of the analytical laboratories; the results in different laboratories never varied systematically and differences rarely exceeded 10% for any individual sample.

The analytical method for nitrate used in all labs (cadmium reduction to nitrite followed by color development with sulfanilamide and napthylethylenediamine) included nitrite with nitrate. Independent nitrite analyses were done on the AutoAnalyzers frequently, and substantial nitrite concentrations (>10% of nitrate plus nitrite) were never detected in samples from the field measurements or in laboratory incubations.

Three different analytical methods for ammonium were used in the different laboratories, including a phenol method at pH 14 (Washington, New Mexico, New Hampshire), a phenol method at pH 9.5 (Massachusetts), and a salicylate-nitroprusside method (Indiana). All methods were equally effective in determining ammonium, but comparisons with distillation showed that they were differentially subject to positive interferences by free amino acids (White and Gosz 1981). These interferences had little effect on the field results, but they could have inflated $NH_4$-N values by as much as 20–30% in laboratory incubations of forest floor under the worst conditions. The interference was most severe in the pH 14 phenol method (where all amino acid N was read as ammonium), intermediate in the salicylate/nitroprusside (30% of amino acid N appeared as ammonium), and insignificant in the pH 9.5 phenol.

Blanks and standards were made up in distilled water for lysimeter analyses and in KCl (148 g/L) for extractions. Forest floor extracts from several sites had slope interferences for ammonium or nitrate, and method-of-addition analyses were used in those sites.

### *Site characterization*

Our initial choice of sites depended in part on the availability of already existing information on site characteristics. While the laboratory methods used for site characterization were identical in all cases, rather different sampling methods and numbers of replicates had been used in some of the sites. Where necessary, further site characterization was done in this study.

At least three different pits were used for soil description in all sites. Soil was collected from these pits using either three 6 cm diameter soil cores at each depth of excavation or known volumes. The soil was passed through a 2-mm sieve, and the volume of inclusions >2 mm was determined by displacement. The bulk density of the <2 mm fraction was then calculated for each of the horizons, and all further mineral soil measurements were made on this fraction. A different procedure was followed with forest floors, where the horizon mass (with and without wood) was determined.

Samples from these soil pits were used for all of the chemical characterizations of deeper (>15-cm) horizons. Additional soil cores were collected for forest floor and surface mineral soil characterization in several of the sites (10 in the Indiana and Massachusetts sites, 12 in New Mexico).

Soil texture was determined by the hydrometer method (Day 1965). Organic carbon was determined in the mineral soil by trapping $CO_2$ released upon pyrolysis; it was estimated in the forest floor from mass loss upon ashing for 4 h at 500° (assuming carbon was 48% of the volatile material). Total nitrogen was determined by persulfate/peroxide digestion in a block digestor followed by analysis for ammonium on a Technicon AutoAnalyzer II.

Soil pH was determined on freshly collected samples in 2:1 (litres : kilogram) 0.01 mol/L $CaCl_2$. Cation exchange capacity and exchangeable cations were determined following Chapman's (1965) procedure, with the cations analyzed by atomic absorption spectrophotometry following the addition of $LaCl_2$ in 50% HCl. Ammonium fluoride extractable phosphorus was measured following Jackson (1958).

All woody plants >2.5 cm dbh were censused on the study sites (0.2–0.8 ha), and the age and height of several (at least three) canopy dominants were determined. Litterfall was collected for at least 2 yr in litter traps in each site. Fifteen 0.5-$m^2$ rectangular traps were used in the Indiana sites, 20 0.041-$m^2$ rectangular traps were used in Massachusetts, 15 0.114-$m^2$ circular traps in New Hampshire, 4 1-$m^2$ square traps in the New Mexico sites other than the aspen (where 10 0.5-$m^2$ traps were used), and 8 0.25-$m^2$ square traps in the

TABLE 2. Vegetation and stand characteristics, litterfall, and litterfall nitrogen in the study areas. The density and basal area of each stand are for all trees >1 cm dbh; the ages and heights reported are the means of three or more representative canopy trees.

| Site | Density (stems/ha) | Basal area ($m^2$/ha) | Age (yr) | Height (m) | Annual litterfall (kg/ha) | Litterfall nitrogen (kg/ha) | Dominant trees |
|---|---|---|---|---|---|---|---|
| Indiana | | | | | | | |
| Maple | 592 | 21 | 95 | 32 | 5230 | 48 | *Acer saccharum*<br>*Fagus grandifolia*<br>*Quercus rubra* |
| Oak | 1087 | 30 | 81 | 24 | 6800 | 62 | *Quercus rubra*<br>*Quercus velutina*<br>*Quercus alba*<br>*Carya* spp.<br>*Acer saccharum* |
| Shortleaf pine plantation | 2390 | 40 | 33 | 15 | 4960 | 38 | *Pinus echinata*<br>*Acer rubrum* |
| New England | | | | | | | |
| Oak-pine | 2020 | 20 | 65 | 9 | 4220 | 36 | *Quercus alba*<br>*Quercus rubra*<br>*Quercus velutina* |
| Red pine plantation | 1506 | 63 | 55 | 20 | 7260 | 40 | *Pinus resinosa* |
| Oak-red maple | 2365 | 32 | 50 | 17 | 4890 | 41 | *Quercus rubra*<br>*Acer rubrum* |
| Northern hardwoods | 1275 | 33 | 66 | 22 | 4780 | 64 | *Acer saccharum*<br>*Fagus grandifolia*<br>*Betula lutea* |
| Balsam fir | 1625 | 46 | 75 | 11 | 4020 | 62 | *Abies balsamea*<br>*Betula cordifolia* |
| New Mexico | | | | | | | |
| Ponderosa pine | 1422 | 37 | 200 | 18 | 2320 | 6.4 | *Pinus ponderosa* |
| Mixed conifer | 1184 | 56 | 200 | 20 | 3900 | 18 | *Pseudotsuga menziesii*<br>*Abies concolor* |
| Aspen | 2270 | 36 | 60 | 16.5 | 2530 | 15 | *Populus tremuloides* |
| Spruce-fir | 1300 | 42 | 300 | 16 | 1106 | 5.6 | *Picea engelmannii*<br>*Abies lasiocarpa* |
| Pacific Northwest | | | | | | | |
| Coastal hemlock | 370 | 102 | 120 | 45 | 6200 | 44 | *Tsuga heterophylla*<br>*Picea sitchensis* |
| Alder | 700 | 45 | 40 | 21 | 4900 | 90 | *Alnus rubra* |
| Douglas-fir | 420 | 83 | 300 | 62 | 3800 | 27 | *Pseudotsuga menziesii* |
| Douglas-fir | 610 | 40 | 45 | 26 | 3300 | 21 | *Pseudotsuga menziesii* |
| Silver fir | 510 | 74 | 200 | 37 | 2180 | 12 | *Abies amabalis*<br>*Tsuga mertensiana* |

Pacific Northwest sites other than the Pacific silver fir (where 48 0.25-$m^2$ traps were used). Only leaves, reproductive parts, and woody litter <1 cm in diameter were included in the site characterizations. The nitrogen content of litterfall was determined using the procedures outlined above.

## RESULTS

### *Field results*

The vegetation characteristics, litterfall dry mass, and litterfall nitrogen content of each of the sites are summarized in Table 2. Forest floor and soil characteristics are summarized in Table 3. As these results demonstrate, a wide range of site conditions was included in this study. Annual nitrogen return to the soil in litterfall ranged from 5.6 to 90 $kg \cdot ha^{-1} \cdot yr^{-1}$, surface mineral soil pH from 3.2 to 6.8, and forest floor carbon:nitrogen ratios from 19 to 52.

Trenching effects upon ammonium and nitrate concentrations in forest floor and surface mineral soil and nitrate concentrations in lysimeters are summarized in Figs. 3–10. These figures show mean trenched plot minus mean control plot concentrations at each time. No attempt was made to adjust lysimeter concentrations for differences in the volume of water percolating through trenched and control plots. The amount of

TABLE 3. Soil characteristics of the study sites. See text for methods.

