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Effects of excess nitrogen on biogeochemistry of a temperate hardwood forest: Evidence of nutrient redistribution by a forest understory species

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HIGHLIGHTS

- Excess nitrogen (N) deposition negatively impacts eastern U.S. hardwood forests.
- Our study studied biogeochemical effects via foliar analysis of herb layer species.
- Aerial N additions were made to an entire watershed for a 25-yr period.
- Early-dominant Viola and late-dominant Rubus were higher in N, lower in Ca.
- N-mediated increases in Rubus appeared to redistribute Mn to surface soils.

GRAPHICAL ABSTRACT

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ABSTRACT

Excess nitrogen (N) in terrestrial ecosystems can arise from anthropogenically-increased atmospheric N deposition, a phenomenon common in eastern US forests. In spite of decreased N emissions over recent years, atmospheric concentrations of reactive N remain high in areas within this region. Excess N in forests has been shown to alter biogeochemical cycling of essential plant nutrients primarily via enhanced production and leaching of nitrate, which leads to loss of base cations from the soil. The purpose of our study was to investigate this phenomenon using a multifaceted approach to examine foliar nutrients of two herbaceous layer species in one N-treated watershed (WS3—receiving aerial applications of 35 kg N/ha/yr as ammonium sulfate, from 1989 to the present) and two untreated reference watersheds at the Fernow Experimental Forest, WV, USA. In 1993, we analyzed foliar tissue of *Viola rotundifolia*, a dominant herb layer species and prominent on all seven sample plots in each watershed. In 2013 and 2014, we used foliar tissue from *Rubus allegheniensis*, which had become the predominant species on WS3 and had increased, though to a lesser extent, in cover on both reference watersheds. Foliar N and potassium (K) were higher and foliar calcium (Ca) was lower on WS3 than on the reference watersheds for both species. Magnesium (Mg) was lower on WS3 for *Viola*, but was not different among watersheds for *Rubus*. Results support the stream chemistry-based observation that excess N lowers plant-available Ca and, to a lesser degree, Mg, but not of K. Foliar manganese (Mn) of

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Rubus averaged >4 times that of *Viola*, and was >50% higher on WS3 than on the reference watersheds. A Mn-based mechanism is proposed for the N-meditated increase in *Rubus* on WS3. Data suggest that excess N deposition not only alters herb community composition and biogeochemical cycling of forest ecosystems, but can do so simultaneously and interactively.

1. Introduction

Foliar nutrient concentrations of wild plants often, though not always, reflect the availability of nutrients in mineral soil, since foliar nutrients are generally indicative of the balance between nutrient supply in the soil and immediate demand by the plants (Chapin, 1980; Schreeg et al., 2014). Sources of variation in this generalization include uptake of nutrients beyond plant demand—luxury uptake—and a high degree of species-specific variability in nutrient use and allocation, including resorption (Chapin and Kedrowski, 1983; Killingbeck, 1996; May et al., 2005; Baeten et al., 2010). To the extent that this generalization is relevant, foliar nutrient analyses can yield insight into factors (e.g., anthropogenic disturbance) that influence nutrient availability, and others (e.g., plant-soil feedbacks) that control nutrient dynamics (Reiners, 1992; Schreeg et al., 2014).

In the United States, the 1977 and 1990 amendments of the Clean Air Act of 1970 have been effective in decreasing emissions of nitrogen (N) compounds into the atmosphere. Despite this, however, high concentrations of reactive nitrogen (including NH_3, NH_4^+, NO, NO_2, NO_3^-, $2N_2O_5$, HNO_3, and several forms of peroxyacetyl nitrates—Horii et al., 2005) persist, as do high levels of atmospheric deposition of N, in several regions throughout the world (Galloway et al., 2008; Sutton et al., 2014; Vet et al., 2014; Keene et al., 2015), although N remains the nutrient that most commonly limits or co-limits plant growth globally (Vitousek et al., 1997; Elser et al., 2007). Conversely, chronic atmospheric deposition of N in many areas supplies available N in excess of plant and microbial demand, leading to a phenomenon known as N saturation (Aber et al., 2003).

