



Vegetation change alters soil profile $\delta^{15}\text{N}$ values at the landscape scale

Yong Zhou^{*}, Ryan M. Mushinski¹, Ayumi Hyodo, X. Ben Wu, Thomas W. Boutton

Department of Ecosystem Science and Management, Texas A&M University, College Station, TX, 77843, USA



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ABSTRACT

The assessment of spatial variation in soil $\delta^{15}\text{N}$ could provide integrative insights on soil N cycling processes across multiple spatial scales. However, little is known about spatial patterns of $\delta^{15}\text{N}$ within soil profiles in arid and semiarid ecosystems, especially those undergoing vegetation change with a distinct shift in dominance and/or functional type. We quantified how changes from grass to woody plant dominance altered spatial patterns of $\delta^{15}\text{N}$ throughout a 1.2 m soil profile by collecting 320 spatially-specific soil cores in a 160 m \times 100 m subtropical savanna landscape that has undergone encroachment by *Prosopis glandulosa* (an N_2 -fixer) during the past century. Leaf $\delta^{15}\text{N}$ was comparable among different plant life-forms, while fine roots from woody species had significantly lower $\delta^{15}\text{N}$ than herbaceous species across this landscape. Woody encroachment significantly decreased soil $\delta^{15}\text{N}$ throughout the entire soil profile, and created horizontal spatial patterns of soil $\delta^{15}\text{N}$ that strongly resembled the spatial distribution of woody patches and were evident within each depth increment. The lower soil $\delta^{15}\text{N}$ values that characterized areas beneath woody canopies were mostly due to the encroaching woody species, especially the N_2 -fixer *P. glandulosa*, which delivered ^{15}N -depleted organic matter via root turnover throughout the soil profile. Soil $\delta^{15}\text{N}$ increased with depth, reached maximum values at intermediate depths, and slightly decreased at greater depths. This vertical pattern may be related to the decrease of ^{15}N -depleted organic matter inputs with depth, and to the presence of a subsurface clay-rich argillic horizon at intermediate depths across this landscape, which may favor the accumulation of ^{15}N -enriched residues. These results indicate that succession from grassland to woodland has altered the spatial variation in soil $\delta^{15}\text{N}$ across the landscape and to considerable depth, suggesting significant changes in the relative rates of N-inputs vs. N-losses in this subtropical system after vegetation change.

1. Introduction

The stable nitrogen isotope composition ($\delta^{15}\text{N}$) of bulk soil, as an integrator of the soil N cycle, reflects the long-term net difference between $\delta^{15}\text{N}$ values of N inputs (e.g. fixation, deposition) and those of N outputs (e.g. gaseous losses, leaching) (Högberg, 1997; Robinson, 2001; Amundson et al., 2003; Hobbie and Ouimette, 2009; Pardo and Nadelhoffer, 2010; Craine et al., 2015a,b; Denk et al., 2017). As a result, soil $\delta^{15}\text{N}$ values can provide integrative insights regarding the behavior of the soil N cycle across a range of spatial and temporal scales.

Soil $\delta^{15}\text{N}$ values can vary by as much as 9–10‰ within a profile (Hobbie and Ouimette, 2009), and generally increase with depth (Bundt et al., 2001; Huygens et al., 2008; Yang et al., 2015). In some cases, maximum soil $\delta^{15}\text{N}$ values occur at intermediate soil depths, with lower values both near the soil surface and deeper in the profile (Bustamante et al., 2004; Hobbie and Ouimette, 2009). Several

mechanisms have been proposed to explain these vertical patterns of ^{15}N enrichment throughout the soil profile (reviewed in Hobbie and Ouimette, 2009), including: (1) accumulation of ^{15}N -enriched microbial residues at depth as a result of transfer of ^{15}N -depleted N to plants by mycorrhizae, especially ectomycorrhizal fungi (Högberg, 1997; Lindahl et al., 2007; Huygens et al., 2008; Hobbie and Ouimette, 2009; Hobbie and Högberg, 2012; Mayor et al., 2015; Denk et al., 2017); (2) preferential preservation of ^{15}N -enriched compounds during organic N decomposition (Hobbie and Ouimette, 2009); (3) fractionation against ^{15}N during N transformations (e.g. nitrification and denitrification) followed by the subsequent loss of ^{15}N -depleted gases (e.g. NO , N_2O , N_2) produced during those transformations (Nadelhoffer and Fry, 1988; Hobbie and Ouimette, 2009; Craine et al., 2015a,b; Denk et al., 2017).

