Geoderma 336 (2019) 68–80

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Increased microbial uptake and plant nitrogen availability in response to simulated nitrogen deposition in alpine meadows

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ARTICLE INFO

Handling Editor: I. Kögel-Knabner

Keywords:
Alpine
Nitrogen deposition
Nitrogen cycle
Microbial biomass
Critical N loads
Soil
Biogeochemistry

ABSTRACT

As global industry and intensive agriculture increase in response to an expanding human population, oligotrophic ecosystems such as alpine and subalpine habitats are increasingly vulnerable to transported atmospheric nitrogen (N) pollution. Even at low levels, N deposition can alter soil chemistry via changes in decomposition rates and mineralization of N from soil organic matter. We used fertilization to mimic N deposition in three National Park alpine meadow ecosystems in the Pacific Northwest (PNW) of the United States (an area of low ambient N deposition) over a 3-year period. Our sites were two moist heath meadow ecosystems in the western Cascade Mountains and one dry meadow ecosystem in the eastern Olympic Mountains. We assessed alpine soil chemistry and N cycling responses to simulated N deposition, using soil inorganic N availability to plants as a critical loads indicator. Soil solution inorganic N supply as measured by resin probes increased in response to N treatment at all sites by Year 3 in plots fertilized at the 10 kg N ha^{-1} yr^{-1} treatment level. At the heath meadow sites, we observed increased soil NO_3-N during the summer and decreased extractable organic carbon (C) during the fall in response to applied N. We also observed seasonal increases in the proportion of soil N contained in microbial biomass in response to treatment. These data indicate season-specific increases in microbial N uptake and mineralization in response to fertilizer treatment. The carbon-rich, fine-ash volcanic soils of the North Cascades were the most sensitive to N treatment with low microbial N uptake. From those soils, we derived an empirical critical load of 6 kg N per ha^{-1} yr^{-1} for increased soil N availability. However, alpine meadow soils in the Western Cascades undergo N limitation in the fall and may have less potential for N leaching with fall rains. In contrast, soils at the dry meadow site had much greater potential for N mineralization, and are temperature- and moisture-limited rather than N limited. Changes in soil chemistry in response to N deposition were site-specific and resulted from differences in plant uptake and soil N mineralization capacity, indicating two very different regimes for response to N deposition for N-limited alpine meadows vs moisture-limited alpine meadows.

1. Introduction

The introduction of fertilizer produced by industrial N fixation and the inadvertent oxidation of atmospheric N_2 during fossil fuel combustion have, over the last century, nearly doubled the amount of biologically available N in circulation in Earth's terrestrial ecosystems (Galloway et al., 2008; Vitousek et al., 1997). A portion of this N leaves terrestrial ecosystems through leaching into streams and waterways or through volatilization and particulate transport into the atmosphere (Galloway et al., 2008). Reactive atmospheric N is then deposited elsewhere through either wet or dry deposition, leading to the fertilization of otherwise remote and nutrient-limited ecosystems such as deserts, alpine areas, mires, and boreal forests (Bobbink et al., 2010; Driscoll et al., 2001; Lovett, 1994).

High-elevation ecosystems are particularly sensitive to the effects of air pollution and to climate change. Alpine environments can be subject to large spikes of N deposition not seen at lower elevations due in part to higher precipitation levels (Bowman et al., 2006; NADP, 2017; Reddy et al., 2015; Williams et al., 2017). Nitrogen deposition in alpine ecosystems has become a special concern at National Parks of the mountainous western U.S., since N fertilization could change vegetation communities (Cummings et al., 2014; Fenn et al., 2003; Pardo et al., 2011). In addition, it is likely that climate change will result in higher temperatures, more precipitation in the form of rain as opposed to snow

Abbreviations: MORA, Mount Rainier National Park; NOCA, North Cascades National Park; OLYM, Olympic National Park; PNW, Pacific Northwest

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https://doi.org/10.1016/j.geoderma.2018.08.029
Received 23 April 2018; Received in revised form 27 August 2018; Accepted 28 August 2018
Available online 08 September 2018
0016-7061/

