Nitrification potentials and landscape, soil and vegetation characteristics in two Central Appalachian watersheds differing in NO_3^- export

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Abstract

Two watersheds within 1 km of each other in the Central Appalachian mountains of West Virginia have similar management histories and receive 13 kg of N in atmospheric deposition, but NO_3^- export from one watershed (W4) has increased over the last 30 years, and is now approximately five times greater than NO_3^- export from the other (W10). We measured net nitrification potentials (NNP) and other landscape, soil, and plant community variables (1) to determine whether differences in leaching could be attributed to differences in NNP, (2) to identify other significant differences between the watersheds, (3) to identify variables that could account for both between- and within-watershed variability in NNP, and (4) to identify readily measured variables that distinguish plots with relatively high or low NNP. NNPs in W4 were 0.84 kg N ha^{-1} per day, approximately three times higher than those on W10. Watershed 4 lay at a slightly higher elevation, had gentler slopes, a thinner forest floor, lower C:N in the 0–10 cm soil layer, lower tree density, greater basal area in *Acer saccharum*, less basal area in *Quercus prinus* and *Amelanchier arborea*, more frequent occurrences of *A. saccharum* seedlings, *Laportea canadensis*, *Polystichum acrostichoides*, *Trillium* sp., *Uvularia sessilifolia* and *Viola* spp., and fewer occurrences of *Gaultheria procumbens*, and *Viburnum acerifolum*. NNPs were correlated with many soil characteristics related to base cation supply, C:N and water holding capacity (WHC). Several two- and three-variable regression models, which were mostly based on soil characteristics, accounted for a large proportion of the variability in NNP (adjusted $R^2 > 0.60$), as well as for the difference between watershed means (*t*-test of residuals indicate no significant difference). A regression model based on basal area of *A. saccharum* and *A. rubrum* and the presence or absence of *Trillium* accounted for 50% of the variability in NNP. At this high-deposition site, plots with soils that had higher pHs, greater base cation supply and WHC, and lower C:N were more susceptible to NO_3^- leaching and N saturation. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Net nitrification potential; Nitrogen saturation; Central Appalachia; Base cations; C:N; Species composition

1. Introduction

Nitrate export in stream-water from many forests is low (<5 kg N ha^{-1} yr^{-1}, van Miegroet et al., 1992). Low NO_3^- export, significant growth responses to N

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fertilization (e.g., Auchmoody and Smith, 1977), and correlations between net primary production and N cycling rates, such as N in litterfall (Cole and Rapp, 1981) or net N mineralization (Pastor et al., 1984), are all consistent with a pattern of N limitation in temperate forests. Higher NO_3^- fluxes in stream- or soil-water can usually be attributed to factors that increase N supply to vegetation, such as fertilization (Kahl et al., 1993) or the presence of substantial populations of N fixing species (van Miegroet and Cole, 1984; Montagnini et al., 1991), or factors that decrease biotic demand for N, such as tree removal (Likens et al., 1970) or injury (Eshleman et al., 1998). A pattern of increasing NO_3^- concentrations in streams from forests where such conditions do not apply has been identified as a symptom of "N saturation", and is usually attributed to a gradual change in the balance of N supply and demand caused by the long-term, atmospheric deposition of N from anthropogenic sources (Ågren and Bosatta, 1988; Aber et al., 1989). Increased nitrification and nitrate leaching, because of N deposition or any other cause, have the potential to leach base cations from forest soils (Reuss and Johnson, 1986; Edwards and Helvey, 1991), transfer H^+ and Al^{n+} to or increase eutrophication in aquatic ecosystems, and change N_2O fluxes from forest soils to the atmosphere (Aber et al., 1989).

A number of watersheds in the Fernow Experimental Forest, in the Central Appalachian region of West Virginia, USA, receive large amounts of atmospheric N and S deposition (National Atmospheric Deposition Program, 1993) and provide examples of a syndrome of N saturation (Peterjohn et al., 1996). Symptoms include a long-term increase in NO_3^- concentrations in a stream draining a mature forest in watershed 4 (W4), high NO_3^- concentrations in a stream draining an aggrading forest in watershed 3, low retention of inorganic N in comparison with other sites, little seasonality in stream-water NO_3^- concentrations, and high relative nitrification rates (net nitrification as a proportion of net N mineralization).

Not all areas within the Fernow Experimental Forest, however, appear N saturated. Areas on the eastern side of W4 have low concentrations of NO_3^- in lysimeter solutions, low nitrification rates in soil, and a stronger root-growth response to N additions than to P additions, in contrast to areas on the western side of the watershed (Peterjohn et al., 1999). Furthermore, while W4 exports approximately 5 kg N ha^{-1} yr^{-1}, watershed 10 (W10) which lies within 1 km of W4, exports only one-fifth as much N per hectare (P.J. Edwards, unpublished data; Williard et al., 1997; Fig. 1). Because these two watersheds have similar management histories (Adams et al., 1994) and similar deposition regimes (Gilliam and Adams, 1996), differences in NO_3^- leaching rates indicate differences in susceptibility to N saturation.

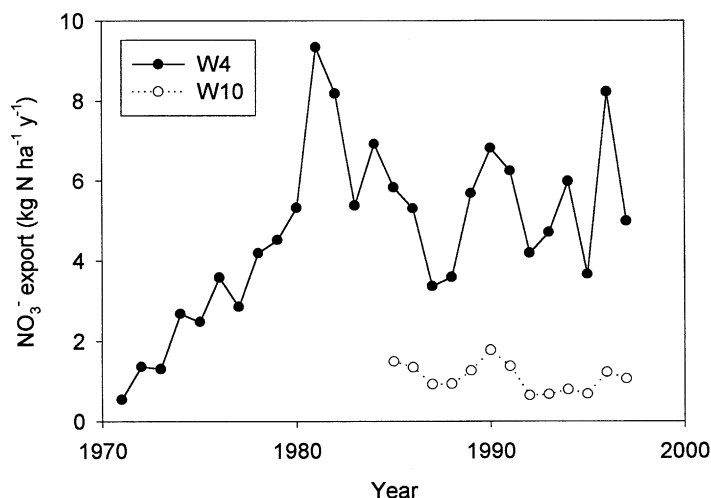Fig. 1. Calendar year export of NO_3^- from W4 and W10 at the Fernow Experimental Forest. Means for W4 and W10 are 5.3 and 1.1 kg NO_3^- ha^{-1} yr^{-1} ($P = 0.0001$), respectively, for the period from 1981 to 1997.