| | Bulk density (g/cm³)* | Inclusion volume (%) | Sand (%) | Silt (%) | Clay (%) | Organic C (%) | pH | Ca meq/100 g | Mg meq/100 g | K meq/100 g | CEC meq/100 g | Total N (%) | Extractable P (mg/kg) | Mean† extractable $NH_4$-N (mg/kg) | Mean† extractable $NO_3$-N (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Indiana | | | | | | | | | | | | | | | |
| Maple | | | | | | | | | | | | | | | |
| FF | 9750 | | | | | 36.8 | 5.7 | 37.8 | 6.6 | 2.2 | 84 | 1.07 | 0.08‡ | 90 | 11.9 |
| 0–15 cm | 0.64 | 4.3 | 14 | 80 | 6 | 1.85 | 5.8 | 6.5 | 0.8 | 0.3 | 16.6 | 0.20 | 55.5 | 4.5 | 2.4 |
| 15–30 cm | 0.76 | 3.5 | 12 | 73 | 15 | 1.21 | 4.3 | 1.6 | 0.4 | 0.3 | 10.8 | 0.11 | 28.4 | 5.3 | 1.4 |
| 30–70 cm | 0.95 | 6.2 | 14 | 70 | 16 | 0.56 | 4.6 | 2.8 | 0.7 | 0.3 | 13.3 | 0.08 | 8.0 | 4.1 | 1.5 |
| Oak | | | | | | | | | | | | | | | |
| FF | 19 400 | | | | | 44.4 | 5.2 | 33.1 | 6.9 | 1.6 | 93 | 1.60 | 0.09‡ | 97 | 4.2 |
| 0–15 cm | 1.0 | 9.4 | 11 | 78 | 11 | 1.83 | 3.8 | 0.8 | 0.3 | 0.3 | 11.1 | 0.13 | 52.4 | 2.1 | 0.4 |
| 15–30 cm | 1.25 | 5.1 | 15 | 78 | 7 | 0.67 | 3.6 | 0.6 | 0.3 | 0.6 | 7.5 | 0.05 | 43.3 | 5.2 | 0.5 |
| 30–70 cm | 1.91 | 18.3 | 16 | 70 | 14 | 0.35 | 4.1 | 1.6 | 1.0 | 0.4 | 12.1 | 0.05 | 29.5 | 4.2 | 0.2 |
| Shortleaf pine | | | | | | | | | | | | | | | |
| FF | 17 250 | | | | | 44.0 | 3.4 | 17.7 | 3.4 | 1.4 | 71 | 0.84 | 0.05‡ | 30 | 1.4 |
| 0–15 cm | 1.07 | 1.0 | 8 | 74 | 18 | 1.07 | 3.7 | 3.0 | 0.7 | 0.3 | 14.4 | 0.07 | 8.8 | 1.0 | 0.3 |
| 15–30 cm | 1.15 | 0.8 | 8 | 70 | 22 | 0.48 | 3.7 | 3.4 | 1.1 | 0.3 | 16.7 | 0.04 | 2.1 | 1.6 | 0.2 |
| 30–70 cm | 1.16 | 2.4 | 14 | 64 | 22 | 0.35 | 3.7 | 3.8 | 2.0 | 0.4 | 19.7 | 0.03 | 0.9 | 1.4 | 0.05 |
| New England | | | | | | | | | | | | | | | |
| Oak-pine | | | | | | | | | | | | | | | |
| FF | 58 200 | | | | | 42.0 | 4.0 | 9.7 | 2.4 | 0.8 | 85 | 1.13 | 0.05‡ | 10.7 | 0.2 |
| 0–15 cm | 1.06 | 15 | 85 | 14 | 1 | 1.07 | 4.5 | 0.1 | 0.1 | 0.1 | 2.2 | 0.05 | 0.6 | 0.2 | 0.1 |
| 15–30 cm | 1.30 | 20 | 83 | 12 | 5 | 0.07 | 4.9 | 0.1 | 0.1 | 0.1 | 1.0 | 0.02 | 0.2 | 1.1 | 0.2 |
| 30–70 cm | 1.38 | 10 | 97 | 2 | 1 | 0.4 | 4.8 | 0.1 | 0.1 | 0.1 | 0.8 | 0.03 | 0.1 | 0.9 | 0.1 |
| Red pine | | | | | | | | | | | | | | | |
| FF | 61 900 | | | | | 32.0 | 3.2 | 10.1 | 4.4 | 4.6 | 72 | 1.22 | 0.06‡ | 54 | 0.3 |
| 0–15 cm | 1.10 | 42 | 62 | 32 | 6 | 6.1 | 3.7 | 0.3 | 0.1 | 0.1 | 8.4 | 0.26 | 1.2 | 1.4 | 0.2 |
| 15–30 cm | 1.53 | 48 | 65 | 30 | 5 | 2.5 | 4.1 | 0.1 | 0.1 | 0.1 | 3.2 | 0.09 | 0.5 | 3.0 | 0.1 |
| 30–70 cm | 1.63 | 43 | 69 | 27 | 4 | 2.2 | 4.4 | 0.1 | 0.1 | 0.1 | 1.2 | 0.04 | 0.2 | 0.8 | 0.1 |
| Oak-red maple | | | | | | | | | | | | | | | |
| FF | 59 600 | | | | | 31.8 | 3.8 | 14.2 | 6.3 | 0.7 | 67 | 1.42 | 0.07‡ | 32.6 | 0.1 |
| 0–15 cm | 1.09 | 30 | 62 | 31 | 7 | 5.9 | 4.0 | 0.4 | 0.1 | 0.1 | 8.6 | 0.29 | 1.4 | 1.4 | 0.2 |
| 15–30 cm | 1.48 | 50 | 63 | 30 | 7 | 3.7 | 4.3 | 0.2 | 0.1 | 0.1 | 3.5 | 0.12 | 0.6 | 4.2 | 0.1 |
| 30–70 cm | 1.54 | 44 | 71 | 25 | 4 | 3.5 | 4.4 | 0.1 | 0.1 | 0.1 | 1.1 | 0.05 | 0.3 | 1.1 | 0.1 |
| Northern hardwoods | | | | | | | | | | | | | | | |
| FF | 58 850 | | | | | 42.7 | 4.0 | 6.2 | 1.3 | 1.1 | 77.9 | 2.01 | 2.2 | 81 | 7.0 |
| 0–15 cm | 0.28 | 7.3 | 68 | 31 | 1 | 15.2 | 4.1 | 0.5 | 0.3 | 0.3 | 33.4 | 0.86 | 2.1 | 12.5 | 2.8 |
| 15–30 cm | 0.62 | 27.9 | 69 | 29 | 2 | 6.1 | 4.3 | 0.5 | 0.2 | 0.2 | 23.2 | 0.34 | 1.6 | 5.6 | 1.4 |
| 30–70 cm | 1.01 | 27.4 | 74 | 23 | 3 | 1.6 | 4.5 | 0.2 | 0.05 | 0.07 | 5.3 | 0.08 | 3.3 | | |
| Balsam fir | | | | | | | | | | | | | | | |
| FF | 117 000 | | | | | 40.2 | 3.1 | 2.7 | 1.0 | 1.1 | 75.9 | 1.55 | 6.3 | 74 | 2.8 |
| 0–15 cm | 1.64 | 35.8 | 62 | 37 | 1 | 7.5 | 3.2 | 0.4 | 0.3 | 0.2 | 26.4 | 0.43 | 2.8 | 9.8 | 1.4 |
| 15–30 cm | 1.64 | | | | | 3.4 | 4.0 | 0.6 | 0.07 | 0.06 | 23.4 | 0.11 | 1.8 | 5.6 | 0 |
| 30–60 cm | 2.5 | 62 | 68 | 28 | 3 | 2.7 | 4.3 | 0.3 | 0.05 | 0.09 | 14.4 | 0.07 | 2.9 | 1.4 | 0 |
| New Mexico | | | | | | | | | | | | | | | |
| Ponderosa pine | | | | | | | | | | | | | | | |
| FF | 113 0000 | | | | | 31.7 | 6.4 | 25.9§ | 4.6§ | 1.1 | 55.7 | 1.10 | 14.5 | 28 | 1.4 |
| 0–10 cm | 1.3 | 24 | 76 | 15 | 9 | 2.4 | 6.8 | 5.2 | 0.8 | 0.6 | 13.0 | 0.08 | 2.1 | 2.1 | 0.1 |
| 10–20 cm | 1.6 | 29 | 64 | 25 | 11 | 1.4 | 5.1 | 3.7 | 0.7 | 0.3 | 9.7 | 0.05 | 1.1 | 1.0 | <0.1 |
| 20–40 cm | 1.7 | 42 | 72 | 18 | 10 | 0.8 | 6.3 | 2.4 | 0.7 | 0.1 | 7.7 | 0.02 | 0.5 | 0.4 | <0.1 |
| Mixed conifer | | | | | | | | | | | | | | | |
| FF | 82 000 | | | | | 42.2 | 5.4 | 91.3§ | 8.9§ | 1.9 | 65.6 | 1.09 | 27.7 | 70 | 2.8 |
| 0–10 cm | 0.80 | 30 | 80 | 12 | 9 | 3.5 | 5.8 | 9.0 | 0.9 | 0.8 | 17.8 | 0.09 | 17.1 | 7.0 | 0.1 |
| 10–40 cm | 1.20 | 40 | 74 | 17 | 9 | 0.8 | 4.0 | 2.5 | 0.4 | 0.5 | 7.4 | 0.08 | 6.9 | 3.5 | 0.1 |
| 40–60 cm | 1.70 | 47 | 76 | 16 | 8 | 0.5 | 5.1 | 3.5 | 0.3 | 0.2 | 6.9 | 0.04 | 7.8 | 2.1 | <0.1 |
| Aspen | | | | | | | | | | | | | | | |
| FF | 28 900 | | | | | 34.6 | 5.0 | 69.4§ | 6.9§ | 2.1 | 89.5 | 1.80 | 25.4 | 98 | 2.5 |
| 0–10 cm | 0.83 | 29 | 67 | 20 | 13 | 3.3 | 4.6 | 3.1 | 0.4 | 0.9 | 19.0 | 0.24 | 2.2 | 12.4 | 0.1 |
| 10–20 cm | 1.10 | 26 | 60 | 24 | 16 | 2.0 | 4.5 | 2.6 | 0.5 | 0.9 | 18.0 | 0.12 | 1.3 | 3.9 | 0.1 |
| 20–60 cm | 1.60 | 22 | 61 | 22 | 16 | 1.3 | 4.6 | 2.0 | 0.4 | 0.3 | 14.8 | 0.11 | 2.3 | 2.4 | <0.1 |
| Spruce-subalpine fir | | | | | | | | | | | | | | | |
| FF | 65 100 | | | | | 37.0 | 5.2 | 45.9§ | 7.3§ | 3.3 | 98.6 | 1.51 | 22.6 | 56 | 0.7 |
| 0–20 cm | 0.93 | 27 | 66 | 13 | 21 | 2.4 | 4.7 | 1.5 | 0.2 | 0.2 | 19.2 | 0.29 | 1.0 | 9.8 | 0.2 |
| 20–40 cm | 1.50 | 51 | 69 | 22 | 9 | 1.5 | 4.2 | 0.4 | 0.04 | 0.1 | 14.1 | 0.14 | 0.4 | 2.8 | <0.1 |

TABLE 3. Continued.

