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Spruce-fir forest changes during a 30-year nitrogen saturation experiment

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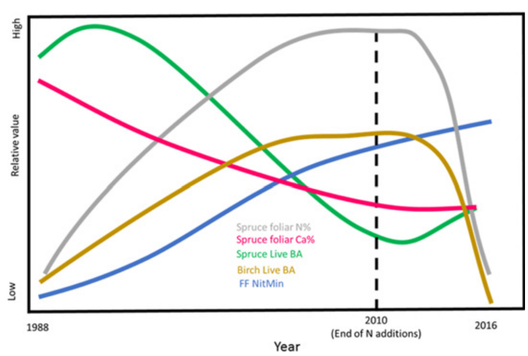
HIGHLIGHTS

- Indicators of nitrogen saturation were observed in plots having a total inorganic nitrogen input of ≥20 kg N ha^{-1} yr^{-1}.
- Control plots aggraded forest floor nitrogen at a rate equal to net N mineralization plus inorganic N deposition.
- Nitrogen treatment plots had a net loss in forest floor nitrogen.
- Drought, heat and thaw-freeze events in conjunction with nitrogen inputs likely contributed to forest decline.
- Despite reduced nitrogen deposition, climate change will make spruce-fir forest regeneration unlikely.

GRAPHICAL ABSTRACT



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ABSTRACT

A field experiment was established in a high elevation red spruce (*Picea rubens* Sarg.) – balsam fir (*Abies balsamea*) forest on Mount Ascutney Vermont, USA in 1988 to test the nitrogen (N) saturation hypothesis, and to better understand the mechanisms causing forest decline at the time. The study established replicate control, low and high dose nitrogen addition plots (i.e., 0, 15.7 and 31.4 kg NH_4Cl-N ha^{-1} yr^{-1}). The treatments began in 1988 and continued annually until 2010, but monitoring has continued to present. During the fertilization period, forest floor C:N, net *in situ* N mineralization, spruce foliar Ca%, and live spruce basal area decreased with increasing N addition, while foliar spruce N% and forest floor net nitrification increased with increasing N addition. The control plots aggraded forest floor N at a rate equal to the sum of the net *in situ* N mineralization plus average ambient deposition. Conversely, N addition plots lost forest floor N. Following the termination of N additions in 2010, the measured tree components returned to pre-treatment levels, but forest floor processes were slower to respond. During the 30 year study, site surface air temperature has increased by 0.5 °C per decade, and total N deposition has decreased 5.5 to 4.0 kg N ha^{-1} yr^{-1}. There have also been three significant drought years and at least one freeze injury year after which much of the forest mortality on the N addition plots occurred. Given that there was no control for the air temperature increase, discussion of the interactive impacts of climate and change and N addition is only subjective. Predicted changes in climate, N deposition and other stressors suggest that even in the absence of N saturation, regeneration of the spruce-fir ecosystem into the next century seems unlikely despite recent region-wide growth increases.

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1. Introduction

Large-scale forest decline was observed across parts of New England beginning in the 1960s, with much of the mortality located within the high elevation red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea*) forests (Johnson, 1983). Researchers agreed that acidic atmospheric deposition of nitrous and sulfur oxides (i.e., NO_x and SO_x) were the primary cause of this decline, but the mechanisms for the mortality were uncertain (Pitelka and Raynal, 1989).

Agren and Bosatta (1988) and Aber et al. (1989) were the first to discuss the nitrogen (N) saturation hypothesis as a contributing cause of forest mortality. The theory proposes that under conditions of very high N availability (alone), adverse physiological and morphological changes could occur at the tree and forest level. The nitrogen saturation hypothesis proposed that the elevated chronically increased supply of plant available N would initially stimulate net primary productivity and foliar biomass, but both would reverse several years after the termination of N additions. Additionally, root biomass would decrease, while foliar N concentration and total tree N content would increase. At the ecosystem level, N saturation would increase net N mineralization, nitrification, N_2O emissions and NO_3 leaching. If N additions continued, the tree would progress through four N saturation stages that would ultimately lead to tree mortality and overall forest decline (Aber et al., 1989, 1998).

The N saturation hypothesis needed to be tested to prove (or disprove) the theory. The ultimate goal of the research was to minimize future forest decline through changes in forest management or regulatory constraints on pollutant emissions. Therefore, a pair of field studies were conducted to examine the nitrogen saturation. The objective was to first observe the initial stages of N saturation in real time by first locating high elevation red spruce and balsam fir forests across New England with similar soils and climate, but with different rates of N deposition. From 1987 to 1988, over 150 spruce-fir sites were sampled for foliar nitrogen, macro- and micronutrient concentration, forest floor N and carbon (C) concentration, and N mineralization and nitrification potential (McNulty et al., 1990, 1991). Several components of the nitrogen saturation hypothesis were well correlated with observed measurements including foliar and forest floor N concentration. The study also suggested that a forest floor N concentration of 1.4% strongly correlated with the onset of nitrification and N saturation in these highly acidic (pH < 3.0) soils (McNulty et al., 1991). Based on the regional survey, a field site located on Mt. Ascutney in southeastern Vermont was selected in 1988 to test the impact of chronic, low-dose, N additions in combination with and ambient atmospheric deposition.

