Agriculture, Ecosystems and Environment 185 (2014) 188–196

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Patterns of root decomposition in response to soil moisture best explain high soil organic carbon heterogeneity within a mesic, restored prairie

Adam C. von Haden[a,*], Mathew E. Dornbush[b]

[a] Environmental Science and Policy Graduate Program, University of Wisconsin-Green Bay, Green Bay, WI 54311, USA
[b] Department of Natural and Applied Sciences, University of Wisconsin-Green Bay, Green Bay, WI 54311, USA

ARTICLE INFO

Article history:
Received 29 August 2013
Received in revised form
13 December 2013
Accepted 16 December 2013
Available online 27 January 2014

Keywords:
Root biomass
Root distributions
Root production
Soil organic matter
Tallgrass prairie
Wisconsin, USA

ABSTRACT

Spatially heterogeneous patterns of soil organic carbon (SOC) are related to topographically-defined soil moisture levels within Midwestern tallgrass prairies. While roots are regarded as the main contributor to SOC formation, relatively little is known about how fine root dynamics respond to landscape-level changes in soil moisture, and thus the mechanisms promoting spatial heterogeneity of SOC remain uncertain. We evaluated SOC, fine root (≤2 mm) biomass, production, decomposition, and vertical rooting distributions among landscape positions varying in soil moisture within 25+ year old restored tallgrass prairies in Wisconsin, USA. We hypothesized that SOC, root biomass, and root production would increase, while root decomposition would decline with increasing soil moisture. Additionally, we hypothesized that relative root biomass and production distributions would become shallower as soils became wetter. We found no relationship between soil moisture and root biomass, production, or their vertical distributions, but decomposition decreased and SOC increased as expected with increasing soil moisture. However, we also observed a strong relationship between soil moisture and species assemblages, suggesting that community composition changed in response to soil moisture. Our findings indicate that SOC was highest in seasonally wet, lowland landscape positions due to greatly reduced root decomposition, not due to changes in root production or relative distributions. We suggest that species turnover may have reduced the effect of soil moisture on root biomass and production, thereby maintaining similar root production under notably disparate soil moisture conditions. Considering continued interest in monoculture biofuel plantings and their potential to sequester C in roots and soils, additional research is necessary at the landscape scale to elucidate the importance of species spatial heterogeneity on grassland belowground C dynamics.

1. Introduction

Cultivated soils have lost 30–75% of historically stored carbon (Lal et al., 2007), but now offer a large potential sink for atmospheric CO_2 through biological carbon sequestration (Lal, 2004). For example, the conversion of row crop agricultural land to perennial grasslands for the USDA Conservation Reserve Program (Gebhart et al., 1994) and for perennial biofuel feedstocks (Lemus and Lal, 2005; Tilman et al., 2006; Anderson-Teixeira et al., 2009) is expected to re-sequester carbon in soils over the course of decades (McLauchlan et al., 2006) to centuries (Matamala et al., 2008). However, soil carbon sequestration rates are unlikely to be equal across the landscape, as soil organic carbon (SOC) stocks are notoriously heterogeneous (Cambardella et al., 1994; Lane and BassiriRad, 2005).

Differences in SOC accumulation rates have been noted between relatively drier and wetter areas within restored perennial grasslands (O'Brien et al., 2010), suggesting that field-scale spatial heterogeneity of SOC may be related in part to topographically-defined patterns of soil moisture (Lane and BassiriRad, 2005). In regions with a history of relatively recent glaciation, landscapes are relatively flat, and even small differences in absolute elevation can produce marked differences in soil moisture (Link et al., 1974; Winter, 1989), thereby potentially influencing the spatial heterogeneity of SOC stocks and sequestration rates. However, relationships between soil moisture and SOC can result from changes in species composition, root production, decomposition, or a combination of interacting factors (Lane and BassiriRad, 2005; O'Brien et al., 2010). In addition, soil moisture may alter the relative depth-distribution of root biomass and production (Hendricks et al., 2006), thereby altering the vertical distribution and security of

* Corresponding author at: Great Lakes Bioenergy Research Center, University of Wisconsin-Madison, Madison, WI 53726, USA. Tel.: +1 608 265 9039.
E-mail address: avonhaden@wisc.edu (A.C. von Haden).

0167-8809/$ – see front matter
http://dx.doi.org/10.1016/j.agee.2013.12.027

sequestered SOC (Post and Kwon, 2000). Thus, a better understanding of the effects of soil moisture on plant input, output, and depth-distributions is necessary for improving predictions of how landscape-level differences in soil moisture, or changing rainfall patterns with global climate change, will affect heterogeneity in grassland SOC dynamics (Norby and Jackson, 2000).

In water-limited tallgrass prairie systems, increased moisture increases aboveground net primary productivity (Briggs and Knapp, 1995; Knapp et al., 2001). However, root turnover, not aboveground litter, is widely accepted as the major contributor to SOC formation in grasslands, due in part to the relatively large allocation of net primary productivity to roots (Hui and Jackson, 2006) and to the relatively greater recalcitrance of roots than aboveground biomass (Gholz et al., 2000; Rasse et al., 2005; Freschet et al., 2013). In grassland agriculture systems where aboveground biomass is harvested annually (e.g for hay or bioenergy feedstocks), the contribution of aboveground biomass to SOC formation is even further minimized. As seen with aboveground production, grassland root biomass and productivity also generally increase in wetter conditions (Hayes and Seastedt, 1987; Fiala et al., 2009), although trends are often weaker or non-significant for roots and far less studied than aboveground plant components (Bai et al., 2010). Across large spatial scales, ecosystem carbon outputs, such as root, litter, and soil organic matter decay rates also increase with increasing precipitation (Epstein et al., 2002; McCulley et al., 2005; Bontti et al., 2009). Yet, decomposition rates are often reduced as moisture becomes excessive (Neckles and Neill, 1994; Conn and Day, 1997) and anaerobic conditions reduce microbial activity (Linn and Doran, 1984). For these reasons, a greater emphasis on understanding changes in grassland fine root dynamics across landscape-scale soil moisture gradients would improve site selection for agricultural or conservation programs geared at sequestering SOC.