A watershed difference in rates of either net nitrification or NO_3^- uptake may account for the difference in NO_3^- leaching. Net nitrification rates can be compared using laboratory or field incubations. While laboratory incubations, or net nitrification potentials (NNPs), are usually much greater than field rates (Knoepp and Swank, 1995), they are more convenient and eliminate effects of unusual weather. They may not account, however, for different microclimatic conditions in soils from different locations. The largest component of N uptake, immobilization by vegetation, can be approximated as a proportion of tree biomass.

While net nitrification rates affect NO_3^- leaching, they are in turn controlled by or correlated with other factors, such as landform and landscape position (e.g., Pastor et al., 1984; Zak et al., 1986; Garten et al., 1994), the physical and chemical composition of the soil (e.g., Robertson, 1982; Donaldson and Henderson, 1990; Boerner and Sutherland, 1995), or vegetation at the site (e.g., Pastor et al., 1984; Zak et al., 1986; Garten et al., 1994). If differences in watershed NO_3^- exports are due to differences in nitrification rates, and if nitrification rates are in turn explained by other variables, then the differences in NO_3^- export may be completely accounted for by differences in those other variables. In contrast, if the difference between watershed means for NNP could not be explained by other variables, it would imply a watershed effect mediated by plot characteristics that were not measured, or by an undetermined effect of watershed as a whole.

Many of the variables that may be correlated with NNP and susceptibility to N saturation are costly to measure, particularly those dealing with soil properties. Regression analysis has the capacity to identify models that might be useful for predicting NNP using easily measured variables, such as the presence or absence of a herb species, or the basal area of tree species.

The purpose of this study was (1) to determine whether differences in average NNP could account for differences in NO_3^- leaching, (2) to identify how the watersheds differ with respect to landscape, soil and vegetation, (3) to identify variables that account for within- and between-watershed variability in NNP, and (4) to propose easily measured indicators for susceptibility to N saturation.

2. Methods

2.1. Study area

The two watersheds lie between 717 and 869 m elevation in the Fernow Experimental Forest (latitude $39°03'$, longitude $79°41'$), West Virginia, in the Allegheny Plateau physiographic province. The soils of the two watersheds (loamy-skeletal, mixed, mesic Typic Dystrochrepts, mostly of the Berks and Calvin series) are derived from residuum and colluvium from acidic sandstones and shales of the Hampshire and possibly the Price and Chemung formations (Taylor, 1999). Soils are <1 m deep. Slope in the two watersheds averages 25%. Precipitation averages 1457 mm in W4 and is generally within 50 mm of that value for other nearby rain gauges (Adams et al., 1994; Gilliam and Adams, 1996). Precipitation is distributed evenly throughout the year. Mean monthly air temperatures range from -1 to $5\,°C$ in January to $25\,°C$ in July (Adams et al., 1994).

Both watersheds were cut heavily between 1905 and 1910 (Adams et al., 1994; Schuler and Fajvan, 1999) and have remained uncut since then, with the exception of salvaging logs that were killed by Chestnut blight in W4. Species present include red oak (*Quercus rubra*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), tulip poplar (*Liriodendron tulipifera*), black cherry (*Prunus serotina*), chestnut oak (*Q. prinus*), black gum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*) and white ash (*Fraxinus americana*).

The USDA Forest Service has monitored stream-flow from W4 (38.7 ha) since 1951 and NO_3^- concentrations (weekly samples) since 1969. Both stream-flow and NO_3^- concentrations for W10 (15.2 ha) have been measured since 1984 (Adams et al., 1994). Evapotranspiration, as estimated by precipitation minus stream-flow, was 810 and 863 mm for W4 and W10, respectively, from 1985 to 1990 (Adams et al., 1994; the average precipitation values for Fernow watersheds 1–7 in those years were used for W10, which has no rain gauge).

2.2. General sampling design

Grids, $100\,m \times 100\,m$, were established in each watershed using a hand-held compass, a tape measure,

and a clinometer for slope correction. Watersheds 4 and 10 contained 35 and 16 gridpoints, respectively. A subset of points for sampling was selected by dividing W4 into 12 sets of two or three adjacent gridpoints, and selecting one point randomly from each set. Four additional points were selected, two of which had low topographic indices (see below) and two of which had high topographic indices. One point representing a high topographic index site was moved approximately 30 m from the original gridpoint, to a convergence of small valleys, which was consistent with the high topographic index obtained for that plot. Because only 16 gridpoints fit onto W10, its high and low topographic index plots were already represented. Plots were defined as the area within a 10 m radius of selected gridpoints.

2.3. Landscape variables

Slope was measured at each plot with a hand-held clinometer. Aspect was measured with a compass, and was expressed with two variables, the sine and cosine of the angular distance between the azimuth and southwest (the azimuth usually associated with drier conditions, e.g., Yawney and Trimble, 1968). Elevation was estimated from topographic maps. Topographic index was calculated for 30 m × 30 m pixels using data from the USGS digital elevation model: first, the program ERDAS (ERDAS, Atlanta, GA) was used to calculate slope and aspect for each pixel; then a spreadsheet was used to calculate flow paths from each pixel using the D8 algorithm (O'Callaghan and Mark, 1984). Topographic index was calculated for each of the pixels as the natural log of the ratio of area draining through each pixel (proportional to the number of drainage pathways passing through that pixel) divided by the percent (tangent of) slope. Topographic index for each plot was then taken from that of the closest pixel. Slope position was calculated as the distance from the ridge above the plot to the plot divided by the distance from the ridge to the base of the slope.