Many studies have been conducted since the Mt. Ascutney study was initiated 30 years ago, particularly as N saturation relates to forest productivity and carbon sequestration. A fertilization study at Harvard Forest found that 20 years of N addition lead to lower fungal abundance and higher rates of lignin accumulation compared to non-fertilized plots in both deciduous and coniferous N additions (Frey et al., 2014). Globally, Tian et al. (2016) found that N additions of 5–6 g m^{-2} yr^{-1} created a threshold for severely reducing net primary productivity (NPP), while De Schrijver et al. (2008) estimated that 25% of European forests are N saturated. Other studies examined the relationship between N saturation and soil N mineralization and nitrification (Lovett and Goodale, 2011), nitrate leaching (Fenn et al., 1998), and relationships between root and foliar N isotopes and N saturation (Pardo et al., 2006, 2007).

However, very few N saturation studies have examined so many structural and functional variables over so long a period as was conducted on Mt. Ascutney. This paper brings together previous and current data as well as other studies to more fully explore the ecological and physiological changes that have occurred since 1988 on the Mt. Ascutney N saturation study plots. The paper also projects how high elevation New England forests may change in the coming years and decades under changing patterns of atmospheric deposition and climate.

2. Materials and methods

2.1. Study plots

After a scouting trip to the site in the fall of 1987, a long-term site in southeastern Vermont adjacent to the Mt. Ascutney State Park (43°26′ N, 72°27′ W) was chosen to test the N saturation hypothesis of forest decline in 1988 for several reasons. First, the initial sampling of red spruce and balsam fir foliar N concentration, and forest floor N concentration suggested that the Mt. Ascutney site had not yet begun to experience symptoms of N saturation. However, the site had elevated N levels compared to other spruce-fir forests further east (McNulty et al., 1991). Nitrogen deposition increases from east to west in New England (NADP, 2017) so placing the site just to the east of forests showing signs of N saturation should predispose the selected plots to develop the initial phase of N saturation with supplemental N additions. Second, Mt. Ascutney had a large area of red spruce (*Picea rubens*) – balsam fir (*Abies balsamea*) forest above 750 m elevation. Finally, the site was located within 200 m of an access road, allowing for convenient movement of equipment, fertilizer, samples and personnel.

Red spruce often grows in pockets surrounded by other deciduous species on Mt. Ascutney. Therefore, plot size needed to be relatively small to accommodate the replicate plots within the same slope and elevation. The establishment ten 15 × 15 m red spruce dominated plots occurred in June 1988 at elevations between 750 and 770 m. Initially, red spruce comprised >80% of the total basal area; with the remainder divided between balsam fir, mountain maple (*Acer spicatum*), red maple (*Acer rubrum*) and birch (*Betula* spp.) (McNulty and Aber, 1993). The location of study plots and treatments within the larger forest stand was randomly selected. Pre-treatment sampling found no statistically significant (paired *t*-test, $p \leq 0.05$) differences in stand species composition, stand structure, net nitrification and net N mineralization of the forest floor or foliar chemistry among plots (McNulty et al., 1991; McNulty and Aber, 1993).

The site soil class is a Houghtonville, classified as frigid Typic Haplorthods located on broad areas between rock outcrops. These soils have 3 to 15% slopes and are well-drained (USDA Soil Conservation Service, 1989). Houghtonville soils have a discontinuous and narrow mineral layer. The mineral soil was not often present on flat surfaces but instead accumulated in rock crevasses. Tree root mass was almost exclusively located in the forest floor and not in this nutrient poor mineral horizon. For these reasons, only forest floor material was collected, and not the mineral horizon.

Climatically, the area has warm summers (average July air temperature 21 °C), and cold winters (average January air temperature −12 °C) (https://www.esrl.noaa.gov/gmd/ccgg/trends/index.html). Total annual precipitation was the only meteorological variable directly measured (1989 to 1991) on the site (McNulty and Aber, 1993).

On-site, bulk deposition inorganic N deposition measured on Mt. Ascutney averaged 5.4 kg N ha^{-1} yr^{-1} in open areas adjacent to the research plots from 1988 to 1991 (McNulty and Aber, 1993). Estimates total inorganic N deposition for Mt. Ascutney after 1991, were derived from the nearest National Atmospheric Deposition Program monitoring station (VT99) located approximately 75 km northwest of Mt. Ascutney. From 1988 to 2016, Station VT99 recorded total inorganic N deposition ranged from a high of 6.8 kg N ha^{-1} yr^{-1} (1990) to a low of 3.7 kg N ha^{-1} yr^{-1} (2009), with a mean of 5.0 kg N ha^{-1} yr^{-1} (NADP, 2017). These deposition values are consistent with the 5.4 kg N ha^{-1} yr^{-1} total inorganic N deposition values measured in open areas adjacent to the research plots from 1988 to 1991 (McNulty and Aber, 1993). The total inorganic N deposition values were not significantly different ($p = 0.48$) during the time of Mt. Ascutney and VT99 measurement overlap (i.e., 1988 to 1991). VT99 total inorganic N deposition has been declining at a rate of approximately 0.5 kg N ha-1 yr-1 during the experiment (i.e., 5.5 to 4.0 kg N ha^{-1} yr^{-1} from 1988 to 2016).

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