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Patterns of nitrogen availability within a forested watershed exhibiting symptoms of nitrogen saturation

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Abstract

Watershed 4 (WS 4) at the Fernow experimental forest in West Virginia shows several symptoms of N saturation. Surprisingly, however, past measurements of N₂O production suggest that a portion of WS 4 (the south-facing slopes) may still be strongly limited by the lack of available N. To examine this possibility more fully, we measured four indices of N availability in two sections of WS 4—slopes with easterly aspects that are located on one side of the main stream channel and slopes with southerly aspects that are located on the opposite side of the stream. Compared to the portion of WS 4 with more east-facing slopes (78% of the total area), we found that south-facing slopes had lower extractable NO₃⁻ pools (14 versus 554 mg N m⁻²), lower rates of net nitrification (2 versus 35 mg N m⁻² day⁻¹), a greater response of root growth to N-rich microsites (4.5× versus 1.6× > controls), and lower concentrations of NO₃⁻ in water leaching below the A, B, and C soil horizons (ca. 0.066 versus 2.3 mg N l⁻¹). The two sections of WS 4 also differed in the composition of their woody vegetation. Slopes with more easterly aspects had a greater relative importance of *Acer saccharum* and *Prunus serotina*. The south-facing slopes were characterized by a greater importance of *Nyssa sylvatica* and *Fagus grandifolia*. From these results we hypothesize that aspect-related differences in species composition can strongly influence the susceptibility of a forested stand to the early onset of N saturation. If this hypothesis is proven, then community composition may account for a significant proportion of the variable response of forested watersheds to similar levels of elevated N deposition. It would also imply that management practices which favor certain species might delay or accelerate the onset of N saturation and the potentially negative changes associated with this process. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Forest ecosystems in central and southern Appalachia receive high amounts of nitrogen (N) from atmospheric deposition which makes them susceptible to

the process of N saturation. Nitrogen saturation has been variously defined (Ågren and Bosatta, 1988; Aber et al., 1989; Stoddard, 1994), but in this study we will view it as a continuum of changes that results in a sustained excess of available N relative to an ecosystem's ability to retain it (Aber, 1992).

An increase in N availability during the process of N saturation may lead to several undesirable effects.

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These include: (1) an increase in surface-water NO_3^- concentrations (Stoddard, 1994); (2) enhanced losses of nutrient cations from forest soils (Likens et al., 1996; Adams et al., 1997); (3) nutrient imbalances, reduced frost hardiness and increased sensitivity of vegetation to attacks by insects and pathogens (Schulze, 1989); (4) declining tree growth and vigor in evergreen stands (Aber et al., 1995; McNulty et al., 1996); and (5) increased emissions of nitrous oxide (N_2O) to the atmosphere by denitrification and/or nitrification (Tietema and Verstraten, 1991).

In central and southern Appalachia, several forest ecosystems exhibit a least a few symptoms of N saturation (Johnson et al., 1991; Nodvin et al., 1995; DeWalle and Pionke, 1996; Williard et al., 1997). However, the best documented example of N saturation in this region is probably watershed 4 (WS 4) at the Fernow Experimental Forest in West Virginia. From over 20 years of research at this site, several symptoms of N saturation have been identified (Peterjohn et al., 1996). These symptoms include a 20-year increase in stream-water concentrations of NO_3^- and base cations, a low retention of inorganic N inputs, a high proportion of net N mineralization being nitrified, and little seasonal variability in stream-water NO_3^- concentrations. Surprisingly, however, measurements of N_2O production in WS 4 suggest that part of this watershed may still be limited by a lack of available N (Peterjohn et al., in press). More specifically, soils from the south-facing slopes of WS 4 had N_2O production rates that were 93% lower than soils from more east-facing slopes, and their mean production rates increased ca. $5\times$ in response to NO_3^- additions. In contrast, soils from more east-facing slopes did not respond to NO_3^- additions. The purpose of this paper is to more fully examine the possibility that portions of a watershed showing symptoms of N saturation may be strongly limited by N availability.