2.4. Soil sampling

Within each plot, we collected 10 samples from the 0–10 cm layer, and five samples from the 10–30 cm layer with a 1.9 cm diameter soil augur. Soils from

each layer were composted and sealed in plastic bags, and stored at 4 °C.

2.5. Nitrification potential measurement

Field moist soils were passed through a 2 mm sieve and mixed by hand. A subsample of the sieved material was packed into a PVC cylinder (∼4 cm diameter) to a height of approximately 2 cm. Soil-filled cylinders were sealed in plastic bags and stored at 4 °C until water-potential equilibration.

To bring all soil samples to a single water potential, the cylinders were placed in a pressure chamber constructed from ∼25 cm diameter PVC pipe, O-rings, transparent plastic plates, and polyethersulfone filter membranes (270 mm diameter, 0.45 µm pore size, Gelman Sciences), connected to an air pressure of ∼34 kPa (5 lb in.$^{-2}$) and allowed to equilibrate for 2 days. At the end of the equilibration, soils were transferred to plastic cups, weighed, and placed in a 21 °C incubator. For the duration of the incubation experiment, we maintained soils at the same moisture status by adding enough deionized water to bring each sample back to its original weight. Intervals between moisture corrections were ≤2 days.

After 1 week of incubation, time-zero subsamples were taken as follows. Water was added to return the samples to their original moisture levels, soils were mixed with a metal spatula, and 3–5 g subsamples were transferred to tared plastic bottles and weighed. Approximately 100 ml 1 M KCl was added to the subsample, and its mass was recorded. The weight of the soil remaining for further incubation was then recorded, and that weight was then used for later moisture corrections. Subsamples with KCl solution were shaken at 200 rpm for 1 h, and allowed to stand overnight. Solutions were filtered through a glass fiber filter (nominal pore size 0.7 µm), and stored at 4 °C until automated colorimetric analysis of NO_3^- and NH_4^+ concentrations using a Lachat Quikchem AE system (methods 12-107-04-1-B and 12-107-06-2A, respectively, Zellweger Analytics, Milwaukee, WI). The subsampling procedure was repeated 8 weeks after the time-zero sampling. Concentrations of extractable NH_4^+ and NO_3^- in soil at time zero and after 8 weeks were used to calculate net N mineralization (accumulation of $NH_4^+ + NO_3^-$) and NNP. Subsamples (∼4.5 g) were also taken at

the 2-week period, using the same procedure for maintaining constant water potentials, for measurement of water holding capacity (WHC), which was defined as gravimetric moisture content at a water potential of -34 kPa.

2.6. Other soil analyses

Measurements taken for soil characterization included pH in distilled water and in 0.01 M $CaCl_2$ (McLean, 1982), exchangeable H^+ and Al^{n+} (Thomas, 1982), exchangeable base cations, and total N and C. Exchangeable base cations were extracted three times from ~4.5 g soil with 50 ml 1 M NH_4Cl. For each extraction, soil and solution were shaken for 1 h at 200 rpm, centrifuged 10 min ($3000g$), and supernatants were decanted into a tared container. Final extractant volume was measured as solution mass. Base cation concentrations were determined using atomic emission or atomic absorption spectrophotometry (Baker and Suhr, 1982). Total N and C were determined by Dumas combustion (Nelson and Sommers, 1982) using a Carlo Erba NA 1500 N, C, S elemental analyzer.

2.7. Vegetation and forest floor characterization

The plant community was characterized by recording diameter, and species of all living stems with diameter at 1.37 m above the ground (DBH) ≥ 5 cm, and then recording counts of all plants <1 m tall on three 50 cm radius subplots, which were chosen randomly at each sampling point. Raw data were used to calculate basal area of living trees by species, total basal area, density and species richness for the tree stratum, and frequency (zero, one, two or three out of three subplots) of each herb species, as well as species richness of the herb stratum. We encountered 25 species of woody vegetation with diameter ≥ 5 cm, and 32 species in the herb layer. Species in the tree layer (*Aralia spinosa*, *Castanea dentata*, *Carya* spp., *F. americana*, *Hamamelis virginiana*, *Magnolia fraseri*, *Ostrya virginiana*, *O. arboreum*, *P. serotina*, *Robinia pseudoacacia*, *Sassafras albidum* and *Tilia americana*) or herb layers that occurred on less than 10% of the plots were not included in the statistical analyses. Plants >1 m tall but <5 cm in diameter were also tallied on the circular subplots, but that procedure

yielded an inadequate amount of data for analysis. Aboveground tree biomass was calculated using allometric equations (Brenneman et al., 1978). Forest floor depth was measured at each corner of a 15 cm × 15 cm square in each subplot, from which the forest floor had been removed.

2.8. Calculations and statistics

Area-based estimates for NNP were calculated using bulk densities derived from the average masses of the core samples for the 0–10 and 10–30 cm depth increments: 621 and 939 kg m^{-3}, respectively. Bulk densities for similar soil series are 1100–1200 kg m^{-3} in A horizons, and 1300–1500 in B horizons (J.C. Sencindiver, West Virginia University, personal communication). Although our values are low, they probably do not distort comparisons of NNP from plot to plot.

Watershed means for NNP and other variables were compared using a *t*-test. Other differences between the watersheds were identified using *t*-tests on measurements of landscape, soil and vegetation characteristics.

Regression and multiple regression analyses were used to identify a set of variables that could account for a large proportion of the within-watershed variability in NNP, as well as the difference between watersheds. We examined models with one, two and three variables. The adjusted R^2-statistic was used to assess the amount of within-watershed variability that a particular model could account for. The five models of each rank with the highest adjusted R^2 were examined for their ability to account for the between-watershed difference, which was tested by comparing the means of residuals within each watershed using a *t*-test.

The presence or absence of herb-layer species and the basal area of tree species were identified as easily measured plant community variables. We used multiple regression of NNP against those data to identify the best one-, two- and three-variable models predicting NNP.

