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Chronic nitrogen deposition reduces the abundance of dominant forest understory and groundcover species

Alan F. Talhelm [a,*], Andrew J. Burton [b], Kurt S. Pregitzer [a], Marcella A. Campione [c]

[a] *Department of Forest, Rangeland, and Fire Sciences, College of Natural Resources, University of Idaho, Moscow, ID 83844, USA*
[b] *Ecosystem Science Center, School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931, USA*
[c] *Department of Wildland Resources, College of Natural Resources, Utah State University, Logan, UT 84322-5200, USA*

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ABSTRACT

Humans have altered the global nitrogen (N) cycle, greatly increasing atmospheric nitrogen deposition in industrialized regions of the world. Groundcover plants can be sensitive indicators of nitrogen deposition impacts. Here, we report results from repeated measurements over a 7 year period of groundcover (plants <1.4 m tall) and understory (plants with a diameter <5 cm at 1.4 m in height) vegetation in four mature northern hardwood forests in the north-central United States receiving experimental additions of N ($3\ g\ m^{-2}\ year^{-1}$ as $NaNO_3$ for 18 years). Experimental N deposition reduced the average abundance of sugar maple (*Acer saccharum* Marsh.) seedlings in the groundcover by >50% ($P < 0.001$). This reduction occurred at all four sites, but was only statistically significant at the two sites where these seedlings were most abundant (site × nitrogen: $P < 0.001$). Our observations of mortality within a large cohort of sugar maple seedlings across three sites provide further evidence of this effect. For these seedlings, experimental N deposition significantly ($P < 0.05$) increased mortality in the weeks following germination, as well as over the longer term, reducing overall survival after 5 years by almost 90%. Although groundcover plants accounted for <0.5% of aboveground plant biomass, they contributed up to 10% of ecosystem leaf area and 5% of aboveground litter. At the two sites where sugar maple seedlings were infrequent, understory vegetation was more abundant and dominated by hop-hornbeam (*Ostrya virginiana* (Miller) K. Koch; 42% of all stems). At these two sites, experimental N deposition significantly reduced the abundance of understory hop-hornbeam by more than 75% (site × nitrogen: $P = 0.008$). The effects of experimental N deposition on the understory and groundcover vegetation occurred without significant decreases in reproductive litter or increases in canopy leaf area. Instead, the negative effects are more likely a by-product of other documented changes caused by the experimental N deposition: increased forest floor mass, decreased mycorrhizal abundance, and increased production of potentially alleopathic phenolic compounds. Because the late-successional species in these forests rely upon groundcover and understory plants for regeneration, the effects of added N on this vegetation have potential implications for future forest composition, particularly given the likely loss of some species in these forests due to exotic pests and pathogens.

1. Introduction

Human activities in sectors such as transportation, industry, and agriculture now add more reactive nitrogen (N) compounds (e.g. NO_x, NH_y) to the biosphere than do natural processes (Galloway et al., 2008). In industrialized regions, large quantities of these reactive N compounds are emitted into the atmosphere and subsequently enter downwind terrestrial ecosystems through atmospheric deposition (Galloway et al., 2008). Over the next century, growing global development and industrialization are expected to increase the amount of atmospheric N deposition added to terrestrial ecosystems around the world (Dentener et al., 2006) and many regions of the world are expected to experience increased atmospheric N deposition even in the most optimistic global change scenarios (Lamarque et al., 2011). Therefore, it is important to identify the effects of N deposition in order to understand how terrestrial ecosystems will function in the future.

In North America, northern temperate forests in the eastern half of the US and Canada receive large amounts of atmospheric N deposition (Townsend et al., 1996) and there is evidence that this has increased the availability of N in these forests (Aber et al., 2003; Talhelm et al., 2012). This increase in N availability has led to greater tree growth and forest carbon (C) storage in

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* Corresponding author. Tel.: +1 208 885 6770; fax: +1 208 885 6564.
E-mail addresses: atalhelm@uidaho.edu (A.F. Talhelm), ajburton@mtu.edu (A.J. Burton), kpregitzer@uidaho.edu (K.S. Pregitzer), marcella.campione@aggiemail.usu.edu (M.A. Campione).

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aboveground biomass (Thomas et al., 2010) and may also be reducing water quality and species diversity (Aber et al., 2003; Pardo et al., 2011). However, attempts to determine "critical loads" of N deposition have shown that there is still considerable uncertainty regarding the impacts of N deposition on northern temperate forests (Bobbink et al., 2010; Pardo et al., 2011).

Among forest ecological indicators, groundcover plants (seedlings, shrubs, and herbaceous plants) are considered to be potentially more sensitive to N deposition than overstory trees (Pardo et al., 2011). There are numerous reports that N deposition has altered the plants species composition in grasslands and other non-forested ecosystems (Bobbink et al., 2010; Pardo et al., 2011) and N deposition has had clear impacts on forest groundcover composition in Europe (Gilliam, 2006). However, there have been relatively few studies examining the influence of N deposition on groundcover plants in the northern temperate forests of North America (Pardo et al., 2011) and these studies have reported conflicting results. Both Hurd et al. (1998) and Rainey et al. (1999) found that experimental N additions decreased the abundance of the most common herbaceous species in forests in New York and Massachusetts, respectively. In contrast, Gilliam et al. (2006) found that 6 years of N amendments had not affected the groundcover of a forested watershed in West Virginia.