| | Bulk density (g/cm³)* | Inclusion volume (%) | Sand (%) | Silt (%) | Clay (%) | Organic C (%) | pH | Ca meq/100 g | Mg meq/100 g | K meq/100 g | CEC meq/100 g | Total N (%) | Extractable P (mg/kg) | Mean† extractable $NH_4$-N (mg/kg) | Mean† extractable $NO_3$-N (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pacific Northwest | | | | | | | | | | | | | | | |
| Coastal hemlock | | | | | | | | | | | | | | | |
| FF | 21 000 | | | | | 40.8 | 4.1 | | | | 95 | 0.78 | | 31 | 0.2 |
| 0–15 cm | 0.52 | 13 | 20 | 65 | 15 | 13.4 | 3.7 | 5.5 | 10.1 | 1.6 | 62 | 1.29 | 85 | 12 | 4.5 |
| 15–30 cm | 0.79 | 15 | 17 | 60 | 23 | 8.6 | 4.1 | 1.3 | 1.8 | 0.2 | 47 | 0.75 | 27 | | |
| 30–70 cm | 0.92 | 13 | 15 | 62 | 23 | 5.8 | 4.2 | 0.7 | 1.0 | 0.1 | 40 | 0.56 | 0.11 | | |
| Alder | | | | | | | | | | | | | | | |
| FF | 15 000 | | | | | 33.6 | 5.5 | | | | 86 | 1.5 | | 43 | 12.5 |
| 0–15 cm | 0.80 | 20 | 61 | 18 | 21 | 2.2 | 5.1 | 4.1 | 0.9 | 0.3 | 40 | 0.2 | 7.1 | 3.5 | 0.8 |
| 15–30 cm | 1.02 | 50 | 49 | 21 | 30 | 1.5 | 4.5 | 2.9 | 0.6 | 0.2 | 38 | 0.1 | 10.2 | | |
| 30–70 cm | 1.35 | 45 | 51 | 24 | 25 | 0.6 | 4.6 | 1.5 | 0.5 | 0.2 | 40 | 0.08 | 2.2 | | |
| Douglas-fir | | | | | | | | | | | | | | | |
| FF | 12 000 | | | | | 38.4 | 5.1 | | | | 90 | 0.93 | | 37 | 1.1 |
| 0–15 cm | 0.94 | 10 | 42 | 38 | 20 | 1.5 | 4.6 | 3.1 | 1.1 | 0.2 | 45 | 0.19 | 6.1 | 2.2 | 0.1 |
| 15–30 cm | 1.12 | 30 | 46 | 30 | 24 | 1.0 | 4.5 | 2.2 | 0.8 | 0.1 | 40 | 0.17 | 4.1 | | |
| 30–70 cm | 1.35 | 45 | 51 | 24 | 25 | 0.6 | 4.6 | 1.5 | 0.5 | 0.2 | 40 | 0.08 | 2.2 | | |
| Douglas-fir | | | | | | | | | | | | | | | |
| FF | 18 000 | | | | | 35.5 | 4.9 | | | | 95 | 0.98 | | 67 | 1.2 |
| 0–15 cm | 1.31 | 55 | 75 | 20 | 5 | 0.9 | 4.3 | 1.2 | 0.08 | 0.1 | 18 | 0.11 | 3.1 | 2.7 | 0.2 |
| 15–30 cm | 1.40 | 60 | 81 | 15 | 4 | 0.24 | 4.7 | 0.2 | 0.03 | 0.04 | 6 | 0.04 | 1.1 | | |
| 30–70 cm | 1.64 | 80 | 87 | 10 | 3 | 0.14 | 5.1 | 0.1 | 0.02 | 0.02 | 4 | 0.01 | 1.2 | | |
| Pacific silver fir | | | | | | | | | | | | | | | |
| FF | 145 000 | | | | | 35.0 | 3.4 | | | | 120 | 1.1 | | 38 | 0.5 |
| 0–15 cm | 0.65 | 10 | 68 | 2 | 30 | 2.4 | 4.0 | 0.25 | 0.25 | 0.21 | 10 | 0.1 | 2.5 | 4.4 | 0.1 |
| 15–30 cm | 0.65 | 40 | 75 | 5 | 20 | 5.9 | 4.4 | 0.1 | 0.1 | 0.1 | 38 | 0.2 | 5.4 | | |
| 30–70 cm | 1.05 | 75 | 27 | 33 | 40 | 10.1 | 4.4 | 0.1 | 0.1 | 0.1 | 44 | 0.4 | 4.9 | | |

* Forest floor horizon mass in kg/ha.
† Mean of all growing season samples for FF and 0–15; usually only one sample date for deeper horizons.
‡ Total P.
§ These high values for exchangeable calcium and magnesium may in part reflect the presence of calcium and magnesium salts made soluble during the extractions.

water was always greater in trenched than in control plots, however, so that the effects of trenching on nitrate losses are understated by the lysimeter results.

To provide a baseline for the concentration differences presented in Figs. 3–10, mean ammonium and nitrate concentrations in the forest floor and mineral soil of the control plots in each site are summarized in Table 3. Results for ammonium concentrations in the lysimeters are not reported in the figures because ammonium nitrogen concentrations in control lysimeters were always very low (<0.1 mg/l), and concentrations in trenched plot lysimeters were equally low in all sites except the New England oak-pine. $NH_4$-N concentrations of up to 1 mg/L were observed there in the first growing season following trenching. Mean nitrate nitrogen concentrations in the control lysimeters were low (<0.25 mg/L) in all sites except the New Hampshire northern hardwoods and Indiana maple-beech sites (both ≈0.5 mg/L) and the Pacific Northwest alder site (≈4.2 mg/L), so the differences between trenched and control plot lysimeter nitrate concentrations largely reflect the trenched plot concentrations.

A. *Indiana sites.*—Ammonium and nitrate concentrations in the forest floors of the Indiana sites were rather variable, and few statistically significant ($t$ test on log-transformed data, $\alpha = .05$) increases in trenched relative to control plots were observed (Fig. 3). Concentrations of ammonium and nitrate in the mineral soils were more consistent. The maple site trenched plots had increased nitrate concentrations early in the first growing season following trenching (Fig. 4). The delay over the first winter was probably caused by low temperatures, since additional plots trenched in late May 1978 had soil nitrate concentrations as high as the older trenched plots by late June 1978. Ammonium concentrations in the surface mineral soil increased significantly early in the first growing season in the oak site, followed 3 mo later by an increase in soil nitrate concentrations. In the pine site, ammonium concentrations in the mineral soil increased slowly through the first growing season, and no increase in soil nitrate was observed until the second growing season following trenching.

Substantially elevated nitrate concentrations in the trenched plot lysimeters were observed in the maple and oak sites several months after the increase in mineral soil nitrate in those sites (Fig. 4). Much smaller (but still significant) increases in nitrate concentrations in trenched plot lysimeters were observed in the pine

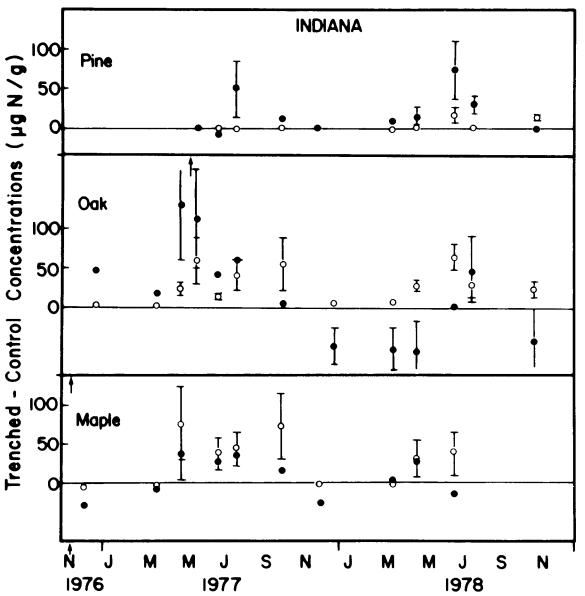


FIG. 3. Responses of extractable $NH_4$-N (●) and $NO_3$-N (○) to trenching in the Indiana forest floors. Values reported are the mean (± SE) of the trenched plot minus the control plot concentrations. Where no error bars are shown, SE is smaller than the symbol. The arrows on the *X* axes show when the plots were trenched in that site.

site several months after the peak in soil nitrate concentrations. Distinct seasonal variations in both mineral soil and lysimeter nitrate concentrations in the trenched plots occurred in the maple site, with peak soil concentrations in the summer and peak lysimeter concentrations several months later (Fig. 4). A similar pattern was observed in the oak mineral soil in both years and in the pine mineral soil in the 2nd yr.

B. *New England sites.*—Significant differences in ammonium concentrations between trenched and control plot forest floors were evident in all of the New England sites (Fig. 5). This result suggests that root uptake is more important in the heavier New England forest floors (Table 3) than in Indiana, and we did observe more fine roots in New England forest floors.

The patterns of changes in mineral soil ammonium and nitrate concentrations following trenching were similar in all three Massachusetts sites, although the magnitude of response differed among sites. In each site there was a significant increase in soil ammonium concentrations in the first growing season, followed by a significant increase in soil nitrate concentrations sometime in the second growing season (Fig. 6). Lysimeter nitrate concentrations increased slightly but significantly during the first growing season in the oak-pine site, then increased to much higher levels in the second and third growing seasons. Lysimeters in the other two sites did not show significant increases until the second growing season, and neither had lysimeter nitrate concentrations approaching those in the oak-pine. All three sites had seasonal cycles in nitrate concentrations in trenched-plot lysimeters. The peak concentrations in the oak-pine site were displaced towards midsummer relative to the others, perhaps because of the low water-holding capacity and rapid leaching of this sandy soil.

The sampling record is constricted in the two New Hampshire sites because of frozen soils and extended snow cover. Both ammonium and nitrate concentrations were elevated in each growing season in the mineral soil of these sites, and the increase in soil nitrate concentrations was particularly striking in the northern hardwoods sites (Fig. 6). Nitrate concentrations below the rooting zone were also significantly elevated in lysimeter samples in each growing season.

We were concerned that we could have missed a delay in nitrate loss below the rooting zone in the balsam fir site, so five additional trenched plots were installed in this site in June 1978. Significantly elevated nitrate concentrations were observed below the rooting zone in these plots only 24 d after trenching.

C. *New Mexico sites.*—Soils at all of the New Mexico sites were frozen and snow covered during the winter months, preventing sample collection. During the summer and fall months of 1977 the soils were too dry to permit any lysimeter collections at the pine and mixed conifer sites. At the aspen and spruce-fir sites the trenched plots were moist enough to allow lysimeter collections, but the control plots were dry due to plant water uptake. The wetter summer conditions in 1978 allowed lysimeter collections from the trenched plots of all sites, but again the control plots were dry.

The pine site had elevated ammonium concentrations in both forest floor and mineral soil in trenched plots in the second growing season after trenching (Figs. 7, 8). Soil nitrate concentrations in trenched plots then rapidly exceeded those in control plots, followed by an increase in trenched plot lysimeter nitrate concentrations at the end of the second growing season (Fig. 8).