3. Results

3.1. NNPs in W4 and W10

Plot-level NNPs (the sum of the NNPs for the two soil layers) were between -0.06 and 2.28 kg N ha^{-1} per day. The means (with standard deviation) in
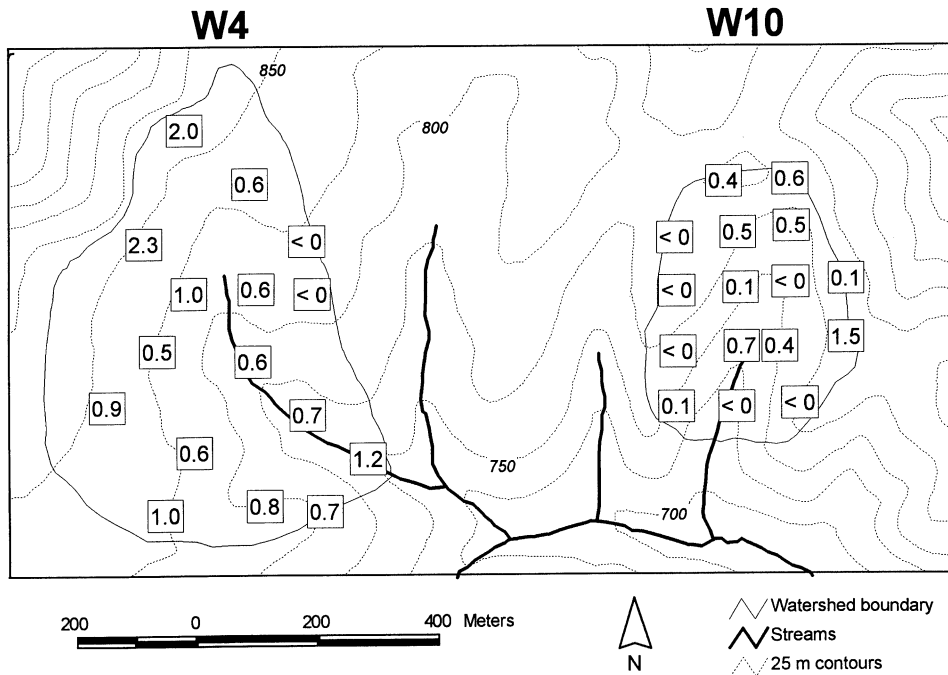
Fig. 2. Spatial pattern of plots and NNP (kg N ha⁻ per day) in W4 and W10.

W4 and W10 were 0.84 ± 0.62 and 0.28 ± 0.41 kg N ha^{-1} per day, respectively, and were significantly different ($P = 0.006$). Values were highest along the northwest ridge of W4, and were lowest along the northeast ridge of W4, and along the east and west ridges of W10 (Fig. 2). Plot-level NNP values fall into three categories: those with NNP ≤ 0.1 kg N ha^{-1} per day (many of which have negative NNP values), those with NNP > 0.1 but ≤ 1.5 kg N ha^{-1} per day, and those NNP > 2 kg N ha^{-1} per day (Fig. 3). While W4 exports
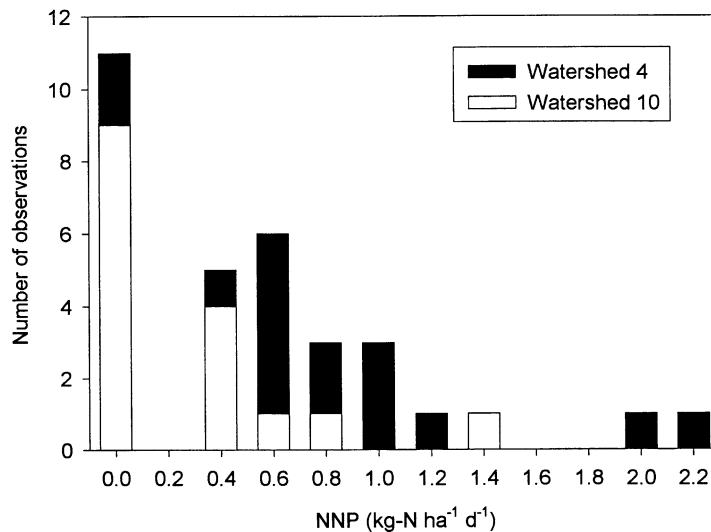

Fig. 3. Distribution of NNP measurements from W4 and W10.

Table 1

Comparison of watershed means (and standard deviations) for landscape variables in two watersheds with differing NO_3^- exports in the Fernow Experimental Forest[a]

Variable	W4	W10	*P*-value
Elevation (above sea level, m)	814.0 ± 30	767.0 ± 21	0.0001
Slope (%)	20.0 ± 8	30.0 ± 13	0.02
Slope position	54.0 ± 33	45.0 ± 30	
Aspect—cosine of angle from SW	0.00 ± 0.66	0.31 ± 0.51	
Aspect—sine of angle from SW	-0.52 ± 0.58	-0.18 ± 0.82	
Topographic index	6.9 ± 1.3	6.0 ± 1.5	

[a] *P*-values are shown for significant ($P \leq 0.05$) watershed differences.

approximately five times as much NO_3^- as W10, NNP was only three times greater in W4.

3.2. Watershed comparisons

Watersheds differed significantly in a number of landscape, soil and vegetation characteristics as well as in mean NNP. Landscape measurements indicated that W4 lies at a higher elevation, while W10 has steeper slopes (Table 1). Watershed 4 as a whole opens to the southeast, while W10 opens to south–southwest

(Fig. 2). Watershed 10, therefore, has a higher cosine of the angle between SW and aspect, although the difference was not significant. Topographic index is somewhat higher on W4 ($P = 0.09$) than on W10. The difference is consistent with both the steeper slopes on W10, and with the larger area of W4: plots in W4 are likely to have larger areas upslope than those in W10.