2. Methods

2.1. Study site

This study was conducted on WS 4 of the Fernow Experimental Forest near Parsons, West Virginia

($39^\circ 3' 15''\text{N}$, $79^\circ 41' 15''\text{W}$). WS 4 is a 38.7 ha catchment that we divided into two sections. The first section lies to the west and south of the main stream channel, consists of slopes with a predominantly easterly aspect, and comprises ca. 78% of the total area (Fig. 1). The second section lies to the east and north of the main stream channel, and consists of slopes with a strong southerly aspect. For convenience, we will refer to these two sections by their aspect throughout this paper. WS 4 has been undisturbed since it was heavily cut around 1905, except for the removal of dead American chestnut trees (*Castanea dentata*) in the 1940s (Adams et al., 1993, 1997). Currently, the forest on WS 4 is a mature stand of trees dominated by *Acer saccharum*, *Quercus rubra*, *Acer rubrum*, and *Prunus serotina* (Table 1). The soils on WS 4 have an average depth of <1 m and are mapped as predominantly a Calvin channery silt loam (loamy-skeletal, mixed, mesic Typic Dystrochrept) that is derived from the acidic sandstone and shale of the Hampshire formation (Losche and Beverage, 1967). A more detailed description of the soils in WS 4 was obtained from 15 soil pits distributed throughout the watershed (M.B. Adams, unpublished data). The more detailed soil survey revealed a complex pattern of mostly the Berks and Muskingum soil series, and differences in soil depth between the two sections of WS 4. More specifically, soils on the more east-facing slopes had an average solum thickness of 64.3 cm and an average depth to bedrock of 83.4 cm. In contrast, soils on the south-facing slopes had an average solum thickness of 39.0 cm and an average depth to bedrock of 55.5 cm. Annual precipitation and streamflow average about 146 and 64.0 cm, respectively (Adams et al., 1994). Precipitation is uniformly distributed throughout the year, whereas streamflow exhibits peak flows between November and April. Mean monthly air temperatures range from about -2°C in January to about 20°C in July (Adams et al., 1994). The mean annual temperature is about 9°C . During the growing season (May–October), the winds at a nearby weather station are most often from the WNW or the ESE. During the dormant season (November–April) winds are generally from the WNW (Adams et al., 1994). Inputs of inorganic N in bulk precipitation average about $11.3 \text{ kg ha}^{-1} \text{ year}^{-1}$, and 55% of these inputs are in the form of NO_3^- -N (Adams et al., 1997).

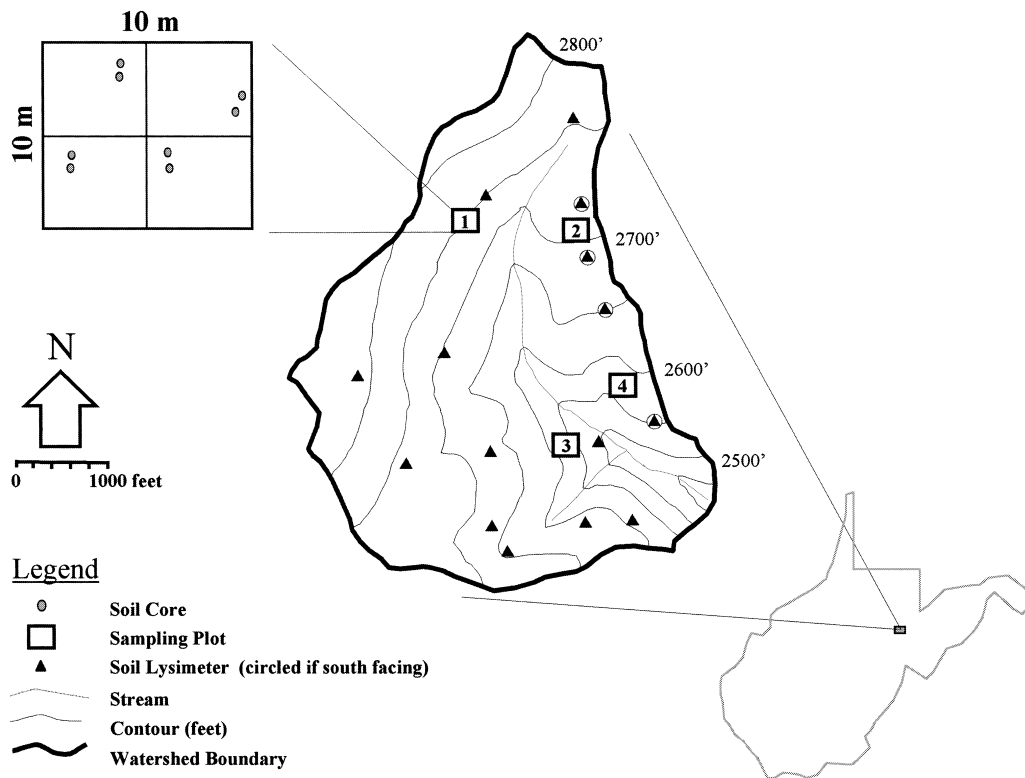


Fig. 1. Location of sampling sites within watershed 4 (WS 4) in the Fernow Experimental Forest, Parsons, West Virginia.