Nitrate concentrations in the soil and forest floor of trenched plots increased and ammonium concentrations decreased following trenching in both the aspen and mixed conifer sites. The increases in nitrate concentrations were more rapid in the aspen, where the eventual magnitude of increase was also greater (Figs. 7, 8). Significantly elevated nitrate concentrations in lysimeters were observed in both the mixed conifer and aspen sites in the second growing season following trenching (Fig. 8); in the third growing season, trenched-plot lysimeters in the mixed conifer site had the highest nitrate concentrations observed in any of our sites.

The spruce-fir site had significantly elevated ammonium concentrations in the forest floor and soil of trenched plots in the second growing season. No increase in nitrate concentrations in soil was observed, however (Figs. 7, 8). Lysimeter nitrate concentrations

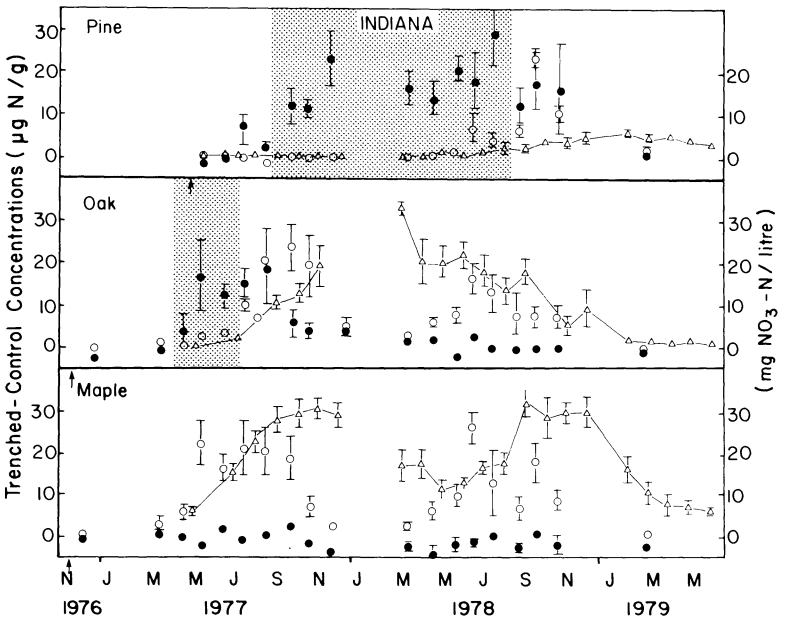


FIG. 4. Responses of extractable $NH_4$-N (●) and extractable $NO_3$-N (○) to trenching in surface mineral soil (0–15 cm) in the Indiana sites. Responses of nitrate-nitrogen concentrations in lysimeters below the rooting zone (△—△) are also reported. Values reported are the mean (± SE) of the trenched plot minus the control plot concentrations. The shaded area represents the time that ammonium concentrations were significantly elevated in trenched plots before nitrate concentrations also became significantly elevated. Ammonium-nitrogen concentrations in lysimeters are not reported because they were <0.1 mg/L in both trenched and control plots. The arrows on the *X* axes show when the plots were trenched in that site.

remained low until 34 mo after trenching, when a small but significant increase in lysimeter nitrate concentrations was finally observed.

D. *Pacific Northwest sites.*—Forest floor and mineral soil ammonium and nitrate concentrations in the Northwest sites were highly variable both spatially and temporally, and many of the large observed differences between trenched and control plots (Fig. 9) were not statistically significant. The results of the lysimeter measurements in these sites (Fig. 10) were much less variable. High concentrations of nitrate below the rooting zone in trenched plots were observed in the first growing season following trenching in the alder and coastal hemlock sites, and a distinct seasonal pattern of high nitrate concentrations in trenched plots similar to that observed in several northeastern hardwood sites was apparent in the hemlock site. The old-growth Douglas-fir site had high but somewhat delayed elevated nitrate concentrations in trenched plot lysimeters, while trenched plots in the poor-site Douglas-fir had only small increases in lysimeter nitrate concentrations. No significant increase in nitrate concentrations in trenched plots was observed in the silver fir site in four growing seasons of sampling.

## *Laboratory results*

The results of the laboratory incubation studies for 14 sites are summarized in Figs. 11–14. For these laboratory measurements, we defined lags in nitrogen mineralization as occurring (a) when there was no net production of mineral nitrogen in a horizon, or (b) when the rate of net production of mineral nitrogen accelerated over time. Lags in nitrification were similarly defined. We defined the end of a lag period for nitrification as occurring (a) when the slope of the net accumulation curve for nitrate (the upper bound on the shaded areas in Figs. 11–14) equalled or exceeded the slope of the net accumulation curve for total mineral nitrogen (the uppermost line on Figs. 11–14), or (b) when the nitrate accumulation curve approached a straight line with a positive slope.

A. *Indiana sites.*—Net mineralization and nitrification both proceeded rapidly with no lags in either the forest floor or mineral soil of the maple site. Nitrogen mineralization was also rapid in the oak forest floor and mineral soil, but nitrification lagged behind mineralization in both. Once nitrification rates equalled mineralization rates, which occurred rapidly in the forest floor, the proportion of the ammonium oxidized per week was much less in the oak than in the maple, and consequently the ammonium pool size remained larger in the oak site. The pine forest floor had a much slower rate of net nitrogen mineralization, and no nitrate was produced in the 8-wk incubation (although some was generally produced by the 13th wk). No net nitrogen mineralization occurred in the pine mineral soil (Fig. 11).

B. *New England sites.*—The northern hardwoods sites had the highest nitrogen mineralization potential in both forest floor and mineral soil that we observed,

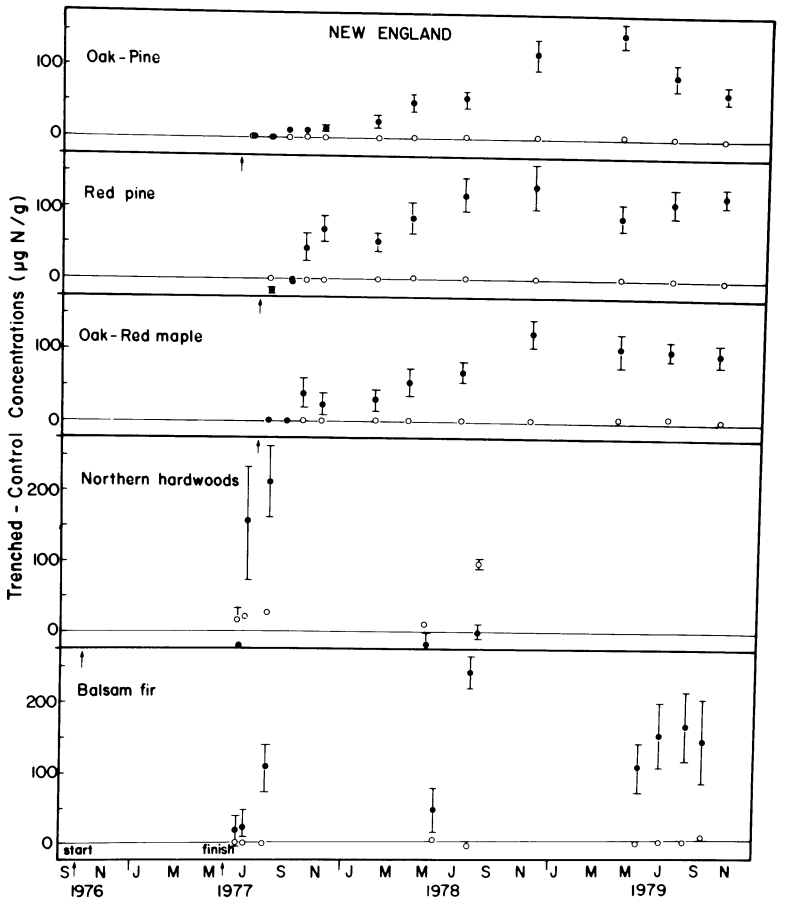


FIG. 5. Responses to trenching in the New England forest floors. See Fig. 3 for definitions of the values and symbols.

and more than half of the total nitrogen mineralization in forest floor occurred in the 1st 2 wk of incubation. No lags in nitrification (as defined above) were observed in northern hardwoods, although net nitrate production was slower than net mineralization and a substantial ammonium pool accumulated (Fig. 12). The balsam fir site also had a relatively high mineralization potential (the second highest of all of our mineral soils), but appreciable net nitrate production occurred only in the mineral soil. The two Massachusetts sites had much lower net mineralization and net nitrate production (Fig. 12).

C. *New Mexico sites.*—An initial decrease in mineral nitrogen concentrations upon incubation was observed in all of the New Mexico forest floors. Subsequent nitrogen mineralization was substantial in the aspen and mixed conifer soils and forest floors, and net nitrate production occurred immediately in the aspen soil and after a brief lag in the mixed conifer soil. Lags in net nitrate production were longer in the forest floor than in the mineral soil in both sites. The ponderosa pine site had a low net nitrogen mineralization in both the forest floor and mineral soil, and nitrate was produced after a lag in the soil but not at all in the forest floor. Net nitrogen mineralization was also low in the spruce-fir site, and nitrate production was negligible in both the forest floor and mineral soil (Fig. 13).

D. *Pacific Northwest sites.*—Nitrogen mineralization was relatively rapid in the coastal hemlock site, and net nitrate production was not delayed in forest floor and briefly if at all delayed in mineral soil. The proportion of available ammonium oxidized was relatively small in the hemlock forest floor but large in the mineral soil. Nitrogen mineralization was slower in the poor-site Douglas-fir and nitrate production was delayed for 4 wk in both forest floor and mineral soil. Net nitrogen mineralization was slow and nitrate production was absent in the silver fir site (Fig. 14).

## DISCUSSION

We used the results of the field trenched plot studies and laboratory incubations for three purposes. First, we identified those sites which had rapid nitrate mobilization to below the rooting zone after trenching. Second, for those sites where nitrate production or mobilization was prevented or delayed, we determined where in the nitrogen cycle the delay occurred (Fig.

