



Cross-biome assessment of gross soil nitrogen cycling in California ecosystems



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ABSTRACT

Microbial transformations of nitrogen (N) largely determine whether N is retained in ecosystems via net primary productivity or lost via gaseous emissions and leaching. The controls on soil N cycling are often studied at single locales, making it difficult to predict N cycling at regional to global scales. We hypothesized that contemporary soil properties exhibit consistent relationships with instantaneous gross N cycling rates across diverse biomes that create a continuum in these properties. We measured ex situ gross N cycling rates and soil properties at 33 study sites representing five biome classifications in California including deserts, grasslands, shrublands, forest, and wetlands. Desert soils had significantly lower total N, organic carbon (C), microbial biomass N, and soil moisture as well as higher pH than all other biomes, whereas forests and wetlands had significantly lower soil nitrate (NO_3^-) concentrations ($P < 0.001$ for all). Gross mineralization rates were best predicted by the combination of soil moisture and soil C:N ratios ($R^2 = 0.46$), which exerted positive and negative controls, respectively. Grasslands exhibited marginally higher gross mineralization than all other biomes, whereas deserts had the lowest rates due to low soil moisture ($P = 0.09$). Gross nitrification rates were positively correlated to soil NO_3^- concentrations ($R^2 = 0.34$) and negatively correlated to soil C:N ratios ($R^2 = 0.31$). The negative relationship between gross nitrification and soil C:N ratios was driven by forest soils, which had significantly higher C:N ratios and lower gross nitrification than all other biomes ($P < 0.05$). Dissimilatory NO_3^- reduction to NH_4^+ (DNRA) occurred in soils from all biomes. The strong positive correlation between DNRA rates and soil NO_3^- ($R^2 = 0.41$) suggests NO_3^- limitation of DNRA. Predictable patterns in gross N cycling across biomes in California suggest that contemporary soil properties are important drivers of instantaneous soil N cycling rates that integrate over differences in vegetation type, atmospheric N deposition rates, and local climate.

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1. Introduction

Nitrogen (N) is a critical nutrient that is often limiting to plants and microbes in temperate and boreal ecosystems (Vitousek and

Howarth, 1991). Soil internal N cycling helps regulate the potential for N retention and loss in ecosystems. Changes in soil N cycling in response to anthropogenic N deposition and global change can lead to changes in net primary productivity (NPP), soil nitrous oxide (N_2O) emissions, and nitrate (NO_3^-) leaching into groundwater (Fowler et al., 2013; Galloway et al., 2003; Vitousek et al., 1997). Differences in soil N cycling rates have been demonstrated in cross-site comparisons of single species forest plots (Lovett et al., 2004; Zak et al., 1986), different topographic positions within a landscape (Zak and Grigal, 1991), grasslands versus forests (McKinley et al., 2008), similar ecosystems that experience a range in background N deposition rates (Rao et al., 2009) or climate (Barrett and Burke, 2000), and even different genotypes of the same species (Schweitzer et al., 2004). Despite these differences, a meta-analysis of woodlands, grasslands, and agricultural land suggested that

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controls on instantaneous N cycling rates are consistent across broad classes of ecosystems (Booth et al., 2005). However, desert ecosystems are also often not included in cross-ecosystem comparisons because it is assumed that limited water availability causes inherently different N cycling patterns (Amundson et al., 2003; Wang et al., 2014; Whitford and Wade, 2002). In addition, relatively few gross N cycling studies have been conducted in ecosystems with Mediterranean climates characterized by cool wet winters and hot dry summers (e.g., Davidson et al., 1992; Hawkes et al., 2005; Herman et al., 2003; Schimel et al., 1989). In ecosystems with strong seasonality in precipitation, N cycling processes may be subject to seasonally dependent controls (Mack and D'Antonio, 2003). The question remains whether the controls on instantaneous N cycling rates in arid and Mediterranean ecosystems are consistent with those in more mesic ecosystems.

Nitrogen mineralization, the process by which organic N is transformed into the inorganic form of ammonium (NH_4^+), is often considered the regulator of N availability for plant uptake. However, in ecosystems with strong N limitation to NPP such as tundra, boreal forests, and deserts, organic N can be directly taken up by plants (Näsholm et al., 1998). Schimel and Bennett (2004) reevaluated the N mineralization paradigm suggesting that, without large exogenous N inputs, mineralization plays an increasingly important role in supporting NPP as available N becomes more abundant. A positive correlation between N mineralization rates and total available N in soils has been observed (Stanford and Smith, 1972; Wang et al., 2001), supporting this hypothesis. Mineralization can also be negatively correlated with soil C:N ratios because at high C:N ratios, microbes must immobilize rather than mineralize N to maintain the stoichiometric ratio of C:N in their biomass (Hart et al., 1994; Mack and D'Antonio, 2003). In their meta-analysis, Booth et al. (2005) found that gross N mineralization was positively correlated to total N and microbial biomass N (MBN) in soils, and negatively correlated to soil C:N after soil organic C concentration was taken into account. The meta-analysis also documented a strong positive correlation between gross N mineralization and soil moisture. Soil water can increase connectivity within the soil matrix to better distribute N among N-rich and N-poor microsites, thus increasing N abundance across microsites to support higher bulk soil N mineralization rates (Stark and Hart, 1999). Given that the microbial community in arid systems can be dominated by drought tolerant fungi that differ from bacteria in their biomass C:N ratios and response to soil moisture (Adebayo and Harris, 1971; Clark et al., 2009; Cleveland and Liptzin, 2007; Wilson and Griffin, 1975), the relationships of these soil properties to gross N mineralization rates may differ from those observed in mesic ecosystems.