Soil moisture may also affect the vertical patterns of root pools and fluxes within the soil profile, as shallower biomass distributions often occur in water saturated soils on a global scale (Jackson et al., 1996). Similarly, at the landscape scale, relatively shallower rooting distributions have been observed in hydric versus xeric forests (Hendricks et al., 2006). Although it seems likely that vertical root biomass distributions would also vary in relation to soil moisture within tallgrass prairie ecosystems, this or related (e.g., Nippert et al., 2012) questions have rarely been addressed. For example, in accordance with global observations of non-forest temperate vegetation (Schenk and Jackson, 2002), species with relatively deeper root biomass distributions may be more common in drier prairie landscape positions. As plant litter is the primary source for SOC formation (Kögel-Knabner, 2002), root production distributions directly influence the vertical distribution of potential SOC formation within the soil profile. Thus, an improved understanding of landscape-level changes in root biomass and production distributions in response to soil moisture would inform SOC management practices that aim to increase the quantity of deep, and seemingly better protected, SOC (Post and Kwon, 2000; Lorenz and Lal, 2005).

Species assemblages change across landscapes, and soil moisture is known to play a significant role in the spatial structuring of grassland plant communities (Silvertown et al., 1999; Silvertown, 2004; Yang et al., 2011). Yet, our current understanding of the effects of soil moisture on grassland root dynamics is derived primarily from studies holding species assemblages relatively constant among moisture treatments (e.g., Hayes and Seastedt, 1987; Fiala et al., 2009; Bai et al., 2010). These studies elucidate the physiological effect of soil moisture on root dynamics for individual species, or for a specific species assemblage, but they do not account for the natural turnover of species that characterizes diverse grasslands. As carbon sequestration benefits are central to current discussions regarding the establishment of low verses high diversity grasslands for biofuel feedstocks (Tilman et al., 2006), an improved understanding of fine root dynamics in response to soil moisture within spatially diverse grasslands is necessary to improve predictions of realized SOC sequestration resulting from land management choices.

Our broad objective was to evaluate the relationship between soil moisture and fine root dynamics within diverse perennial grasslands to improve our understanding of the factors contributing to SOC heterogeneity across landscapes. To this end, we evaluated trends in SOC, fine root ($\leq$2 mm) biomass, production, and decomposition in response to changes in soil moisture across the landscape in a diverse, 25+ year old restored tallgrass prairie in northeastern Wisconsin. We hypothesized that fine root biomass and production would increase with increasing soil moisture, based largely upon patterns of aboveground dynamics previously reported from manipulative studies in grasslands (e.g., Knapp et al., 2001). Additionally, we hypothesized that fine root decomposition would decrease with increasing soil moisture, as wet soils are more likely to support anaerobic conditions that are unfavorable for microbial decomposition (Linn and Doran, 1984). Finally, we hypothesized that vertical distributions of root biomass and production would become relatively shallower with increasing soil moisture, due to the need for deeper roots in dry soils for resource uptake and due to the increasingly anaerobic conditions expected at depth in wet soils.

2. Materials and methods

2.1. Study site

The study site was the Keith White Prairie located on the University of Wisconsin-Green Bay campus in Green Bay, WI, USA (44.5277°N, 87.9264°W). The annual average temperature is 6.9 °C with a low monthly average temperature of −9.2 °C in January and a high monthly average temperature of 21.1 °C in July. The annual average total precipitation is approximately 740 mm per year. In 2009, the year preceding our root biomass harvest, temperature and precipitation were slightly below normal at 6.4 °C and 703 mm, respectively, while in 2010, the year capturing root production and decomposition measurements, temperature and precipitation were both significantly higher than normal at 8.3 °C and 974 mm, respectively. The restored tallgrass prairies that we utilized were located on historically cultivated fields that had been planted to tallgrass prairie 27–36 years prior to plot establishment in 2009. The prairies contain a diverse mixture of species that change in dominance across the landscape. Common species in include *Andropogon gerardii* Vitman, *Silphium integrifolium* Michx., *Solidago canadensis* L., *Monarda fistulosa* L., and *Phalaris arundinacea* L., but the individual plots vary greatly in terms of occurrence and relative abundance (Table 1). The prairies are burned approximately every 2–5 years to maintain prairie species composition (G. Fewless unpublished data).

As part of a larger experiment (Dornbush et al., 2012), we established six plots in three separate prairies (n = 2 prairie^{-1}), with each prairie corresponding to a historically independent agricultural field. To avoid spatial autocorrelation of soil moisture and species assemblages, we established one relatively wet and one relatively dry plot within each segregated prairie unit (Fig. 1). Thus, soil moisture status was not related to the spatial proximity of plots. The plots were 15 × 5 m to conform to lowland swale size, and were further subdivided into 5 × 5 m subplots (n = 3 plot^{-1}). The subplots served as the units of within plot replication, allowing for multiple estimates per plot and providing consistency among SOC, root biomass, production, and decomposition methods. The plots were located on the Kewaunee-Manawa silt loam association that