Soils in both watersheds had low pH values and low base saturation (Table 2). The forest floor was significantly thicker in W10, which also had a higher C:N ratio. The pH in 0.01 mol l^{-1} $CaCl_2$ was substantially,

Table 2

Comparison of watershed means for soil characteristics in two watersheds with differing NNP in the Fernow Experimental Forest[a]

Variable	0–10 cm layer			10–30 cm layer		
	W4	W10	*P*-value	W4	W10	*P*-value
NNP (kg N ha^{-1} per day)	0.62 ± 0.56	0.22 ± 0.31	0.02	0.21 ± 0.20	0.06 ± 0.12	0.01
Forest floor depth (cm)	2.6 ± 1.2	4.4 ± 1.6	0.001			
pH in H_2O	3.97 ± 0.28	3.96 ± 0.37		4.38 ± 0.16	4.27 ± 0.12	0.03
pH in 0.01 mol l^{-1} $CaCl_2$	3.72 ± 0.31	3.59 ± 0.29		3.97 ± 0.11	3.78 ± 0.10	0.0001
ECEC (meq kg^{-1})[b]	87.0 ± 19	85.0 ± 21		56.0 ± 10	57.0 ± 10	
Base saturation (%)	21.0 ± 19	14.0 ± 7		11.0 ± 6	9.0 ± 3	
Exchangeable H (meq kg^{-1})	217.0	24.0 ± 12		8.0 ± 4	11.0 ± 6	
Exchangeable Al (meq kg^{-1})	48.0 ± 16	50.0 ± 13		42.0 ± 9	41.0 ± 7	
Exchangeable Ca (meq kg^{-1})	12.0 ± 20	5.0 ± 3		2.9 ± 1.8	1.7 ± 0.9	0.03
Exchangeable Mg (meq kg^{-1})	2.9 ± 1.7	2.2 ± 0.8		1.1 ± 0.6	0.8 ± 0.3	
Exchangeable K (meq kg^{-1})	3.5 ± 2.2	3.1 ± 1.3		2.0 ± 0.9	2.1 ± 1.5	
Exchangeable Na (meq kg^{-1})	0.6 ± 1.0	0.5 ± 0.3		0.3 ± 0.3	0.3 ± 0.5	
C content (g kg^{-1})	64.0 ± 34	62.0 ± 23		22.0 ± 5	20.0 ± 8	
N content (g kg^{-1})	4.1 ± 2.8	3.1 ± 0.8		1.5 ± 0.3	1.2 ± 0.3	0.03
C:N (kg kg^{-1})	16.0 ± 3	19.0 ± 3	0.006	15.0 ± 3	17.0 ± 3	
WHC (kg kg^{-1})[c]	0.46 ± 0.15	0.39 ± 0.08		0.25 ± 0.04	0.21 ± 0.03	0.003

[a] The 0–10 cm layer includes the Oe and Oa horizons, where present.

[b] Effective cation exchange capacity (sum of cation charge extracted with 1 mol l^{-1} KCl or NH$_4$Cl.

[c] Water content at water potential, ψ, of -34 kPa.

Table 3

Comparison of watershed means for tree (DBH $\geq$ 5 cm) community variables in two watersheds in the Fernow Experimental Forest Basal area ($m^2\,ha^{-1}$) is recorded for each individual species

Variable	W4	W10	*P*-value[a]
Species richness	6.3 ± 2.1	7.4 ± 1.4	
Density (stems ha^{-1})	625.0 ± 134	746.0 ± 184	0.04
Total basal area ($m^2\,ha^{-1}$)	34.0 ± 13	28.0 ± 11	
Biomass ($Mg\,ha^{-1}$)	326.0 ± 154	233.0 ± 105	
A. pensylvanicum	0.08 ± 0.16	0.12 ± 0.28	
A. rubrum	4.4 ± 5.5	5.0 ± 3.2	
A. saccharum	4.1 ± 6.9	0.5 ± 0.8	0.05
A. arborea	0.09 ± 0.23	0.32 ± 0.30	0.02
Betula lenta	0.9 ± 1.6	0.4 ± 0.8	
F. grandifolia	0.3 ± 0.7	1.4 ± 3.6	
L. tulipifera	4.7 ± 9.2	0.6 ± 2.0	
M. acuminata	1.2 ± 2.2	1.4 ± 2.9	
N. sylvatica	1.3 ± 4.3	2.6 ± 4.2	
Q. alba	2.2 ± 4.6	2.3 ± 3.5	
Q. prinus	0.6 ± 2.3	6.4 ± 6.6	0.003
Q. rubra	9.7 ± 9.9	6.2 ± 6.0	

[a] *P*-values are shown for comparisons with significant ($P \leq 0.05$) differences.

but not significantly, lower in W10 in the 0–10 cm layer. In the 10–30 cm layer, however, pH in both water and 0.01 mol l^{-1} $CaCl_2$ were lower for W10. Soils from the deeper layer in W10 had less N and less exchangeable Ca, and lower WHC. NNPs were higher in W4 for soils from both depth strata.

There were few significant differences in the tree communities of the two watersheds (Table 3). Watershed 10 contained a higher density of stems, and larger basal areas of *Q. prinus* and *Amelanchier arborea*, while W4 carried a larger basal area of *A. saccharum*. Although the differences were not significant, a larger number of species was found on plots in W10, whereas plots on W4 had larger mean basal area and biomass. Individual plots on W4 contained as much as 34 $m^2\,ha^{-1}$ of *L. tulipifera*, which was a small component of the vegetation on W10, and as much as 38 $m^2\,ha^{-1}$ of *P. serotina*, which does occur on W10, but did not occur in any of our plots.