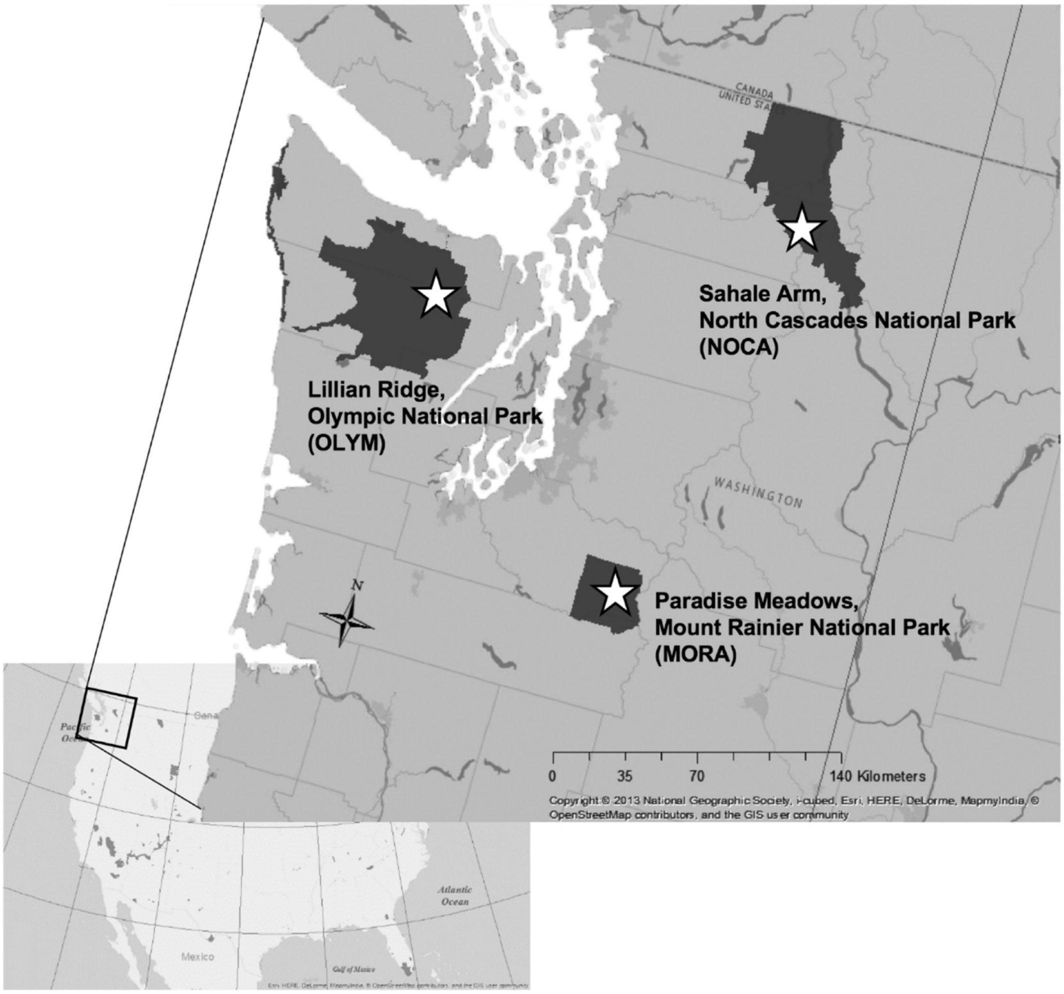

Fig. 1. Site locations.
Locations of research sites at Mount Rainier (MORA), North Cascades (NOCA) and Olympic (OLYM) National Parks, Washington State, USA.

in the fall, higher snowlines, and earlier snowmelt (Beniston et al., 1997; Inouye, 2008; Karl et al., 2009; Mote et al., 2005). These changes could increase alpine soil acidity, weathering rates, decomposition, leaching of NO_3-N into surface waters (Bowman et al., 2014) and the likelihood of invasion by opportunistic plant species (Porter et al., 2012). Since these effects can also result from N deposition, climate change is likely to exacerbate detrimental effects of increasing N pollution, making the need for further research and policy change in this area ever more urgent.

Determining critical N loads, defined as “the highest load that will not cause chemical changes leading to long-term harmful effects on the most sensitive ecological systems” (Nilsson, 1988), is essential if air quality regulations are to protect alpine ecosystems that have not yet been strongly affected by N deposition. Estimates of critical N loads are lacking for many alpine soils and ecosystems. At present, published critical N loads for increased soil inorganic N availability in alpine meadows are 9–10 kg N ha^{-1} yr^{-1} at Rocky Mountain National Park, CO (Bowman et al., 2012), 20 kg N ha^{-1} yr^{-1} at Niwot Ridge, CO (Bowman et al., 2006) (both located in the mountainous western United States), and between 10 and 40 kg N ha^{-1} yr^{-1} on the Tibetan Plateau (Zong et al., 2015).

Nitrogen deposition studies in alpine ecosystems have found a number of different depositional effects on soil chemistry and soil N cycling, including increased decomposition of particulate organic C (Fang et al., 2014a), changes in CO_2 flux (Fang et al., 2011), increased soil inorganic N pools (Bowman et al., 2006), changes in microbial access to root-derived C and fungal:bacterial ratios (Farrer et al., 2013) and changes in soil pH and in abundance of different microbial phyla (Yuan et al., 2016). One of the most detrimental effects of N deposition on soils is leaching of inorganic N, especially the more mobile NO_3-N, which can lead to eventual eutrophication of streams and lakes (Fenn et al., 2003; Pardo et al., 2011). An increase in soil NH_4-N or NO_3-N, even if ephemeral, means that soil, microbial and plant N sinks are inadequate to retain excess N and that the potential for inorganic N leaching is increased. The time of year at which a change in N chemistry occurs is also significant; N chemistry changes must be coupled with environmental factors such as precipitation and temperature in order to assess leaching potential. For example, ephemeral increases in inorganic N are considerably more harmful if they occur at times of greatest precipitation and lowest plant uptake.

A general model of the soil N processes for an ecosystem is therefore important to provide context for developing critical N loads for that ecosystem. Several studies investigating alpine N dynamics (Jaeger et al., 1999; Lipson et al., 1999; Nemergut et al., 2005) have suggested a model of alpine N availability in the Rocky Mountains: a pulse of high organic N availability upon snowmelt and turnover of the microbial community, followed by mineralization and high plant uptake, followed by late-summer and fall microbial immobilization of N. However, availability of labile C and N and microbial processing of N in alpine soils is strongly influenced by snow depth and snowpack duration (Brooks et al., 2011) and the very heavy snowpack and dry summers (NOHRSC, 2017) of the maritime-influenced alpine PNW may