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Testing associations between tree species and nitrate availability: Do consistent patterns exist across spatial scales?

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ABSTRACT

In forest ecosystems there are numerous factors that influence nitrate (NO_3) availability and retention in ways that can significantly affect receiving waters. Unfortunately these factors often co-exist and interact making it difficult to establish the importance of each individually. Three reference watersheds at the Fernow Experimental Forest (FEF) provide a unique opportunity to evaluate the influence of tree species on soil NO_3 availability across spatial scales because they differ in stream-water NO_3 concentrations despite sharing the same macro-climate, geology, hydrology, dominant soils series, stand age, pollution regime, and land-use history.

To test the strength of plant/soil associations inferred from previous work in two watersheds in the FEF, we measured NO_3 availability and the composition of tree species in a third watershed that has intermediate stream-water NO_3 concentrations. We also examined plant/soil relationships in these watersheds at the scale of individual trees.

Across the spatial scales examined – from individual trees to small watersheds – there were consistent associations between tree species and soil NO_3 availability. For individual trees, species with high underlying soil NO_3 availability included *Acer saccharum* and *Lireodendron tulipifera*, whereas species with low underlying soil NO_3 availability included *Acer rubrum*, *Nyssa sylvatica*, and *Quercus prinus*. For small plots we found plant/soil relationships that were consistent with those made apparent by sampling under individual trees of *A. saccharum*, *A. rubrum*, *N. sylvatica*, and *Q. prinus*. And at the scale of entire watersheds, those with higher stream-water NO_3 had a greater importance of tree species associated with high NO_3 availability at finer spatial scales than did the watershed with low stream-water NO_3.

The spatially-robust relationships between tree species and soil NO_3 availability at the FEF suggest that well-characterized relationships between dominant tree species and soil properties should improve our understanding of how changes in the species composition of forest trees due to human activities, or natural causes, will alter rates of NO_3 production and loss.

1. Introduction

The increased production of nitrate (NO_3) is a pivotal event during the process of nitrogen (N) saturation in terrestrial ecosystems that can, in turn, significantly affect N losses and downstream ecosystems (Aber et al., 1998; Driscoll et al., 2003). Several empirical studies suggest that the composition of tree species may make a significant contribution to the variability in NO_3 production and loss from forest ecosystems (Lovett and Rueth, 1999; Peterjohn et al., 1999; Lovett et al., 2000). In general, these studies indicate that sugar maple trees are associated with high NO_3 availability and a lower capacity to retain NO_3 than oak and American beech trees. For example, Lovett and Rueth (1999) found a significant, and positive, correlation between N deposition and potential rates of net nitrification for soil collected from seven sites containing sugar maple, but not for soil collected from nearby sites containing American beech. From these observations they concluded that soils under the two species responded differently to increasing levels of N deposition, and that species differences should be considered in the prediction of forest response to N deposition, and in forest management practices.

Numerous factors, however, influence NO_3 availability and retention in forest ecosystems. These include climate, geology, hydrology, soils, stand age, pollution, species composition, natural

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disturbances (insect defoliation, fire, frost, etc.), and land-use history (e.g., Vitousek and Reiners, 1975; Mitchell et al., 1996; Lewis and Likens, 2000; Aber et al., 1998, 2002; Eshleman et al., 1998; Goodale and Aber, 2001; Mitchell, 2001; Hong et al., 2005; Williard et al., 2005). Unfortunately, the frequent co-existence and interaction of these factors can confound attempts to firmly establish the importance of each individually.

Several small reference watersheds at the Fernow Experimental Forest (FEF) provide a unique opportunity to evaluate the importance of tree species because they have large differences in stream-water NO_3 concentrations despite sharing the same macro-climate, geology, hydrology, dominant soils series, stand age, pollution regime, and land-use history. Furthermore, none of the forests in these watersheds have experienced severe insect defoliation (M.B. Adams *personal communication*) and fire has not been recorded since the federal government purchased the FEF in 1915 (Schuler and Gillespie, 2000).

Previous work comparing two of these watersheds (WS 4 and WS 10) suggests there may be a relationship between the composition of tree species and NO_3 availability that persists across several spatial scales (Christ et al., 2002; Peterjohn et al., 1999). At the scale of an entire catchment (∼14–34 ha), the watershed with the highest levels of stream-water NO_3 (WS 4) had a greater relative importance (dominance + density + frequency) of *Acer saccharum*, *Lireodendron tulipifera*, and *Prunus serotina* – species often associated with high nutrient requirements, high foliar N levels, and high soil N availability. The same watershed had a lower relative importance of *Acer rubrum*, *Nyssa sylvatica*, *Fagus grandifolia*, and *Quercus prinus* – species with low nutrient requirements and typical of moderate-to-low soil N availability (Abrams, 1998, 2007; Lovett and Rueth, 1999; Christ et al., 2002). Although we are unaware of generalizations about relative nutrient requirements of *Amelanchier arborea*, this species also had a lower relative importance in WS 4.

At a finer spatial scale within WS 4 (the watershed with high stream-water NO_3 levels), Peterjohn et al. (1999) found a region (∼8.5 ha) with very low NO_3 availability and a lower relative importance of two tree species associated with high soil N availability (*A. saccharum* and *P. serotina*), and a greater importance of tree species associated with low N availability (*N. sylvatica*, *F. grandifolia*, and *Q. prinus*). This region also had greater relative importance of *A. arborea*.