There were several herb-layer species with significantly different frequencies of occurrence on the two watersheds (Table 4). *A. saccharum* seedlings did not occur on W10, but were present on one of every six subplots on W4. Species that were more frequent on W10, *Gaultheria procumbens* and *Viburnum acerifolium*, were perennials; those more frequent on W4,

Table 4

Comparison of watershed means (and standard deviations) for variables describing herb (height $\leq$1 m) communities in two watersheds with differing NNP in the Fernow Experimental Forest[a]

Variable	W4	W10	*P*-value[b]
Species richness	10 ± 4	9 ± 2	
A. saccharum	17 ± 27	0	0.02
Dennstaedtia punctilobula	12 ± 27	0	
Dioscorea quaternata	2 ± 8	8 ± 19	
G. procumbens	0	17 ± 27	0.02
L. canadensis	40 ± 49	6 ± 25	0.02
L. tulipifera	21 ± 29	6 ± 13	
Medeola virginiana	10 ± 20	2 ± 8	
Monotropa uniflora	2 ± 8	6 ± 13	
P. acrostichoides	8 ± 15	0	0.03
Q. rubrum	4 ± 11	10 ± 16	
Rubus spp.	10 ± 20	2 ± 8	
Smilax rotundifolia	33 ± 39	40 ± 35	
Trillium sp.	17 ± 17	0	0.0005
U. sessilifolia	37 ± 38	8 ± 15	0.008
Vaccinium vacillans	8 ± 19	17 ± 24	
V. acerifolium	0	14 ± 17	0.002
Viola spp.	73 ± 30	46 ± 38	0.04

[a] Frequency (occurrence on zero, one, two or three out of three subplots, expressed as a percentage) is recorded for each individual species.

[b] *P*-values are shown for comparisons with significant ($P \leq 0.05$) differences. Fifteen other species occurred in the herb stratum of fewer than 10% of the plots.

including *Laportea canadensis*, *Trillium* sp., *Uvularia sessilifolia* and *Viola* spp. overwinter belowground. The fern, *Polystichum acrostichoides*, was also more frequent on W4.

3.3. Relationship to soil, landscape and plant community variables

There was a significant correlation between NNP and one of the six landscape variables, 13 of 15 variables describing the 0–10 cm soil layer, five of 14 variables describing the 10–30 cm soil layer, five of 16 variables describing the tree community, and seven of 19 variables describing the herb layer (Table 5). Many of the variables with significant correlations reflected base cation status in the soil, including pH in water or in 0.01 M $CaCl_2$, base saturation, and exchangeable H, Al, Ca, Mg, K, and Na in the 0–10 cm layer, and exchangeable Ca, base saturation, and pH in 0.01 M $CaCl_2$ in the 10–30 cm layer.

Of the five one-variable models with the highest adjusted R^2-values, two accounted for the difference in NNP due to watershed. The three that did not were all related to base cation status of the soil (Table 6). The five best two-variable and three-variable models, however, all accounted for watershed differences (Table 6).

Adjusted R^2-values for the best two- and three-variable models lay within narrow ranges. Most of the variables that occur in these models describe the 0–10 cm layer of the soil, in particular the base cation status (pH in water or 0.01 M $CaCl_2$, base saturation or exchangeable Ca), the content or character of the organic matter (total C, total N or C:N) and WHC.

3.4. Prediction

The presence or absence of *Trillium* explained the greatest proportion of variance of any one-variable model (adjusted $R^2 = 0.30$). Those plots without *Trillium* had an average NNP of 0.37 kg N ha^{-1} per day, whereas those with *Trillium* had an average NNP of 1.13 kg ha^{-1} per day. The best two-variable model (adjusted $R^2 = 0.42$) indicated that plots with *Trillium* had NNP greater than those without by 0.61 kg N ha^{-1} per day, and that NNP increased by 44 g N ha^{-1} per day for each m^2 ha^{-1} of *A. saccharum*

Table 5
Variables with significant ($P \leq 0.05$) correlations to NNP

Variable	Slope[a]
Landscape variables	
Elevation	$8.1 \times 10^{-3**}$
Soil variables, 0–10 cm layer	
pH in 0.01 mol l^{-1} $CaCl_2$	1.39[****]
Base saturation	2.95[****]
C:N	−0.13[****]
Exchangeable Ca	0.03[****]
Exchangeable Al	−0.02[***]
Total N	0.17[***]
Exchangeable Mg	0.24[***]
Exchangeable K	0.18[**]
WHC	2.43[**]
Exchangeable Na	0.40[**]
pH in water	0.87[**]
Forest floor depth	−0.15[*]
Exchangeable H	−0.02[*]
Soil variables, 10–30 cm layer	
Exchangeable Ca	0.21[***]
Base saturation	5.88[**]
C:N	−0.09[**]
pH in 0.01 mol l^{-1} $CaCl_2$	1.78[*]
WHC	4.83[*]
Tree community variables	
A. saccharum	0.06[**]
Species richness	−0.15[**]
A. arborea	−0.91[*]
Q. prinus	−0.04[*]
Aboveground biomass	$1.5 \times 10^{-3*}$
Herb-layer community variables	
A. saccharum	1.73[***]
L. canadensis	0.80[***]
Trillium sp.	2.29[***]
V. vacillans	−1.17[*]
P. acrostichoides	2.15[*]
Viola spp.	0.59[*]
D. punctilobula	1.08[*]

[a] Slopes are calculated for simple linear regressions of NNP against each variable. The numerator for slope units is kg N ha^{-1} per day, and the denominator is the units given for each variable in Tables 1–4. Variables within categories are sorted by decreasing R^2.
[*] Significant at $P \leq 0.05$.
[**] Significant at $P \leq 0.01$.
[***] Significant at $P \leq 0.001$.
[****] Significant at $P \leq 0.0001$.

basal area. The best three-variable model (adjusted $R^2 = 0.50$) indicated an increase of 0.44 kg N ha^{-1} per day in the presence of *Trillium*, an increase of 60 g N ha^{-1} per day for each m^2 ha^{-1} of *A.*

Table 6

Regression and multiple regression models with NNP as the dependent variable, and independent variables drawn from landscape, soil or vegetation characteristics of individual plots in W4 and W10[a]