2.2. Measurements

To assess the extent of N limitation in the two sections of WS 4 (east- and south-facing slopes), we measured four indices of N availability. These indices were: (1) KCl-extractable pools of inorganic N; (2) net rates of N mineralization and nitrification; (3) root ingrowth into fertilized microsites; and (4) NO_3^- concentrations in soil leachate. To better understand any differences between the two sections, we also characterized the composition of the woody vegetation.

2.2.1. Pools and production rates of available N

From May to October 1996, we used the buried-bag technique (Eno, 1960; Westerman and Crothers, 1980; Pastor et al., 1984) to make monthly measurements of the inorganic N pools, and the net rates of N mineralization and nitrification. These measurements were made on intact soil cores obtained from four, $10\text{ m} \times 10\text{ m}$ sampling plots located at mid-slope

positions within the watershed (Fig. 1). Two sampling plots (1 and 3) were positioned in the section of WS 4 that has slopes with easterly aspects. The remaining sampling plots (2 and 4) were located in the section that has slopes with southerly aspects (Fig. 1). On each sampling occasion, four randomly located pairs of intact soil cores (10 cm deep \times 8 cm in diameter) were removed from each plot (one pair from each quadrant of a given plot) and placed separately into polyethylene bags (0.025 mm thickness). Of the two cores taken from each quadrant, one was reinserted into its original hole, covered with litter, and incubated in situ for 1 month. The second core was taken to the lab for analysis of the initial concentration of extractable inorganic N. After approximately 1 month, the buried core was collected for analysis, and another set of cores was sampled in the same manner. Soil cores were also buried in October 1996 and allowed to incubate for 6 months in order to provide one estimate of N availability for the colder months.

In the lab, all soil cores were sieved to pass a 5.6 mm mesh, and a 10 g subsample from each was shaken for 1 h in 100 ml of 2M KCl. After allowing each sample to equilibrate overnight, the supernatant was decanted, centrifuged at 300 rpm for 15 min, decanted again, and stored at 4°C. For each sample, duplicate measurements of NO_3^- and NH_4^+ concentrations were determined colorimetrically with a Lachat QuickChem AE autoanalyzer. Nitrate was determined using cadmium-reduction procedures (QuickChem Method 12-107-04-1-B) and NH_4^+ was determined using a heated salicylate method (QuickChem Method 12-107-06-2-A). The change in the extractable pools of NO_3^- and NH_4^+ over time was used to estimate the net rate of N mineralization. The change in extractable NO_3^- pools over time was used to estimate net nitrification rates.

2.2.2. Root ingrowth cores

As an index of the potential growth response of vegetation to various nutrient additions, we used a fertilized root ingrowth core assay (Raich et al., 1994). Ingrowth cores were made by forming bags from fiberglass window screen (0.143×0.2 cm-mesh) and filling them with calcined clay (Turface[®]). Each core received 90 ml of one of three solutions: $6.76 \text{ g l}^{-1} \text{ NH}_4\text{Cl}$, $8.10 \text{ g l}^{-1} \text{ Na}_2\text{HPO}_4$, or deionized water as a control. In May 1996, we positioned ingrowth cores along four, 35 m transects that began at the outer edge of each sampling plot and ran parallel to the contours of the hillside. Every 5 m along the length of each transect, we buried a cluster of three cores (one from each treatment) to a depth of 10 cm. The three cores in each cluster were within 10 cm of each other and remained in place for 5 months. At the end of 5 months, the cores were retrieved by slicing the soil around each core and carefully removing the core and any adhering soil. All cores were then sealed in plastic bags and frozen until they could be processed. To estimate the amount of root growth into each core, we shaved the soil and roots from the outside of the thawed cores, and sieved the contents through a 5.6 mm mesh to obtain the larger roots. We collected smaller roots by floating them in water to separate them from denser material. Floating roots were collected on a nylon mesh (96 μm), and all roots (both large and small) were dried (65°C for ≥ 48 h) and weighed.