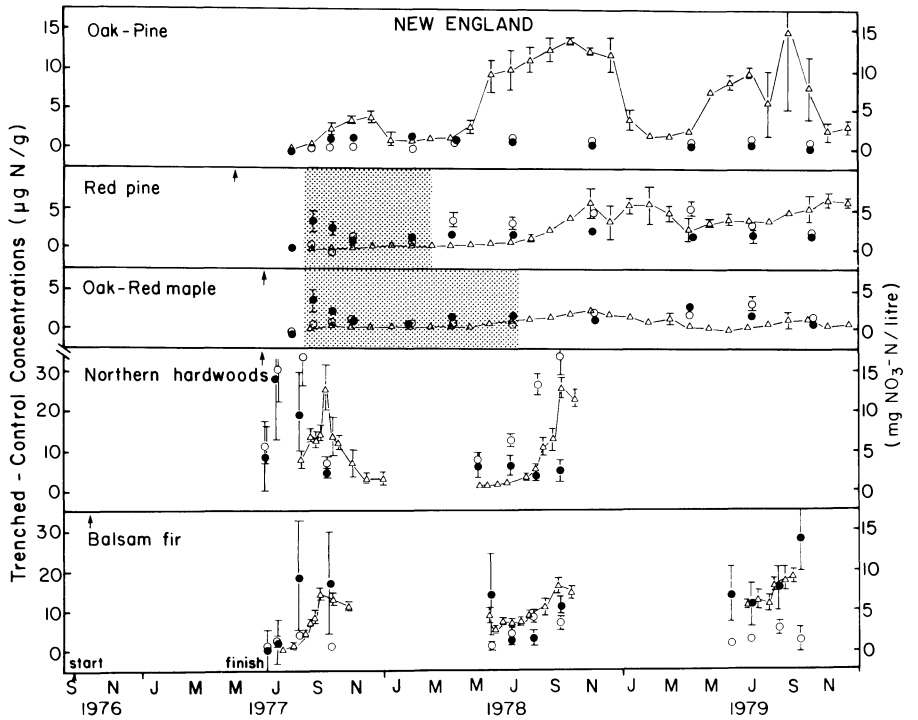


FIG. 6. Responses to trenching in the New England mineral soils and lysimeters. Elevated ammonium concentrations in lysimeters were observed following trenching in the oak-pine site (see text). See Fig. 4 for definitions of the values and symbols.

1) and, if possible, what process caused the delay. Finally, we used the information on site characteristics (Tables 2, 3) to try to determine why particular processes prevented or delayed nitrate mobilization in particular kinds of sites.

### *Identification of sites with high potential losses*

High nitrate concentrations in trenched plot lysimeters appeared relatively rapidly below the rooting zone in the Indiana maple, New England northern hardwoods and balsam fir, and Pacific Northwest hemlock and alder sites. These results cannot be used directly to calculate nitrate losses in kilograms per hectare per year, since water flux was not measured. Nonetheless, water flux through the trenched plots was increased relative to the control plots in all sites, so our results could be used to identify those sites in which nitrate could be rapidly mobilized to groundwater or streamwater.

Where information is available, our trenched plot results are in accord with larger scale studies of commercial clearcutting. We found a high potential for nitrate losses in the New Hampshire northern hardwoods (Fig. 6) and a low potential in poor-site Douglas-fir (Fig. 10): high losses of nitrate were observed following clearcutting of northern hardwoods in New Hampshire (Pierce et al. 1972), while no increase in nitrate movement was detected in clearcut Douglas-fir on an Everett soil in the Puget Sound Lowland (Cole and Gessel 1965).

We had expected that coniferous forests would have lower potential nitrate losses than deciduous forests,

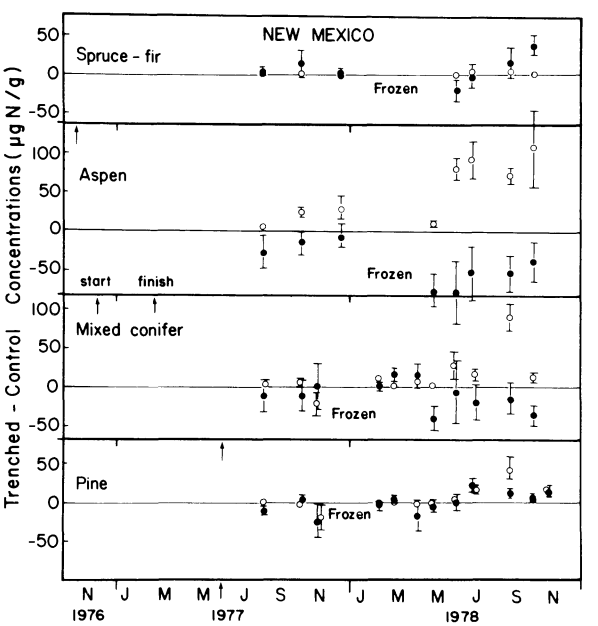


FIG. 7. Responses to trenching in the New Mexico forest floors. See Fig. 3 for definitions of the values and symbols.

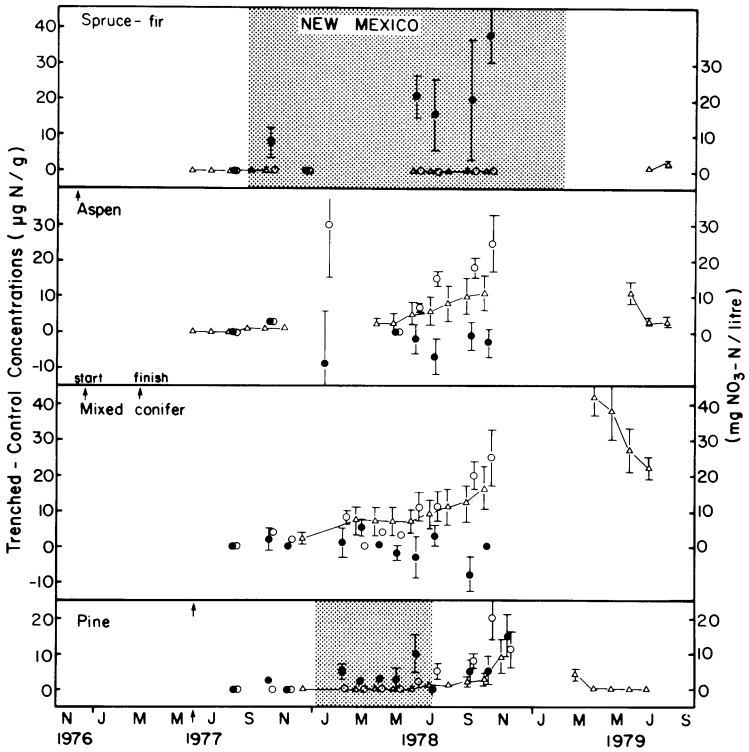


FIG. 8. Responses to trenching in the New Mexico mineral soils and lysimeters. See Fig. 4 for definitions of the values and symbols.

but we observed rapid and substantial increases in nitrate concentrations below the rooting zone in several coniferous forests. Similarly, despite the suggestion that high acidity and low base saturation inhibit nitrification (Stone 1973, Alexander 1976), we found high nitrate concentrations below the rooting zone in trenched plots and high rates of autotrophic nitrification in laboratory incubations in the most acid, base-poor site studied, the New Hampshire balsam fir. We did find that in general the "most fertile" or "highest quality" sites within each region (including the New Mexico mixed conifer and aspen sites in addition to those listed above) lost nitrate to below the rooting zone more rapidly following trenching (Vitousek et al. 1979). These terms are difficult to define precisely, however, especially across regions. In the remainder of this discussion, we will explain these results in terms of the processes which can prevent or delay nitrate losses following trenching.

### *Processes preventing or delaying nitrate losses*

Nitrate losses could be prevented or delayed by processes operating at three points in the nitrogen cycle (Fig. 1). We classified the responses of our sites to trenching as class 1 when no significant increase in forest floor or soil ammonium concentrations was observed following trenching, as class 2 when ammonium concentrations were significantly increased in the forest floor or soil but nitrate concentrations were not, as class 3 when forest floor or soil but not lysimeter nitrate concentrations were significantly increased, and as class 4 when lysimeter nitrate concentrations increased substantially (Vitousek et al. 1979).

*Class 1 responses.*—Class 1 responses clearly occurred during the first growing season following trenching in the Indiana pine, New Mexico pine, and Pacific Northwest silver fir sites. They may have occurred for shorter periods of time in several other sites. Of the processes which could cause response delays in class 1 (Fig. 1), neither ammonia volatilization nor clay fixation could have been primarily responsible for the low net mineralization rates observed. Ammonia volatilization can be ruled out because the soil and forest floor pH were <6 in every site except the New Mexico ponderosa pine, where $^{15}N$ incubation studies demonstrated insignificant gaseous loss (J. R. Gosz, *personal observation*). Clay fixation could not explain low net mineralization rates in forest floor in any site, and the clay content and mineralogy are appropriate for substantial ammonium fixation in mineral soils only in the Indiana pine site.

Accordingly, we concluded that the class 1 responses we observed were caused by a low rate of net nitrogen mineralization. Since we only measured net nitrogen mineralization, we could not determine

whether the class 1 sites had a low gross rate of nitrogen mineralization or a high rate of nitrogen immobilization. Some indirect evidence suggested that low gross rates of mineralization in the class 1 sites were at least partly responsible, however. If immobilization controlled net mineralization across our range of sites, then net nitrogen mineralization in laboratory incubations should be predictable from the C:N ratio of the substrate (Black 1968). Neither forest floor nor mineral soil nitrogen mineralization rates can be predicted in this way ($r^2$ for forest floor = .08, $r^2$ for mineral soil = .03). Perhaps the ratio of available organic carbon:available organic nitrogen actually controls net mineralization, but this ratio can neither be measured directly nor predicted from the total C:total N ratio.

Laboratory nitrogen mineralization potentials were then compared with the amount of nitrogen deposited annually in litterfall at each site, which we used as an index of nitrogen availability. Annual litterfall nitrogen inputs were a good predictor of net nitrogen mineralization potentials in forest floor incubations ($r^2$ for a linear regression = .68), supporting an association between nitrogen availability and above-ground nitrogen circulation in these sites. More important, not only was the rate of nitrogen mineralization (in micrograms per gram of forest floor per unit time) low in the sites with small amounts of nitrogen in litterfall, but the proportion of forest floor nitrogen mineralized (in micrograms per microgram of forest floor N per unit time) under laboratory conditions could also be predicted from the amount of nitrogen in litterfall ($r^2$ for a linear regression = .67; Fig. 15). This relationship suggests that organic nitrogen which is relatively refractory to decomposition is produced in forests which circulate small amounts of nitrogen (Lamb 1975).