Vegetation can directly affect soil $\delta^{15}\text{N}$ through symbiotic N_2 -fixation and mycorrhizal associations (Högberg, 1997; Craine et al., 2015a,b; Mayor et al., 2015), or indirectly through the modification of substrate quality/quantity and/or micro-environmental conditions that

^{*} Corresponding author. Rm 210, Kleberg Center, Department of Ecosystem Science and Management, 474 Olsen Blvd, TAMU, College Station, TX, 77843, USA.
E-mail address: zhouyong1222@tamu.edu (Y. Zhou).

¹ Present address: School of Public and Environmental Affairs, Indiana University, Bloomington, Indiana, 47405, USA.

may influence rates of soil N transformations (Bai et al., 2009a,b; 2013; Wang et al., 2013). For these reasons, when ecosystems undergo disturbances that modify vegetation dominance, primary production, and/or rates of N transformations, soil $\delta^{15}\text{N}$ is likely to be altered (Bai et al., 2013). These potential modifications of soil $\delta^{15}\text{N}$ following vegetation changes represent another complication to the utility of soil $\delta^{15}\text{N}$ as a diagnostic tool for inferring prevalent soil N cycling processes under disturbed conditions.

A notable example of a change in vegetation dominance is the geographically widespread phenomenon of woody plant encroachment into grass-dominated ecosystems in arid and semiarid regions, which appears to be caused by livestock overgrazing, reduced fire frequency, rising atmospheric CO_2 concentration, and climate change (Bond and Midgley, 2000; Eldridge et al., 2011; Archer et al., 2017; Stevens et al., 2017), all of which have the potential to favor the productivity of C_3 woody plants at the expense of C_4 grasses. Woody plant encroachment is a complex social-ecological issue that has long been of concern to land managers because it has the potential to reduce the productivity of grazing livestock (e.g., cattle, sheep, equines) whose diets are strongly grass-based (Archer et al., 2017). In addition, woody encroachment has been shown to have significant impacts on biodiversity, hydrology, and biogeochemistry at ecosystem to global scales (Hibbard et al., 2001; Huxman et al., 2005; Pacala et al., 2007; Ratajczak et al., 2012; Ge and Zou, 2013; Anadón et al., 2014; Poulter et al., 2014).

In the context of soil N cycle, woody plant encroachment has been demonstrated to increase N inputs, intensify rates of soil N cycling processes, and accelerate N losses through leaching and trace gas emissions (Hibbard et al., 2001; Martin et al., 2003; McCulley et al., 2004; Liao et al., 2006; McKinley et al., 2008; Eldridge et al., 2011; Creamer et al., 2013; Soper et al., 2016). Although many studies have found decreased soil $\delta^{15}\text{N}$ after woody plant encroachment (Wheeler et al., 2007; Boutton and Liao, 2010; Sitters et al., 2013), others have found either no net change (Blaser et al., 2014), or even increased soil $\delta^{15}\text{N}$ (Bekele and Hudnall, 2005; Billings and Richter, 2006). Reasons for these discrepancies remain unclear, but may be related to whether or not the encroaching woody species include plants capable of symbiotic N-fixation, and/or the degree of impact that increased woody plant abundance has on individual soil N processes that vary in the extent of fractionation against ^{15}N . More importantly, most of these studies investigating the impact of woody encroachment on soil $\delta^{15}\text{N}$ have focused on surface soils (mostly < 30 cm). However, recent studies have emphasized that woody encroachment can have significant impacts on deep soil biogeochemistry (Chiti et al., 2017; Zhou et al., 2017a), as encroaching woody species generally have root systems that are distributed more deeply than those of the herbaceous species (Schenk and Jackson, 2002). Therefore, there is currently a knowledge gap regarding the direction and magnitude of soil $\delta^{15}\text{N}$ changes in deeper portions of the soil profile following disturbance and vegetation change in arid and semiarid ecosystems.