2.2.3. Soil leachate

To collect soil leachate, 15 soil pits were dug on WS 4 in 1988 as part of a separate investigation (Adams et al., 1997). In each pit, zero-tension lysimeters were positioned at the base of the A and B horizons. Whenever possible, lysimeters were also placed at the base of the C horizon. After a 6 month acclimation period, leachate samples were collected at monthly intervals or whenever the sample volume was sufficient for chemical analysis. All leachate samples were analyzed for NO_3^- using EPA approved protocols at the USDA Forest Service's Timber and Watershed Laboratory in Parsons, WV (Edwards and Woods, 1993).

2.2.4. Vegetation

In order to characterize the vegetation, we sampled woody vegetation in 35 plots within WS 4. A grid of 100×100 m squares, oriented according to the cardinal compass directions, was laid out using a hand-held compass, a clinometer for slope correction, and a tape measure. Center points for circular plots (10 m radius) were established at each gridpoint. Diameter, species, vigor and canopy class was recorded for each stem ≥ 5 cm DBH (diameter at breast height) on each of the circular plots. Importance values for living stems of each species for the watershed as a whole, as well as for each of the two sections of the watershed, were calculated as averages of relative density, relative basal area, and relative frequency of that species in the corresponding set of plots. We also characterized the vegetation on the four soil-sampling plots (Fig. 1) with respect to each species relative density and relative basal area.

2.3. Data analysis

All data were tested for normality using the Shapiro–Wilks' W test, and appropriate transformations (logarithmic or square-root) were performed on non-normal data prior to statistical analysis. Values in data sets containing zeros were increased slightly (0.0005–0.005, depending on detection limits and the magnitude of the data) prior to any log transformations. Analysis of variance was performed to test for significant differences at $\alpha = 0.05$. For extractable N pools and N production rates, the statistical model we used treated sampling plots as a random factor and

included two terms: aspect (easterly or southerly) and sampling plot nested within aspect. For root ingrowth data, we tested for effects on root growth stimulation – the ratio of the mass of roots in a fertilized core to the mass of roots in the control (distilled water only) core from the same cluster. For this analysis, our statistical model treated the sample clusters as a random variable and included the following terms: aspect, sample cluster nested within aspect, treatment (N or P addition), and the appropriate interactions. Finally, the statistical model we used to analyze the soil leachate data included both aspect and soil horizon as fixed variables and the aspect \times horizon interaction. All statistical calculations were performed using the computer program STATISTICA release 5 (StatSoft, 1995).

3. Results

3.1. Pools and production rates of available N

The average amount of KCl-extractable NO_3^- in plots with a more easterly aspect (554 mg N m^{-2}) was

significantly greater ($p = 0.011$) than the amount in plots with a southerly aspect (14 mg N m^{-2} ; Fig. 2). In contrast, KCl-extractable NH_4^+ was not significantly different between the two sections of WS 4.

Consistent with the large differences we measured in extractable NO_3^- , there were also large (>10-fold) differences in the net rates of NO_3^- production between the two sections of WS 4 (Fig. 2). The average rate of net nitrification in sampling plots with more easterly aspects was $35 \text{ mg N m}^{-2} \text{ day}^{-1}$, and this was significantly greater ($p = 0.033$) than the average rate measured in plots with a southerly aspect ($2 \text{ mg N m}^{-2} \text{ day}^{-1}$). The differences in net rates of N mineralization between the two sections of WS 4 were not statistically significant ($p = 0.470$) even though the average rate in plots with a southerly aspect ($23 \text{ mg N m}^{-2} \text{ day}^{-1}$) was about half of the average rate measured in plots on the more east-facing slopes.