No simple relationship between site properties and nitrogen mineralization potentials in mineral soil was found, perhaps because root litter inputs, which generally supply relatively more organic nitrogen to mineral soil than do leaf and branch litterfall, were not estimated.

An interesting set of relationships emerged from the comparative site data (Table 3) which suggest how the nitrogen status of a wide range of sites could be characterized. A graph of the carbon:nitrogen ratio of litterfall vs. the annual circulation of nitrogen in litterfall (Fig. 16) gave an inverse correlation for our sites ($r^2$ for a semilog regression = .70). We tested the limits of this relationship by adding information from other sites. The complete range of sites (Fig. 16) fits the pattern suggested by our sites rather closely. It appears that sites with litterfall nitrogen of $<40$ kg·ha$^{-1}$·yr$^{-1}$ either function on lower nitrogen concentrations or are more effective in retranslocating nitrogen prior to leaf abscission. Above 70 kg·ha$^{-1}$·yr$^{-1}$ in litterfall, the carbon:nitrogen ratio in litterfall apparently stabilizes between 27:1 and 37:1 regardless of the absolute amount of carbon and nitrogen in litterfall. Sites

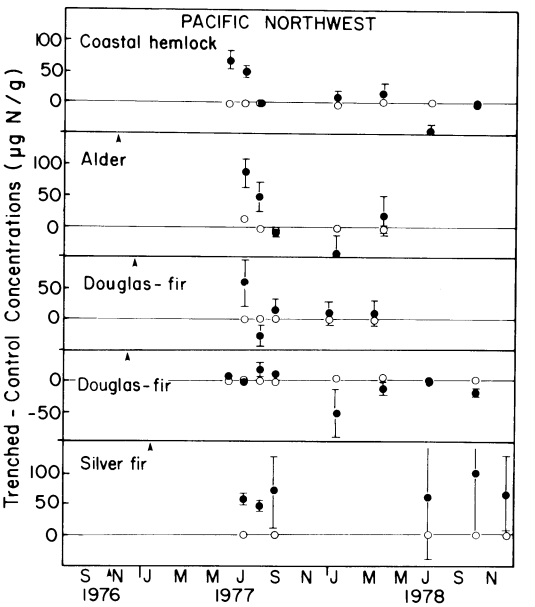


FIG. 9. Responses to trenching in the Pacific Northwest forest floors. Upper Douglas-fir graph is old-growth forest; lower is poor-site Douglas-fir forest. See Fig. 3 for definitions of the values and symbols.

with litterfall carbon:nitrogen ratios in this range may not be strongly nitrogen limited.

The pattern in Fig. 16 also suggests that the overall nitrogen immobilization capacity of litter falling in low-nitrogen sites is greater than that in sites circulating more nitrogen (Aber and Melillo 1980), even though net mineralization potentials in the forest floor are not predictable from the total C:N ratio of the forest floor. Overall, the results in both Figs. 15 and 16 suggest that class 1 responses occur where nitrogen stress prior to disturbance causes the production of organic matter which has a wide C:N ratio and which is refractory to decomposition.

*Class 2 responses.*—Class 2 results were observed in 8 of our 17 sites. In some sites (i.e. Indiana oak mineral soil, Washington poor-site Douglas-fir forest floor and mineral soil), net nitrate production lagged a few weeks or months behind the appearance of elevated ammonium in both the field and the laboratory. In others (i.e., New Hampshire balsam fir forest floor, Massachusetts oak-red maple forest floor), only negligible nitrate production was ever observed in the field or laboratory despite substantially elevated ammonium concentrations.

Class 2 results could occur either because nitrate is not produced or because any nitrate produced is rapidly removed by immobilization or denitrification. Nitrate immobilization is unlikely to be responsible, since heterotrophs exhibit a strong preference for ammonium as a nitrogen source (Jones and Richards 1977) and would immobilize that first. Elevated denitrification potentials have been detected in some of

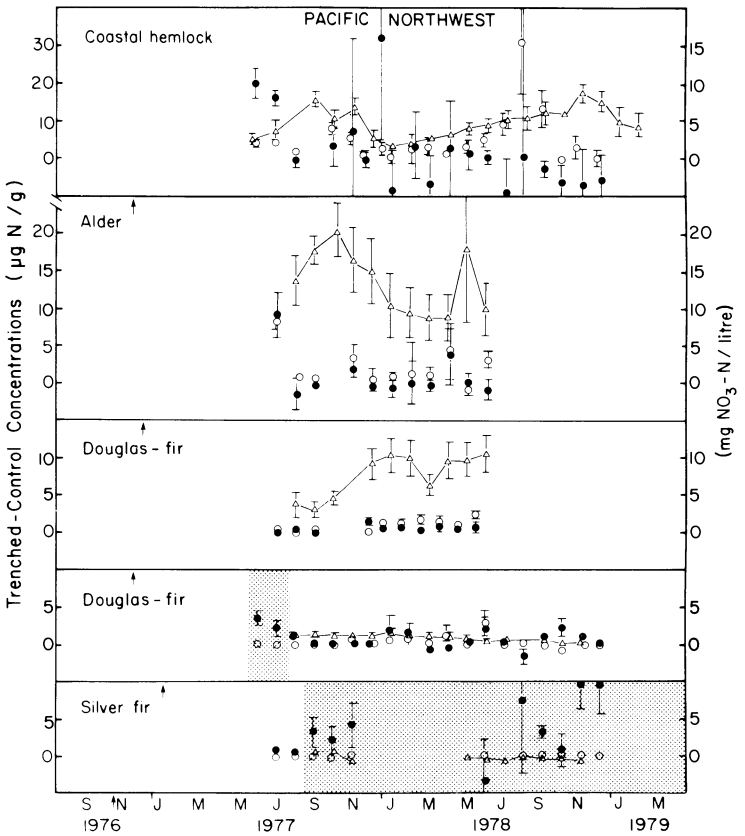


FIG. 10. Responses to trenching in the Pacific Northwest mineral soils and lysimeters. See Fig. 4 for definitions of the values and symbols. Douglas-fir graphs are for old growth (upper) and poor site (lower).

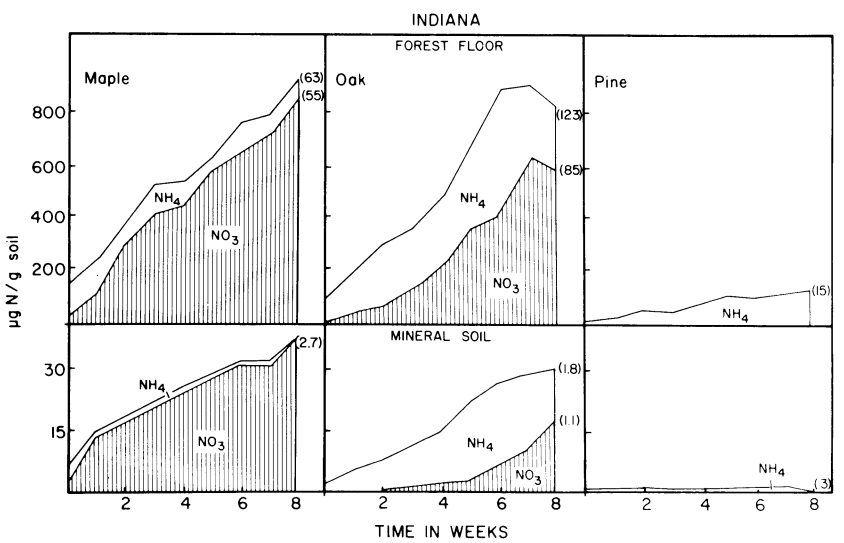


FIG. 11. The results of laboratory incubations of forest floor (upper graphs) and 0–15 cm depth mineral soils (lower graphs) in the Indiana sites. Within each graph, the upper line represents the total concentration of extractable mineral nitrogen (ammonium-nitrogen plus nitrate-nitrogen) at each time, while the lower line (which bounds the shaded area) represents the concentration of nitrate-nitrogen. The numbers in parentheses are the standard errors of the total mineral nitrogen (upper number) and the nitrate-nitrogen (lower number) concentrations at the end of each incubation.

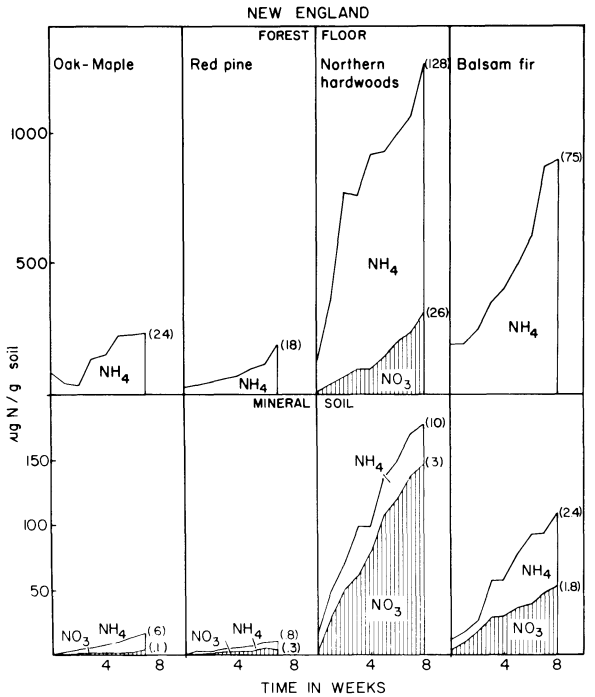


FIG. 12. Results of laboratory incubations in the New England sites. See Fig. 11 for a detailed description.

our trenched plots (J. M. Melillo, *personal communication*), but the results of the aerobic incubations in the laboratory (Figs. 11–14) suggest that lags in nitrification rather than rapid denitrification (an anaerobic process) caused the class 2 responses we observed. Additionally, preliminary $^{15}N$ measurements of incubations in the New Mexico sites showed no detectable gaseous losses of nitrogen in any of those sites.