Nitrification, the process by which NH_4^+ is oxidized to nitrate (NO_3^-), contributes to the potential for ecosystem N loss because NO_3^- is highly susceptible to leaching losses as well as gaseous losses to N_2O and dinitrogen (N_2) via denitrification (Robertson and Tiedje, 1987). For example, in ecosystems that receive high anthropogenic N inputs, increased nitrification is responsible for increased N leaching losses (Venterea et al., 2004). In soil microsites where there is sufficient N available to meet demands of both microbial and plant assimilation, there is likely to be N available for nitrification (Schimel and Bennett, 2004; Stark and Hart, 1999). Thus, NH_4^+ supply to nitrifiers is the proximate control on nitrification rates (Myrold et al., 1998). Indeed, Booth et al. (2005) found that gross N mineralization was the best predictor of nitrification, out of the explanatory variables evaluated. However, in ecosystems impacted by high anthropogenic N inputs that supply excess N, gross nitrification rates may be best predicted by NH_4^+ concentrations rather than gross N mineralization, which represents an internal supply of N.

Dissimilatory nitrate NO_3^- reduction to NH_4^+ (DNRA) can lead to ecosystem N retention by returning NO_3^- to the less mobile form of inorganic N, NH_4^+ . This process decreases ecosystem N losses through leaching and gaseous N_2O and N_2 emissions via denitrification (Silver et al., 2001; Templer et al., 2008). Like denitrification, DNRA occurs under anaerobic conditions when N-oxides (NO_3^- and nitrite, NO_2^-) rather than oxygen (O_2) serve as terminal electron acceptors to yield energy in microbial metabolism. As such, DNRA has been documented as an important fate of NO_3^- in anoxic sediments (Bernard et al., 2015; Giblin et al., 2013; Smith et al., 2015) as well as upland soils that experience anoxic conditions (Huygens et al., 2007; Silver et al., 2001). While some studies have reported DNRA rates in non-flooded, upland soils, DNRA is rarely considered in the terrestrial N cycle (Rutting et al., 2011). The few studies that have quantified both DNRA and denitrification rates in upland soils have shown that DNRA rates can be comparable to or even many times greater than denitrification rates (Chen et al., 2015; Huygens et al., 2007; Rutting et al., 2011; Silver et al., 2001; Templer et al., 2008; Yang et al., 2015). However, to date, few studies on DNRA have been conducted in terrestrial ecosystems. Questions, therefore, remain regarding environmental controls on DNRA and how widespread this process is across bioclimatic zones and soil types.

Here, we present a survey of soil properties and gross N cycling rates in ecosystems from a wide geographical range in California, USA. We classified the ecosystems into five broad biome groups: deserts, forests, grasslands, shrublands, and wetlands. Our goals were to: (1) determine the range of gross N cycling rates across a wide range of ecosystems including arid and Mediterranean climates, and (2) determine if there are consistent relationships between soil properties and gross N cycling rates across biomes. We hypothesized that, while arid and Mediterranean ecosystems would differ in their soil properties compared to mesic ecosystems (Gallardo and Schlesinger, 1992; Post et al., 1985; Wang et al., 2014), contemporary soil properties would exhibit consistent relationships with instantaneous gross N cycling rates across these diverse biomes that create a wide continuum in these properties. Thus, we expected that differences in N cycling rates across biomes would be driven by differences in soil properties. If other factors, such as climate or soil microbial community composition, were more important potential direct drivers of instantaneous N cycling rates, then we would expect to find only weak correlations between N cycling rates and soil properties.

2. Materials and methods

2.1. Study sites

Our study utilized 33 existing research sites at 27 study areas located within 8 out of 10 bioregions in California (Hickman, 1993, Fig. 1; Table S1). The study sites were chosen to represent a wide continuum in soil properties that could elucidate controls on gross N cycling rates using a regression approach. Mean annual precipitation (MAP) for each site over the period of 1980–2015 was obtained from the daily time step, 1-km grid resolution Daymet data set archived and distributed through the Oak Ridge National Laboratory Distributed Active Archive Center (Table S1, Thornton et al., 2016). Soils from the top 10 cm of mineral horizons were collected from 27 sites in January 2007 (wet season), and from six high elevation sites in the Sierra Nevada in May 2007 after snowmelt. A characteristic of Mediterranean climates is dry summers and wet winters, so we timed the soil sampling to avoid the pulses of high microbial activity that occur with the first precipitation events of the wet season (Chou et al., 2008; Xiang et al., 2008). We also timed the soil sampling campaigns to maximize the chances that we would collect the soils under field moist conditions that minimize

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