3.2. Root ingrowth cores

In plots with easterly aspects, root growth was stimulated equally by N and P (ca. $2.5\times$ > controls;

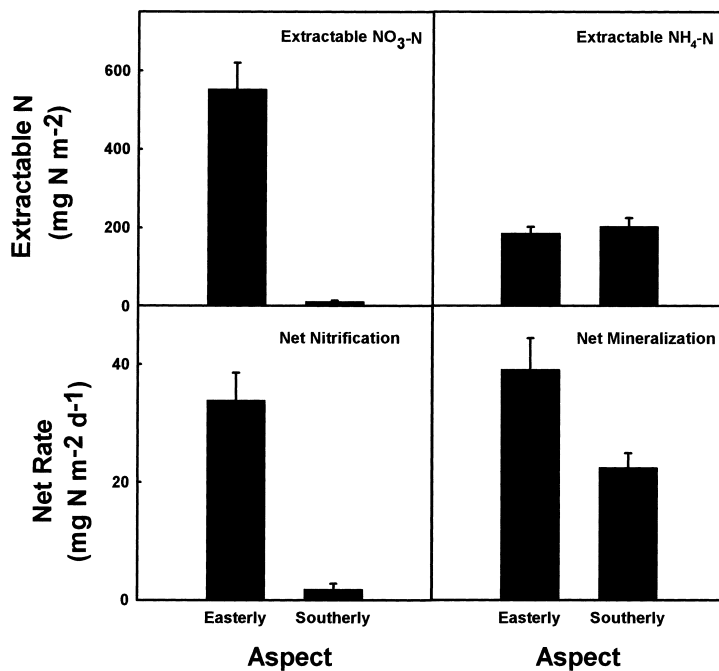


Fig. 2. Pools and production rates of available N for soils located on slopes with different aspects within watershed 4 (WS 4). Bars represent 1 SE of the mean.

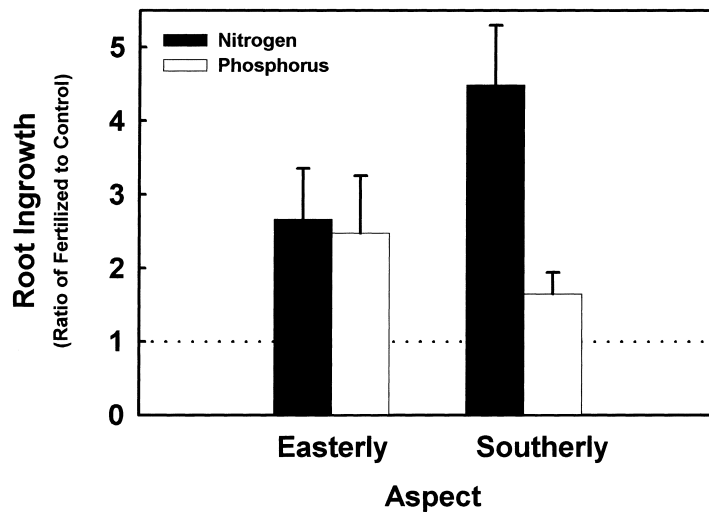


Fig. 3. Interactive effects of nutrient treatments and aspect on the stimulation of root growth. Bars represent 1 SE of the mean. Dotted line indicates no stimulation by fertilization.

Fig. 3). In contrast, root growth in plots with a southerly aspect was strongly stimulated by N ($4.5 \times$ > controls) and only weakly stimulated by P ($1.6 \times$ > controls). When these data were analyzed using a three-way ANOVA, we found a significant treatment effect (N or P addition; $p = 0.0005$) and a significant treatment \times aspect interaction ($p = 0.0048$). When the data for each fertilization treatment were analyzed separately, ANOVA revealed a significantly greater response to N on the south-facing plots ($p = 0.037$), and no aspect-related difference in the response of root growth to P additions.

3.3. Soil leachate

Soil leachate samples were divided into two groups depending on the location of the lysimeters. The first group consisted of all the leachate samples collected from four locations on the south-facing slopes of WS 4 (Fig. 1). The second group consisted of all leachate samples collected from 11 locations on slopes with more easterly aspects. Large and statistically significant differences ($p < 0.001$) were found in the NO_3^- concentrations of leachate moving through the two sections of the watershed (Fig. 4). The average NO_3^- concentrations in leachate from all soil horizons on slopes with an easterly aspect (ca. 2.3 mg N L^{-1}) were $>30\times$ the average concentra-