Several mechanisms could prevent or delay nitrate production in the presence of available ammonium in disturbed forests, trenched plots, or incubated samples (Vitousek and Melillo 1979). These include the allelochemic suppression of nitrification (Rice and Pancholy 1972), competition between heterotrophs and nitrifiers for phosphorus or some other limiting nutrient (Purchase 1974), soil or site conditions (especially of moisture availability and pH) within the tolerance range of some heterotrophs but outside the range of nitrifiers (Alexander 1976), or low initial populations of autotrophic nitrifiers due to competition between roots, mycorrhizae, heterotrophs, and nitrifiers for ammonium prior to disturbance (Belser 1979, Johnson and Edwards 1979).

Not all of these possible causes of lags in nitrification could be distinguished using our results, but we can rule out some possibilities as major causes and set limits on others. There was no significant relationship between pH and nitrate production. Extractable phosphorus was correlated with nitrate production in our mineral soils, but the association was weak ($r^2 = .28$), and other studies suggest that experimental additions of phosphorus and other nutrients only increase nitrification under extremely phosphorus-deficient conditions (Purchase 1974, Melillo 1977, Johnson and Edwards 1979, Robertson 1980).

We found a significant positive correlation between the mean concentration of mineral nitrogen (mostly ammonium) in a horizon (drawn from all of the field measurements in control plots) and the rate of nitrate

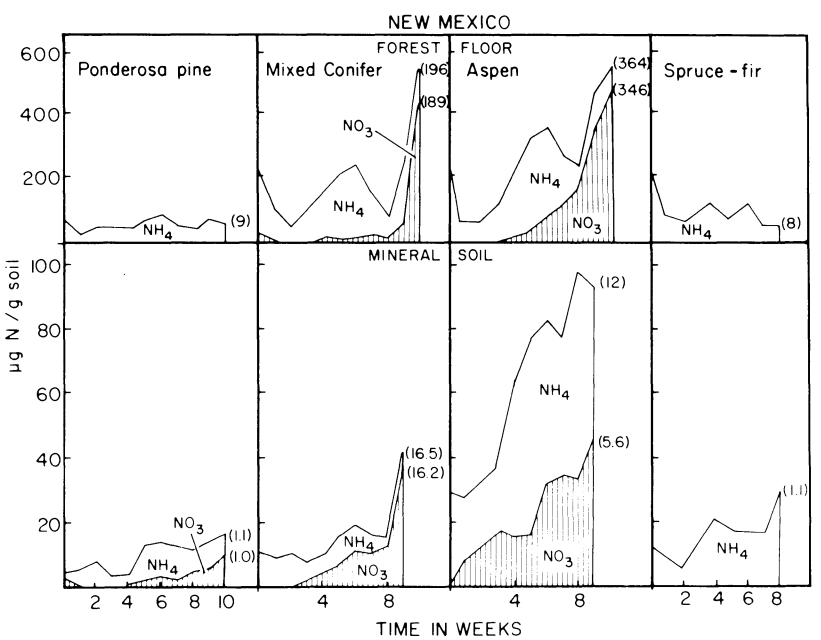


FIG. 13. Results of laboratory incubations in the New Mexico sites. See Fig. 11 for a detailed description.

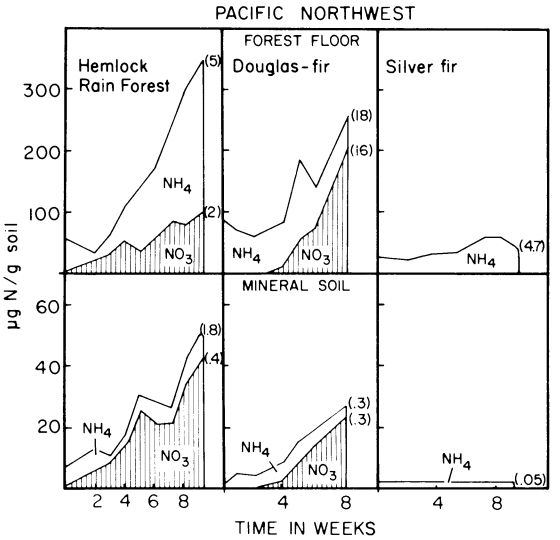


FIG. 14. Results of laboratory incubations in the Pacific Northwest sites. See Fig. 11 for a detailed description.

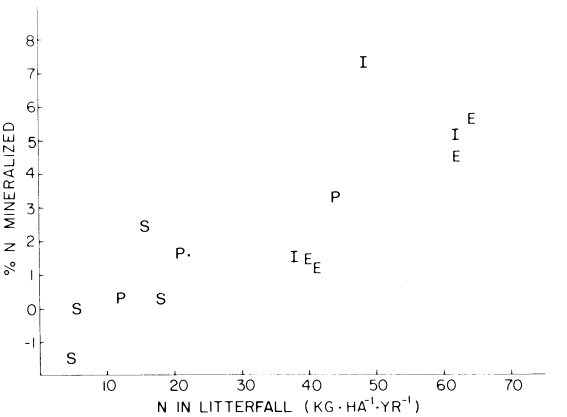


FIG. 15. The relationship between the amount of nitrogen in annual litterfall and the proportion of forest floor nitrogen mineralized in 8-wk aerobic incubations. The symbols are: E = New England; I = Indiana; P = Pacific Northwest; and S = New Mexico. The Indiana site well above the abscissa at 48 $kg \cdot ha^{-1} \cdot yr^{-1}$ is the maple-beech site.

production upon incubation in the laboratory. The pattern for forest floor (Fig. 17) suggests a threshold for N between 60 and 90 $\mu g/g$ soil, above which net nitrate production generally occurred in 8-wk laboratory incubations. The pattern for mineral soil (Fig. 18) is more nearly linear ($r^2 = .48$), with high mean mineral nitrogen concentrations in the field associated with high net nitrate production during the 8-wk incubations and with short or absent lags in nitrification.

These patterns are consistent with either of two explanations. Where nitrogen concentrations are low, the relatively poor affinity of nitrifying bacteria for ammonium (Jones and Richards 1977) could lead to their exclusion from a site by competitive roots, mycorrhizae, and heterotrophs. Once roots and mycorrhizae were killed or suppressed by disturbance or the removal of samples to the laboratory, there would be a lag in nitrate production in low-nitrogen sites while populations of nitrifying bacteria grew on the newly available ammonium. Where competition before disturbance was less, mineral nitrogen concentrations in the field would be higher and populations of nitrifiers could persist in the undisturbed forest.

Alternatively, low nitrogen (or other nutrient) availability could cause plants to produce and eventually to release polyphenols and other compounds which might function as broad-spectrum inhibitors (Del Moral 1972, Lamb 1975, Koeppe et al. 1976). Such compounds could cause a lag in nitrification by suppressing populations of nitrifying bacteria in the field and, if they are persistent in the soil, by continuing to suppress population growth of nitrifiers after disturbance or removal of the soil for incubation. Our ability to discriminate among these alternatives is limited in large part by the techniques available for estimating the population sizes and activity of the diverse autotrophic nitrifying flora in forest soils (Belser and Schmidt 1980, Robertson and Vitousek 1981).

*Class 3 responses.*—Where nitrate concentrations increased in the soil in our sites, the only substantial delay in nitrate loss was the time required for nitrate to percolate from the surface mineral soil to below the rooting zone. This time could vary depending on hydraulic conductivity (fast in the sandy Cape Cod oak-pine site, slower in the Massachusetts red pine plantation), precipitation rate (fast in the New Hampshire northern hardwoods, slower in the New Mexico sites, especially in the dry year 1977), and soil moisture status.

## SYNTHESIS: PREDICTING POTENTIAL NITRATE LOSSES

The results of this study suggest that the amount of nitrogen circulating annually in litterfall and the relative availability of that nitrogen prior to disturbance are useful predictors of the potential for nitrate loss following disturbance. Three major patterns of intrasystem nitrogen circulation are important in forests: reabsorption of leaf nitrogen prior to abscission, net release of ammonium from organic matter by decomposers and subsequent ammonium uptake by roots and mycorrhizae, and nitrate production by nitrifying bacteria and its uptake by roots and mycorrhizae. As long as the intrasystem nitrogen cycle remains intact, nitrogen losses should be relatively low from forests cycling nitrogen by any of these pathways. Once the intrasystem nitrogen cycle is disrupted by disturbance, however, the patterns of nitrogen circulation prior to disturbance could strongly affect the timing and potential magnitude of nitrogen losses.

Nitrogen uptake is relatively low in nitrogen-defi-

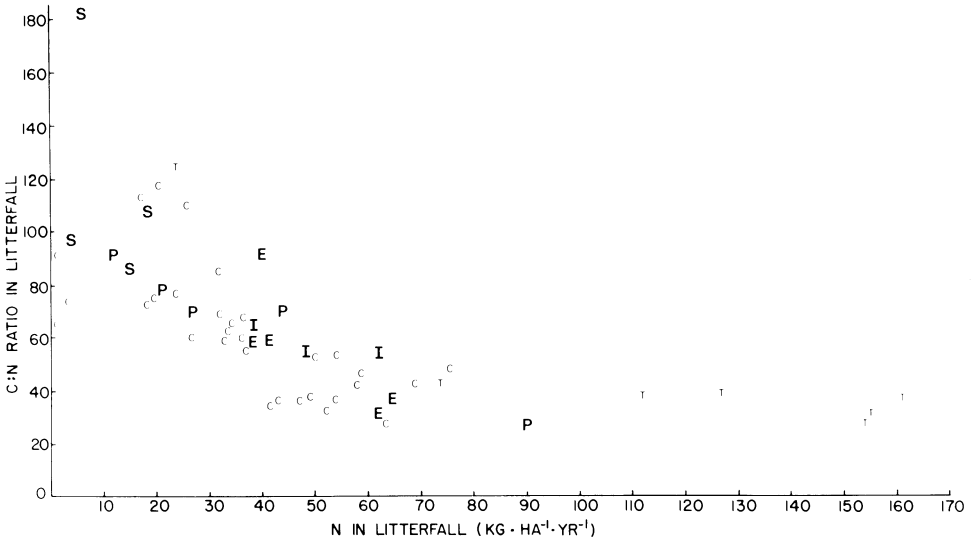


FIG. 16. The relationship between the amount of nitrogen in litterfall and the carbon:nitrogen ratio of that litterfall in our sites (bold-faced letters) and a range of others. Carbon concentrations were estimated as half the dry mass of litterfall in all sites. The symbols for our sites are identical to those in Fig. 15; the additional sites represented by "C" were drawn from Cole and Rapp (1980) (with modifications from Turner et al. 1976 and Sollins et al. 1980), and the sites represented by "T" were reported by Bernhard-Reversat (1975), Franken (1979), and Herrera and Jordan (1981).

cient forests. Nitrogen concentrations in leaves and twigs are also relatively low, and the reabsorption of nitrogen from senescent leaves to stems and/or younger leaves may be relatively more important (Stachurski and Zimka 1975, Turner 1977; but see Chapin 1980 for a thorough review of this sometimes conflicting literature). Nitrogen concentrations in litterfall in such sites are low (Fig. 16), and the overall nitrogen immobilization capacity of the litterfall is thereby increased. Moreover, forest floors in such sites have organic nitrogen which appears to be more refractory to decomposers (Fig. 15). A disturbance in such a system should thus cause relatively small changes in ammonium or nitrate concentrations, as we observed in trenched plots and laboratory incubations.