Finally, at the spatial scale of small plots (∼0.03 ha) within both WS 4 and WS 10, higher net nitrification rates in forest soils were strongly correlated with higher soil pH_{Ca} ($r = 0.75$), lower soil C:N ratios ($r = -0.70$), greater base saturation ($r = 0.72$), and (to a lesser extent) the relative importance of several dominant canopy tree species (Christ et al., 2002; Peterjohn, unpublished data). Specifically, there were positive correlations between potential net nitrification and the relative importance (dominance + density) of *A. saccharum* ($r = 0.66$), and *P. serotina* ($r = 0.41$), whereas negative correlations were found between net nitrification and the importance of *A. rubrum* ($r = -0.47$), *Q. prinus* ($r = -0.44$), *N. sylvatica* ($r = -0.41$), and *A. arborea* ($r = -0.39$). No correlation was apparent at this scale between net nitrification and the importance of *L. tulipifera* ($r = 0.18$), or *F. grandifolia* ($r = -0.001$).

To more rigorously test the strength of the apparent associations observed between tree species and NO_3 availability across spatial scales at the FEF, we measured NO_3 availability and the composition of tree species in a third reference watershed (WS 13) that has intermediate, but fairly high, stream-water NO_3 concentrations (∼39 μM) when compared to the other two reference watersheds (∼56 and ∼16 μM for WS 4 and 10, respectively). We also examined whether associations between tree species and NO_3 availability are detectable at the scale of individual canopy trees (∼0.001 ha) growing across all three reference watersheds.

2. Materials and methods

2.1. Study sites

This study used three forested watersheds located on the FEF near Parsons, West Virginia (39°3′15″N, 79°42′15″W). The watersheds (WS 4, 10, and 13) are <2 km apart and have the same dominant soils series, geology, climate, stand age, and land-use history (Fig. 1). None of the forests in these watersheds have experienced severe insect defoliation and no fire damage has been recorded.

Watershed 4 consists of 38.7 ha with an average slope of 16% and an east–southeasterly aspect. The vegetation is dominated by *A. saccharum*, *A. rubrum*, *Q. rubra*, and *L. tulipifera*. Watershed 10 is smaller (15.2 ha), more steeply sloping (26%), and has a southerly aspect. The vegetation on this watershed is dominated by *A. rubrum*, *Q. prinus*, *Q. rubra*, and *F. grandifolia*. Watershed 13 is the smallest of the watersheds (14.2 ha), with steep slopes (ca. 25%), and a north–northeasterly aspect. The vegetation on this watershed, as will be shown, is dominated by *A. saccharum*, *F. grandifolia*, *Q. rubra*, and *A. rubrum*.

On all three watersheds the dominant soil type is a Calvin channery silt loam (loamy-skeletal, mixed, mesic Typic Dystrochrept) derived from the acidic sandstone and shale of the underlying Hampshire formation (Losche and Beverage, 1967; Taylor, 1999). The depth to bedrock is <1 m. Mean monthly air temperatures range from about −2 °C in January to about 20 °C in July. Annual precipitation (±1 SD) is about 145 ± 14.8 cm and is uniformly distributed throughout the year. Streamflow and stream-water chemistry data exist for all three watersheds since 1988. From available data, the average annual streamflow (±1 SD) for WS 4, 10, and 13 are 64.0 ± 12.8, 64.2 ± 14.7 and 98.1 ± 9.0 cm, respectively (Adams et al., 1994). The average monthly stream-water NO_3 concentrations (±1 SD) from 1990 to 2000 for WS 4, 10, and 13 were about 56 ± 11.4, 16 ± 11.9 and 39 ± 12.3 μM NO_3, respectively. The vegetation on all three watersheds regenerated naturally after being heavily cut ca. 1907. The only known disturbance since that time was a 25% reduction in the volume of standing timber caused by the Chestnut blight in the 1930s and the removal of the dead chestnut trees in the 1940s (Adams et al., 1993; Schuler and Gillespie, 2000). All watersheds at the Fernow Experimental Forest have historically received relatively high inputs of inorganic N from the atmosphere. Between 1986 and 2002, we estimate that these watersheds received an average of ∼10 kg N ha^{-1} yr^{-1} in total N (wet + dry) deposition (Adams et al., 2006). For comparisons between the reference catchments, we used the average monthly stream-water NO_3 concentrations as a measure of NO_3 availability for an entire watershed, and we measured tree data in small plots to calculate species-specific importance values (relative dominance + relative density + relative frequency) for each watershed.

2.2. Plot-based sampling

In the summer and fall of 2000, we characterized the vegetation and NO_3 availability in all three reference watersheds at the FEF. This was done to assess whether patterns between NO_3 availability and tree species composition found for WS 4 and 10 persist with the inclusion of data from WS 13 – a previously un-sampled reference watershed. Following the methods of Christ et al. (2002), the living vegetation with a DBH ⩾ 5 cm was characterized using eleven evenly-spaced plots (10-m radius and 100 m apart) in WS 13 and sixteen plots in both WS 4 and 10. In all plots we also buried three anion-exchange membranes (Dynambio, Madison, Wisconsin, USA) to a depth of 7 cm for one week. This was done five times during the growing season (twice in June, twice in July, and once late in the growing season) in WS 4 and WS 10, and once in WS