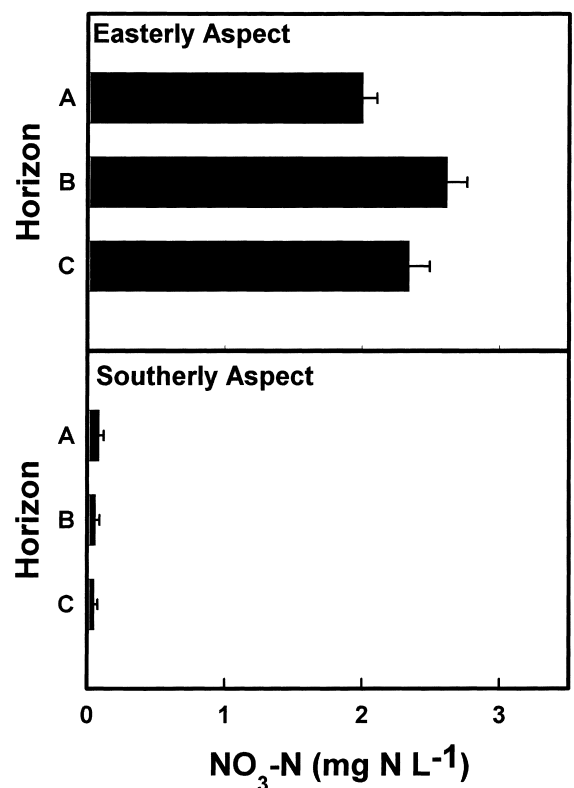


Fig. 4. Average concentrations of NO_3^- -N in water leaching below the A, B, and C soil horizons on slopes with different aspects in watershed 4 (WS 4). Bars represent 1 SE of the mean.

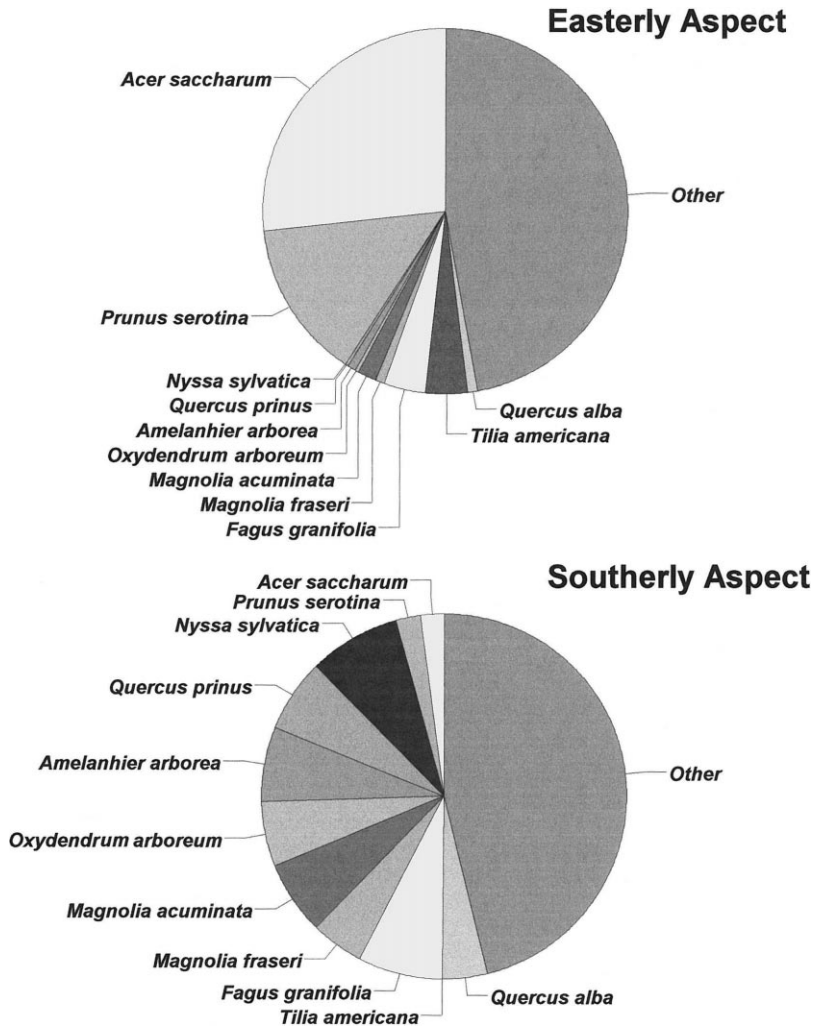


Fig. 5. The importance percentages of woody species growing on slopes with different aspects in watershed 4 (WS 4). Only species with the greatest aspect-related differences in their importance percentages are identified. Data from Table 1.

tions measured on slopes with a southerly aspect (ca. $0.066 \text{ mg N l}^{-1}$).