Adjusted R^2	Variable	Coefficient	Variable	Coefficient	Variable	Coefficient	WS effect
One-variable models							
0.55	pH, 0–10 cm, $CaCl_2$	1.39[****]					0.27[*]
0.51	Base saturation, 0–10 cm	2.95[****]					0.36[**]
0.47	C:N, 0–10 cm	−0.13[****]					0.23
0.39	Exchangeable Ca, 0–10 cm	0.03[****]					0.38[**]
0.36	*A. saccharum*	1.73[***]					0.26
Two-variable models							
0.66	pH, 0–10 cm, $CaCl_2$	1.24[****]	WHC, 0–10 cm	1.70[**]			0.17
0.65	pH, 0–10 cm, water	−1.20[**]	pH, 0–10 cm, $CaCl_2$	2.44[****]			0.06
0.65	C:N, 0–10 cm	−0.12[****]	WHC, 0–10 cm	2.10[***]			0.04
0.64	Total N, 0–10 cm	0.50[****]	Total C, 0–10 cm	−0.03[****]			0.14
0.63	pH, 0–10 cm, $CaCl_2$	1.13[****]	Total N, 0–10 cm	0.10[**]			0.23
Three-variable models							
0.73	pH, 0–10 cm, water	−1.00[**]	pH, 0–10 cm, $CaCl_2$	2.14[****]	WHC, 0–10 cm	1.43[**]	0.01
0.72	pH, 0–10 cm, water	−1.10[**]	pH, 0–10 cm, $CaCl_2$	2.12[***]	Total N, 0–10 cm	0.09[**]	0.04
0.72	Base saturation, 0–10 cm	2.83[****]	WHC, 10–30 cm	5.14[***]	*G. procumbens*	−0.92[**]	0.01
0.71	pH, 0–10 cm, water	−1.19[**]	pH, 0–10 cm, $CaCl_2$	2.43[****]	Total C, 0–10 cm	0.01[*]	0.05
0.71	pH, 0–10 cm, water	−1.18[**]	pH, 0–10 cm, $CaCl_2$	1.93[****]	Base saturation, 0–10 cm	1.52[*]	0.07

[a] An insignificant effect of watershed indicates that the regression model accounted for the variation in NNP due to watershed. The five one-, two- and three-variable models having the highest adjusted R^2 are shown. "WS effect" is the difference between watershed means of the residuals of the regression models. *A. saccharum* and *G. procumbens* denote frequencies of those species in the herb layer.

[*] Significant at $P \le 0.05$.

[**] Significant at $P \le 0.01$.

[***] Significant at $P \le 0.001$.

[****] Significant at $P \le 0.0001$.

saccharum, and a decrease of 43 g N ha^{-1} per day for each m^2 ha^{-1} of *A. rubrum* (Fig. 4).

4. Discussion

4.1. NNPs and NO_3^- leaching

The large and significant difference between NNP in W4 and W10 is consistent with the hypothesis that different rates of NO_3^- export from the two watersheds are caused by inherent differences in the capacity of their soils to produce NO_3^-. Williard et al. (1997), sampling W4 and W10 as well as seven other central Appalachian watersheds, also found that watersheds losing more NO_3^- have soils with greater nitrification rates. Nevertheless, differences in export cannot be attributed solely to differences in NNP until the effects of variation in deposition, biotic demand, and microclimate are considered.

The observed differences in NO_3^- export could theoretically be caused by differences in N inputs, but we consider large differences in atmospheric N deposition unlikely. The two watersheds are located within 1 km of each other, and previous research in this area has shown relatively small variation in chemical loading in wet deposition at higher elevations (Gilliam and Adams, 1996). While the variability in dry deposition in this area has not been studied extensively, there is little to suggest that rates would differ substantially, particularly since the watersheds lie within a narrow elevation band.

If vegetation in one watershed were to have a greater demand for N than vegetation in another watershed with similar N supplies, the watershed with less demand would appear saturated. This possibility, however, cannot account for the greater NO_3^- export from W4. Biomass is substantially, although not significantly, greater on W4 than on W10 (Table 3). Furthermore, there is a significant correlation between
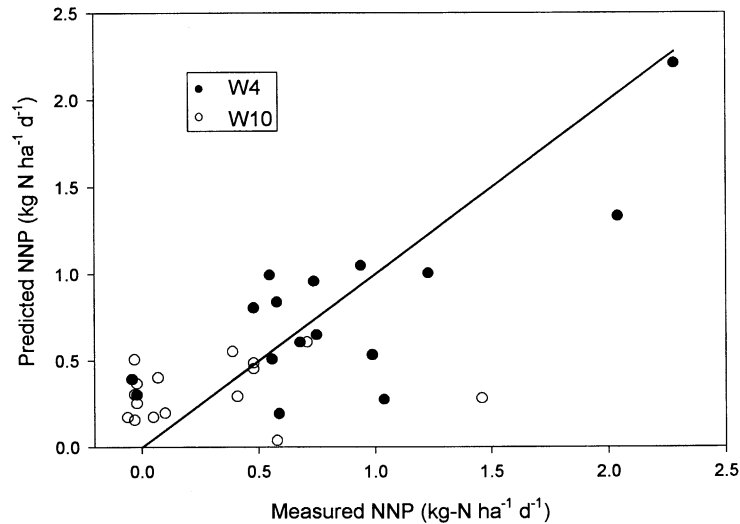
Fig. 4. Performance of a model predicting NNP using basal area of *A. saccharum* (increasing NNP with increasing basal area), *A. rubrum* (decreasing NNP with increasing basal area) and *Trillium* sp. (presence indicates higher NNP). The line is a plot of $Y = X$. The regression model has an adjusted $R^2 = 0.50$.

biomass on each plot and NNP (Table 5). Because nitrate production occurs in locations with higher N demand by vegetation over the life of the stand, low demand cannot account for NO_3^- leaching. This possibility can also be ruled out for the stand in its present condition by considering the scale of net nitrification and uptake rates. Net nitrification is approximately 70 kg N ha^{-1} yr^{-1} on W4 (Gilliam et al., 1996). If net nitrification is approximately one-third that rate on W10, then uptake on W4 must be approximately 45 to 50 kg N ha^{-1} yr^{-1} greater on W4 than on W10, so that NO_3^- leaching is only 5 kg ha^{-1} yr^{-1} (Fig. 1).