Spatial variations in soil $\delta^{15}\text{N}$ could provide integrative insights on the soil N cycle across multiple spatial scales (Craine et al., 2009a,b; Pardo and Nadelhoffer, 2010; Bai et al., 2013; Wang et al., 2013; Rascher et al., 2012; Ruiz-Navarro et al., 2016). Woody plant encroachment into grass-dominated ecosystems is generally associated with the amplification of spatial heterogeneity in soil properties (“islands of fertility”, Schlesinger et al., 1996), making it more difficult to generalize ecosystem processes based on sampling at small spatial scales and limited sample sizes (Throop and Archer, 2008; Liu et al., 2011; Zhou et al., 2017b). Previous studies have demonstrated the existence of spatial variations in soil $\delta^{15}\text{N}$ in arid and semiarid ecosystems and identified driving factors (such as vegetation type, topographic properties, and water availability) responsible for those spatial variations (Bai et al., 2013; Wang et al., 2013; Ruiz-Navarro et al., 2016). However, these studies were largely confined to surface soils, and it remains unclear how changes in plant life forms and/or functional types in arid and semiarid ecosystems may influence spatial

variation in soil $\delta^{15}\text{N}$ values in deeper portions of the soil profile.

In this study, we investigated a well-studied subtropical savanna ecosystem that has undergone encroachment by *Prosopis glandulosa* (an N_2 -fixing tree legume) and other subordinate tree/shrub species during the past century in southern Texas, USA (Archer et al., 1988; Boutton et al., 1998). Prior research in this region has documented that woody plant encroachment has altered spatial patterns of soil $\delta^{15}\text{N}$ in surface soils (0–15 cm) (Bai et al., 2013). To further expand on this work, we collected 320 spatially specific soil cores to a depth of 1.2 m across a 160 m × 100 m landscape in this subtropical savanna to test the following two hypotheses: (1) the deep-rooting characteristics of the encroaching woody species would modify soil $\delta^{15}\text{N}$ values to considerable depth within the soil profile; and (2) landscape-scale spatial patterns of soil $\delta^{15}\text{N}$ in the horizontal plane would be evident throughout the soil profile and correlated with the distribution patterns of the encroaching woody vegetation.

2. Methods and materials

2.1. Study site

Research was conducted at the Texas A&M AgriLife La Copita Research Area (27°40' N, 98°12' W; elevation 75–90 m a.s.l.) in Jim Wells County, Texas, USA (Fig. S1). The climate is subtropical, with mean annual temperature and precipitation of 22.4 °C and 680 mm, respectively. Landscapes consist of well-drained uplands that grade gently (1–3% slopes) to lower-lying drainage woodlands. Soils on upland portions of the landscape are sandy loams (Typic and Pachic Argiustolls) with a laterally extensive but discontinuous clay-rich argillic horizon (B_t) which begins 30–50 cm below the surface (Archer, 1995; Zhou et al., 2017b).

Multiple lines of evidence (i.e. historical accounts, tree-ring analyses, and coupled $\delta^{13}\text{C}$ - ^{14}C analyses of soil organic matter) have indicated that upland vegetation was once almost exclusively dominated by C_4 grasses, and woody encroachment into C_4 dominated grasslands has occurred during the past century due to overgrazing and reduced fire frequency (Archer et al., 1988, 2001; Archer, 1995; Boutton et al., 1998). Current upland vegetation is comprised of discrete woody patches distributed within a remnant C_4 grassland matrix (Archer et al., 1988; Archer, 1995). Woody patches consist of small shrub clusters (generally < 100 m²) and large groves (generally > 100 m²). The formation of woody patches is initiated by the colonization of *Prosopis glandulosa*, an N_2 -fixing tree legume (Zitzer et al., 1996; Soper et al., 2015). Established *P. glandulosa* trees then serve as nurse plants, facilitating the recruitment of other trees/shrubs underneath their canopies to form discrete clusters (Archer et al., 1988). The spatial distribution of clusters across this landscape is random and not related to the spatial heterogeneity in subsurface soil texture (Zhou et al., 2017b). However, if clusters occur on non-argillic inclusions (i.e. coarse-textured soils), they expand laterally and coalesce to form groves (Archer, 1995; Zhou et al., 2017b). In the process of occupying the non-argillic inclusions, groves will often merge with clusters that develop on the argillic soils. Therefore, the peripheral areas of groves often occupy soils where the argillic horizon is present. At present, the remnant grassland matrix is dominated by C_4 grasses, but also includes C_3 forbs and a small portion of crassulacean acid metabolism (CAM) species. Groves are dominated by *P. glandulosa* trees with up to 15–20 other tree/shrub species in the understory. Clusters consist of the same woody species as groves, but *P. glandulosa* in clusters are significantly smaller and younger than those in groves (Boutton et al., 1998). Grasses and other herbaceous species are extremely rare underneath clusters and groves. Species composition can be found in Table S1. Based on the plant and soil properties and processes that characterize grasslands, clusters, and groves, each are unique ecosystems that comprise the upland landscape, and we refer to them as landscape elements (Turner et al., 2001).

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