3.4. Vegetation

In our general survey of the vegetation on WS 4, clear differences were found in the relative importance of woody species on the two sections of WS 4 (Table 1). The largest of these differences were in the relative importance of *Acer saccharum* and *Prunus serotina* (Fig. 5). On the section of WS 4 with more easterly aspects, the importance percentages of *Acer*

saccharum and *Prunus serotina* were 26.7 and 14.1%, respectively. In contrast, on the section of WS 4 with south-facing slopes, the importance percentages for these species were only 2.1 and 2.2%.

When only the vegetation within our soil-sampling plots was compared, we found that plots on more east-facing slopes (1 and 3) were characterized by a greater importance of *Acer saccharum*, *Quercus prinus*, and *Tilia americana*. In contrast, sampling plots on south-facing slopes (2 and 4) were characterized by a greater importance of *Nyssa sylvatica*, *Fagus grandifolia*, *Oxydendrum arboreum*, *Acer rubrum*, and *Quercus rubra*.

4. Discussion

When considered together the results of this study clearly demonstrate that a watershed showing symptoms of N saturation can still contain portions that are strongly limited by the lack of available N. More specifically, we found that a small portion of WS 4 with south-facing slopes had lower extractable NO_3^- pools, lower rates of net nitrification, a greater response of root growth to N-rich microsites, and lower concentrations of NO_3^- in water leaching below the A, B, and C soil horizons.

The underlying causes of the differences in N availability within WS 4 are not known. They are, however, associated with differences in the composition of woody vegetation in a way that is consistent with our current understanding of species-related rates of nutrient cycling. In deciduous forests, rapid rates of litter decomposition and N cycling are frequently measured in stands dominated by sugar maple (*Acer saccharum*) and black cherry (*Prunus serotina*), whereas slower rates are often observed in stands dominated by oak (*Quercus* spp.) and beech (*Fagus grandifolia*; Shanks and Olson, 1961; Melillo et al., 1982; Pastor et al., 1984; Aber et al., 1990; Zak and Pregitzer, 1990). Furthermore, recent studies (Rothstein et al., 1996; Kinney and Lindroth, 1997) suggest that sugar maples (*Acer saccharum*) may have a limited capacity to compete for available NO_3^- -N – a trait which may make sugar-maple stands more susceptible to an early onset of N saturation.

The differences in species composition that we observed between the two sections of WS 4 could result from a variety of factors, and the exact cause cannot be determined from this study. We hypothesize, however, that these differences in vegetation are strongly influenced by differences in aspect. In Appalachian forests, a relationship between aspect, species composition, and some components of site quality has been clearly demonstrated (Trimble and Weitzman, 1956; Auchmoody and Smith, 1979; Tajchman and Wiant, 1983; Frank et al., 1984; Hicks and Frank, 1984). In general, south- and west-facing slopes are less productive and dominated by oaks (*Quercus* spp.), whereas north- and east-facing slopes are more productive and dominated by black cherry (*Prunus serotina*) and maple (*Acer* spp.).

Although the species composition differs between the two sections of WS 4, other factors might also account for the observed differences in N availability. These factors include potential differences in temperature, moisture, pH, and soil depth. However, the data currently available do not strongly support these alternative hypotheses. For example, a previous study of WS 4 during the growing season of 1994 found little difference in soil temperature (17.8 versus 17.4°C for south- versus east-facing slopes), air temperature (14.0 versus 14.0°C), water-filled pore space (37.6 versus 39.1%), or soil pH (3.92 versus 3.91) between the two sections of WS 4 (Peterjohn et al., in press). Furthermore, the shallower soils found on the south-facing slopes indicate that deeper soils are not associated with greater N retention in this watershed. Because the existing environmental data for the two sections of WS 4 are quite limited, more extensive measurements are currently being made to more rigorously examine the importance of factors other than species composition in influencing N availability and retention.

If future studies support the hypothesis that species composition is a good indicator of a forest's susceptibility to N saturation, then community composition may account for a significant portion of the unexplained variability in the response of forested watersheds to similar levels of elevated N deposition (Driscoll et al., 1989; Dise and Wright, 1995; Peterjohn et al., 1996). It would also suggest that management practices, or natural changes, which favor certain species might delay or accelerate the onset of N saturation and the potentially negative changes associated with this process.

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