As discussed by Gilliam (2006), N saturation is a biogeochemical phenomenon that has direct, sometimes immediate, consequences for plant communities, thus integrating the ecological disciplines of both biogeochemistry and vegetation science. Biogeochemically, excess N alters mobility of a variety of essential nutrients, beginning with increased predominance of NO_3^-, the highly mobile form of available N. As NO_3^- accumulates in the available N pool in excess of plant uptake, it becomes susceptible to leaching below the active rooting zone, accompanied by cations, particularly Ca^{++} and Mg^{++}. The result is an imbalance of increasing availability of N leading to decreasing availability of Ca^{++} and Mg^{++} (Peterjohn et al., 1996; Gilliam et al., 1996; Moore and Houle, 2013). Studies have also found that N saturation can initiate phosphorus (P) limitation forest ecosystems, although the specific mechanism is different than for cations (Güsewell, 2004; Gress et al., 2007; Vitousek et al., 2010).

Regarding the plant response to excess N, there are several possible direct and indirect effects on the species composition of forest herb strata via alteration of interspecific competition, herbivory, mycorrhizal infection, pathogenic fungal infection, and invasive species (Gilliam, 2006). This can be especially relevant for the herbaceous layer of forests considering that (1) many, perhaps most, N-saturated ecosystems are forests (Holland and Lamarque, 1997; Aber et al., 2003; Gilliam, 2014), and (2) the herb layer is potentially the most sensitive of forest strata to changes in nutrient availability (Muller, 2014). In addition, the herb layer merits special attention as the forest stratum with highest plant diversity (Gilliam, 2007).

The site for the current study—Fernow Experimental Forest (FEF), West Virginia—has been used for several past and on-going investigations into the ecological sustainability of Appalachian hardwood forests in the context of natural and anthropogenic disturbances, one of which is chronically-elevated N deposition (Adams et al., 2006). Peterjohn et al. (1996) provided clear evidence that several symptoms of N saturation (cf., Aber, 1992) had developed on the long-term reference watershed for on-going studies at FEF (WS4). One such symptom is high absolute and relative (to net N mineralization) rates of net nitrification, which were shown by Gilliam et al. (2001) to exist on an N-treated watershed (WS3) and two untreated reference watersheds (WS4 and WS7). Another symptom relevant to the present study is increased mobility and leaching of Ca^{2+} and Mg^{2+} associated with enhanced nitrification and leaching of NO_3^- (Peterjohn et al., 1996; Gilliam et al., 1996), along with evidence of decreased growth rates of dominant tree species (May et al., 2005; DeWalle et al., 2006). More recent work using root in-growth bags filled with nutrient-amended soil suggests that N saturation has led to P limitation in several FEF watersheds (Gress et al., 2007).

The purpose of this study was to enhance insight into the effects of excess N on the biogeochemistry of a temperate hardwood forest by examining foliar nutrient concentrations of two dominant herb-layer species on one N-treated watershed and two untreated watersheds at two time periods following initiation of N treatments—4 years and 24–25 years post-treatment. Because there has been an unprecedented N-mediated shift in herb layer dominance on these watersheds (Gilliam et al., 2016), this involves an unavoidable confounding of species and time (i.e., from *Viola rotundifolia* Michx. to *Rubus allegheniensis* Porter dominance—see Methods). Nevertheless, this study is unique in assessing biogeochemical responses to experimental N additions over such a time period and doing so using foliar nutrients on the same sample plots.

2. Methods

2.1. Study site

This study is part of long-term, on-going research on the effects of experimental additions of N on a temperate hardwood forest ecosystem carried out at FEF, located in Tucker County, West Virginia (39° 03′ 15″N,7 9° 49′ 15″W). FEF is a ~1900 ha area of the Allegheny Mountain section the unglaciated Allegheny Plateau. Precipitation for FEF averages ~1430 mm yr^{-1}, with precipitation generally increasing through the growing season and with higher elevations. Ambient wetfall deposition of N is ~10 kg N/ha/yr, and has changed little over the study period (Gilliam and Adams, 1996), other than declines in NO_3^- concentrations (Adams et al., 2006).

Soils of the study watershed are predominantly Inceptisols of the Berks (loamy-skeletal, mixed, mesic Typic Dystrochrept) and Calvin series (loamy-skeletal, mixed, mesic Typic Dystrochrept), derived from sandstone, and are generally coarse-textured sandy loams, well-drained, and ~1 m in depth (Adams et al., 2006). Three watersheds were used for the location of sample plots: WS3, WS4,

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