In addition to acting as potential indicators, groundcover plants are an important, but often overlooked, ecological component of northern forests. In part, this is because although there may be hundreds of groundcover plants per m^2 (Curtis, 1959), these plants frequently make up only a small fraction of forest biomass (Gilliam, 2007). However, these plants are both crucial to forest regeneration following disturbance and often disproportionately important within forest ecosystems in terms of species diversity, net primary productivity, nutrient cycling, and litter production (Siccama et al., 1970; Nilsson and Wardle, 2005; Gilliam, 2007). For instance, within the Hubbard Brook Experimental Forest, groundcover herbs and shrubs accounted for less than 0.1% of forest aboveground biomass, approximately 2% of both litterfall and aboveground productivity, 18% of litter N, and 90% of the vascular plant species (Siccama et al., 1970; Gosz et al., 1972; Whittaker et al., 1974). Clearly, an impact of N deposition on groundcover vegetation would likely have consequences for a variety of ecosystem processes (Gilliam, 2006).

In four northern hardwood forests in the north-central United States (Fig. 1), long-term N additions (>10 years) acting as an experimental increase in N deposition have had dramatic effects on ecosystem function. Experimental N deposition has increased the foliar N content (Talhelm et al., 2011) and the growth of overstory trees (Pregitzer et al., 2008), reduced the abundance of arbuscular mycorrhizal fungi (van Diepen et al., 2010), altered the composition of saprotrophic microbial communities (Zak et al., 2011), and slowed the decomposition of organic matter (Zak et al., 2008). Although there is a wealth of information about belowground ecology and the growth of the overstory plants at these sites, the response of the groundcover and understory vegetation to experimental N deposition and the ecological role of this vegetation have not yet been examined. In this context, our objectives were to fill the knowledge gaps surrounding the abundance, composition, and role of this vegetation in ecosystem processes, with an emphasis on the dominant species at these sites, sugar maple (*Acer saccharum* Marsh.). Sugar maple relies on the "seedling bank" strategy for regeneration and can produce hundreds of seedlings per square meter (Curtis, 1959; Hett and Loucks, 1971; Marks and Gardescu, 1998). Based on other N deposition studies in northern temperate forests (Hurd et al., 1998; Rainey et al., 1999), we hypothesized that experimental N deposition would alter groundcover species composition, particularly affecting herbaceous plants. Further, we hypothesized that sugar maple seedlings would respond positively to experimental N deposition in terms of abundance and biomass because overstory trees had increased in growth and earlier measurements suggest that canopy leaf area had not been affected by experimental N deposition (Pregitzer et al., 2008).

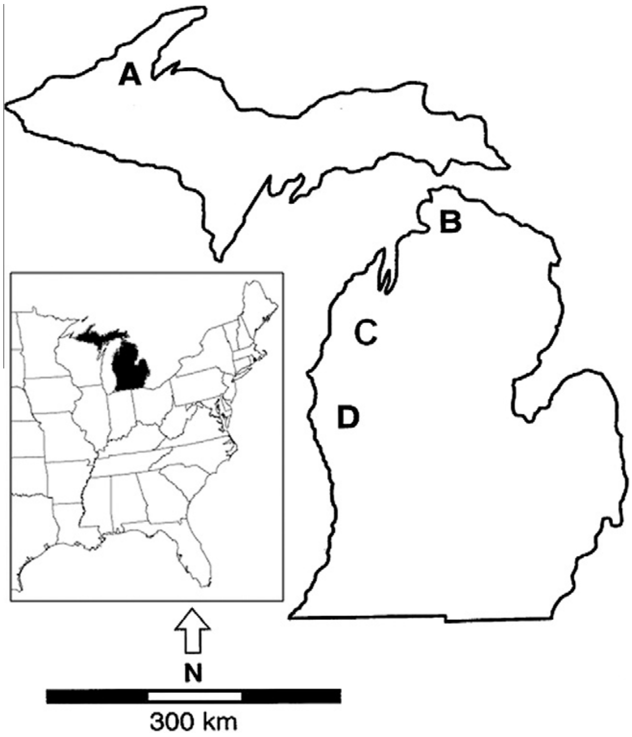

Fig. 1. Study site locations in Michigan, USA.

To meet these objectives, we conducted initial measurements of groundcover plant abundance, biomass, leaf area, and leaf N at one site. Based on results from these initial measurements and the occurrence of an especially large sugar maple seed crop the following year, we expanded our research and measured the abundance of plants in both the groundcover and understory at all four sites repeatedly over a period of 7 years. Our early results inspired a series of mechanistic experiments conducted by Patterson et al. (2011) that were intended to understand how experimental N deposition had affected the establishment and survival of sugar maple seedlings. While we discuss the degree to which these findings apply to our broader survey, we refer interested readers to this work for a more detailed discussion of these experiments.

2. Methods

2.1. Study sites

The four sites in this study are spread 500 km across northern lower and western upper Michigan, in the north-central United States (Fig. 1). These sites encompass the north to south distribution of the northern hardwood forest biome in the upper Great Lakes region (Braun, 1950; Pregitzer et al., 2004). The forests in this study are characteristic of much of the region: mature, second growth stands that originated around the beginning of the 20th century (98–104 years old in 2009; Burton et al., 2012). Sugar maple is the dominant component of these forests (>75% of basal area at each site), which have a basal area near maximum for this forest type (34.7 ± 0.8 m^2 ha^{-1}, Pregitzer et al., 2008). The sites occur across gradients of ambient N deposition, latitude, and temperature. Nitrogen deposition ranges from 0.68 g m^{-2} $year^{-1}$ (wet plus