Many microbial processes in soil are regulated by temperature (e.g. Peterjohn et al., 1994; Kirschbaum, 1995) or moisture (e.g., Kieft et al., 1987; Christ and David, 1996). Differences in NNP measurements may not reflect differences in field rates because soils may be exposed to different temperature and moisture regimes. Moister conditions on W4, which are expected because of its generally higher topographic indices, easterly aspect, and higher WHCs, might cause a further increase in nitrification rates on W4 relative to those in W10. Higher soil temperatures, which are expected on W10 due to its more southerly aspect, might decrease actual net nitrification by

drying the soil, or increase nitrification by warming it. The thinner forest floor in W4 suggests that of these two factors, acceleration of microbial processes due to higher moisture has the stronger effect. Therefore, microclimatic conditions probably increase actual net nitrification rates in W4 relative to those in W10.

4.2. Susceptibility to N saturation

The long-term increase in NO_3^- export from the Fernow Experimental Forest (Edwards and Helvey, 1991) indicates that the supply of NO_3^- gradually increased relative to biotic demand. The NNP measurements made in this study identify characteristics of plots in which the soil produces large amounts of NO_3^-, and have therefore proven susceptible to N saturation. Such plots are distinguished best by soil characteristics, such as relatively high pH and water retention, and relatively low C:N. Watershed 4 has proven more susceptible to N saturation because its soil supplies more bases, and has more WHC and lower C:N. Saturated plots are also distinguished by the presence of certain species, such as *Trillium*, the absence of others, such as *G. procumbens*, or the abundance of others, such as *A. saccharum*.

The suite of soil characteristics that distinguish susceptibility in this study, particularly high WHC and pH, and low C:N, are commonly associated with rapid N cycling, including nitrification, in other studies (Robertson, 1982; Pastor et al., 1984; Donaldson and Henderson, 1990; Boerner and Sutherland, 1995). Furthermore, species that were associated with high NNP values in this study, especially *A. saccharum*, have commonly been associated with sites of higher net nitrification (Zak and Pregitzer, 1990) and higher NO_3^- leaching (Iseman et al., 1999). Many of these characteristics are also associated with higher site indices and greater net primary productivity. *G. procumbens* indicates a poor site class, while *P. acrostichoides* indicates a good site class (Carvell and Perkey, 1997). In Michigan, stands with *A. saccharum* associated with *Q. rubra* or *T. americana* contained 178 and 209 Mg ha^{-1}, respectively, whereas mixed oak stands without a large *A. saccharum* component contained only 151 Mg ha^{-1} (Zak and Pregitzer, 1990). Lovett and Rueth (1999) found that nitrification potentials was correlated with N deposition in stands of *A. saccharum*, but not in stands of *Fagus grandifolia*. "Richer", more productive forests, or those containing *A. saccharum*, are susceptible to N saturation.

In this study, correlations between NNP and soil properties were generally stronger than those between NNP and abundance of various species (Table 5). This correlation, however, does not rule out the possibility that the abundance of certain species not only indicates different levels of NNP, but influences soil chemistry and, therefore, NNP as well. Finzi et al. (1998) examined soil chemistry under trees of various co-occurring species and found that soils (0–7.5 cm) under *A. saccharum* consistently had higher pH than soils under *F. grandifolia*, *Q. rubrum*, and *Tsuga canadensis*.

The positive correlation between nitrification and productivity is well known, and has sometimes been linked with NO_3^- leaching as well. At the Fernow Experimental Forest, however, this pattern occurs in a watershed in which a transition from N retention to NO_3^- loss has been observed. This relationship is one piece of evidence that forests in areas of high N deposition that are currently exporting NO_3^- may have become N saturated within the last few decades, and may not be in an undisturbed state.

4.3. Landscape variables and NNP

The lack of an association between NNP and landscape variables is surprising, considering previous literature. Garten et al. (1994) documented increasing NNP with increasing topographic index and detected an effect of aspect as well. Topographic variables, including aspect and slope position, have frequently been identified as indicators of site index in the central Appalachian region (e.g., Trimble and Weitzman, 1956; Yawney and Trimble, 1968). The failure of topographic relationships to hold may be due to variation in parent material, which affects soil chemistry. For example, two plots on the western ridge of W4 had the highest NNP, whereas plots near the eastern ridge of W4 and the eastern and western ridges of W10 had low NNP (Fig. 2). These two plots had the only pHs > 4 (measured in 0.01 mol l^{-1} $CaCl_2$), the only exchangeable Ca values >20 meq kg^{-1}, and the only base saturation values >40%. Maps by Taylor (1999) of the Fernow Experimental Forest indicate that, due to the dip of the rock strata, bedrock in this part of the study area is from the Canon Hill member of the Devonian Hampshire formation (Greenish-gray, marine–non-marine transitional sandstone, pebbly sandstone and shale), whereas the rest of the study area is underlain by the Rowlesburg member of the Hampshire formation (non-marine sandstone and shale, dark grayish-red in color). This bedrock may contain more weatherable base cations than the bedrock under the rest of the study area. When these two plots are excluded from the analysis, the correlation coefficient between NNP and topographic index increases from 0.20 ($P = 0.28$) to 0.33 ($P = 0.07$).

5. Conclusions

Watersheds 4 and 10 at the Fernow Experimental Forest differ in NO_3^- export and in many other characteristics. The large difference in NNP in the two watersheds suggests that differing tendencies of the soils to nitrify are both sufficient and necessary to explain the difference in NO_3^- leaching. Differences in soil microclimate may cause actual nitrification in W4 to exceed that in W10 by an even greater ratio than that measured for NNP. Several

two- and three-variable models can account for variability in NNP between watersheds and among plots approximately equally well. These models indicate that high NNP and, therefore, susceptibility to N saturation, occur in areas of relatively high base cation supply and acid neutralizing capacity, low C:N, and high WHC.

Relationships between NNP and biomass indicate that low demand for N is not the cause of N leaching. Therefore, high net nitrification, as indexed by high NNP, is the cause of the saturated condition in W4, and of the spatial pattern of saturation within W4. The long-term record demonstrating saturation at the Fernow Experimental Forest, therefore, provides evidence that "rich" sites that are currently found to leach NO_3^- are not necessarily leaching at baseline rates.

Acknowledgements

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