With greater annual nitrogen circulation in litterfall, uptake and leaf nitrogen concentrations are higher and nitrogen reabsorption from foliage may be less. We have shown that the organic nitrogen in such systems is more easily mineralized (Fig. 15). If competition among roots, mycorrhizae, heterotrophs, and nitrifiers

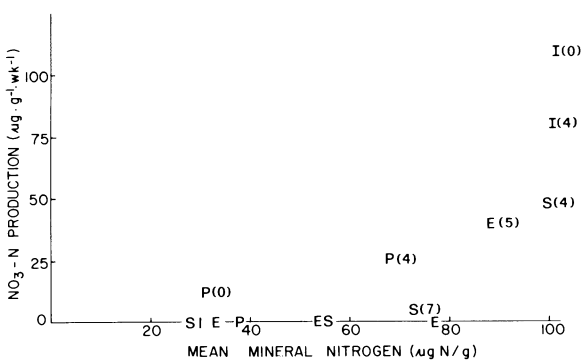


FIG. 17. The relationship between the mean growing season mineral nitrogen concentrations (ammonium-nitrogen plus nitrate-nitrogen) in forest floor and the rate of nitrate production in 8-wk aerobic incubations in our sites. The symbols are as in Fig. 15. The numbers in parentheses next to each symbol represent the length of any lag in nitrification (in weeks).

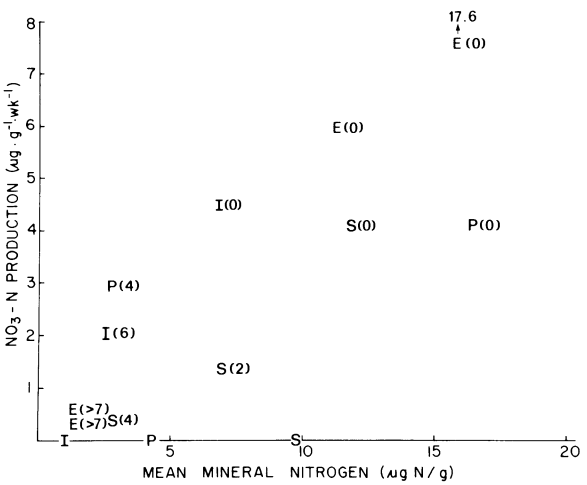


FIG. 18. The relationship between mean growing season mineral nitrogen concentrations (ammonium-nitrogen plus nitrate-nitrogen) in mineral soil and the rate of nitrification in laboratory incubations. The symbols are as in Fig. 15; the numbers in parentheses as in Fig. 17.

for the ammonium released remains intense, however, the concentrations of mineral nitrogen in the soil will remain low (Figs. 17, 18), populations of nitrifying bacteria will be low (Belser 1979), and most plant nitrogen uptake will be of the ammonium form. A disturbance to such a system would result in a rapid increase in ammonium availability, but there would be a delay in nitrate production while populations of nitrifying bacteria became established and grew.

With still greater nitrogen availability, competition for ammonium in an undisturbed forest would be lessened, nitrifying bacteria could maintain higher populations, and plants would obtain more of their nitrogen as nitrate. The vegetation might produce smaller amounts of polyphenols and other potential inhibitors. There would be no delay in net nitrogen mineralization and little or no delay in nitrate production following disturbance in such a site. Any forest in which this pattern is important would thus have a high potential for rapid nitrate losses following disturbance. The association of such responses with the more fertile sites is thus quite reasonable on a process level.

The patterns of nitrogen cycling and nitrogen availability outlined here suggest an important way in which relative nitrogen availability or nitrogen stress can be accentuated in forest ecosystems. Trees growing in low-nitrogen sites produce litter with a relatively high carbon:nitrogen ratio (Fig. 16) and organic nitrogen that appears to be relatively recalcitrant to decomposers (Fig. 15). This has the effect of reducing nitrogen availability in the soil, thus further increasing nitrogen stress to the trees. A positive feedback system towards the development of low nitrogen turnover in a site could occur in this way, especially if the reabsorption of nitrogen from foliage increases in response to nitrogen stress in many species (Gosz 1981). Nitrogen fertilization, on the other hand, should lead to lower carbon:nitrogen ratios in litter (Miller et al. 1976), higher mineralization rates, and the development of greater nitrogen cycling through litterfall.

Why does nitrogen circulation vary so substantially in natural forests? Certainly fire, which volatilizes nitrogen as it mineralizes most other nutrients, has the short-term effect of increasing nitrogen stress in fire-dominated ecosystems (Raison 1979), although post-fire recovery often includes abundant symbiotic and nonsymbiotic nitrogen fixers (Jorgenson and Wells 1971, Gorham et al. 1979). Climatically controlled low decomposition rates can also reduce nitrogen mineralization and place vegetation under nitrogen stress. Relatively low nitrogen levels are present on younger and coarser textured substrates in the Pacific Northwest (Gessel et al. 1973), and very old, degraded soils may have much reduced nutrient availability and nitrogen stores (Walker and Syers 1976). Finally, humans can affect the nitrogen status of sites either through land-use practices which reduce soil fertility (such as continual cultivation of sensitive sites) or through chronic low-level nitrogen fertilization due to anthropogenic fixed nitrogen in precipitation (Heinrichs and Mayer 1977).

### Implications for Resilience and Succession

The mechanisms we suggested here have implications for ecosystem resilience following disturbance as well as resistance. Bormann and Likens (1979) suggested that the flush of nutrients which occurred following disturbance at Hubbard Brook favored rapid revegetation of the disturbed site and thus prevented even more substantial nutrient losses via erosion. Pioneer species, including pin cherry at Hubbard Brook, do respond to the high levels of nutrients in disturbed sites with germination (Peterson and Bazzaz 1978, Auchmoody 1979) and rapid growth (Marks 1974, Covington and Aber 1980, Boring et al. 1981, H. Gholz, *personal communication*).

In sites which circulate relatively little nitrogen prior to disturbance, any flush of nitrogen availability following disturbance would be delayed. Revegetation by rapidly growing successional species could thus be prevented or delayed. It seems reasonable to speculate that nitrogen-poor sites in general have a relatively high resistance to nitrate losses but low resilience, and nitrogen-rich sites are the reverse. High, rapid, and short-lived nitrate losses were in fact observed following clearcutting in high-quality sites in Sweden, while low, long-delayed and relatively long-lasting nitrate losses were observed in lower quality sites (Wiklander 1981).

It has been suggested that nitrification and plant uptake of nitrate are characteristic of early successional ecosystems, but that nitrification is inhibited and plants use primarily ammonium in later successional systems (Rice and Pancholy 1972, Haines 1977, Bormann and Likens 1979). Other studies have found no such trend (Montes and Christensen 1979, Lamb 1980, Robertson and Vitousek 1981). The pathways outlined here suggest why some but not all seres would shift from nitrate to ammonium nutrition in succession. As discussed above, disturbance temporarily decreases competition for inorganic nitrogen in the soil. In sites where most nitrogen circulates by the ammonium pathway prior to disturbance, populations of nitrifying bacteria should eventually increase in response to the increased ammonium availability which follows disturbance (Matson and Vitousek 1981). As succession proceeds, however, competition for nitrogen should increase, the populations of nitrifying bacteria should be outcompeted, and the plants should return to a predominantly ammonium-based nutrition. Allelochemical inhibition of nitrification could reinforce this process, especially if polyphenols are more abundantly produced in nitrogen-poor sites.

Not all ecosystems would be expected to have these successional changes in nitrogen nutrition, however. A relatively fertile site circulating a large amount of

nitrogen through nitrate prior to disturbance could have greatly increased nitrate losses after disturbance, but nitrate could be the major form of nitrogen taken up by plants in both early and late succession (Vitousek 1977). Similarly, a lower quality site with low nitrogen circulation might produce very little nitrate after disturbance or during any stage of succession.

## Conclusions

1) A range of forest sites responded very differently to a trenching experiment designed to elucidate the mechanisms controlling high nitrate losses following disturbance.

2) The most important mechanisms preventing or delaying nitrate production in the lower quality sites were low rates of net nitrogen mineralization and lags in nitrification.

3) Sites which circulated relatively small amounts of nitrogen aboveground produced litter with a much wider carbon:nitrogen ratio than sites which circulated more nitrogen.

4) Although the carbon:nitrogen ratio of forest floor material was a poor predictor of potential nitrogen mineralization, the proportion of forest floor nitrogen mineralized under constant laboratory conditions was positively correlated with the amount of nitrogen in litterfall.

5) The rate of nitrification and the length of the lag period before maximum nitrification rates occurred in laboratory incubations were positively correlated with mean mineral nitrogen concentrations in the field.

6) In general, sites with low or long-delayed nitrate losses were those that had relatively low nitrogen availability prior to trenching.

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