



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

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## 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 ( $\leq 2$  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.

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## 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<sub>2</sub> 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

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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 versus 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

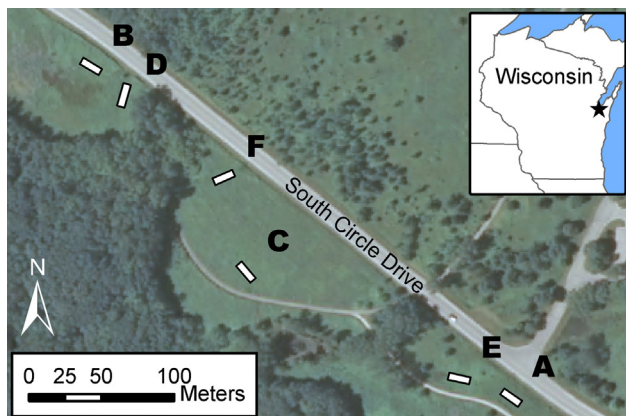
### 2.1. Study site

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 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<sup>−1</sup>), 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<sup>−1</sup>). 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

**Table 1**  
General properties of the six study plots located in a Northeast Wisconsin restored tallgrass prairie. Soil moisture represents average volumetric moisture from May through November 2010. Species surveys were conducted in June and October 2011 to quantify species richness, while aboveground biomass was harvested in August 2011 to quantify ANPP ( $\pm$ SE) and relative graminoid abundance. Dominant species were based on visual estimations of peak biomass in summer 2011.

Plot	A	B	C	D	E	F
Field #	3	1	2	1	3	2
Topography	Upland	Upland	Upland	Lowland	Lowland	Lowland
Slope (%)	2.5	1.2	1.1	2.9	3.1	1.2
Moisture (%)	31.6	32.0	32.1	39.4	51.2	61.3
0–10 cm SOC (%)	2.5	2.0	1.8	2.5	5.1	4.9
Last burned	2004	2006	2009	2006	2004	2009
ANPP ( $\text{g m}^{-2} \text{ year}^{-1}$ )	548.1 (56.8)	724.5 (71.3)	754.9 (84.1)	755.9 (112.9)	788.9 (75.3)	693.6 (81.8)
Species $\text{m}^{-2}$	17.3	19.7	12.0	14.0	14.7	10.0
Graminoids (%)	5	12	63	32	56	95
Dominant species	<i>Eryngium yuccifolium</i> <i>Lespedeza capitata</i> <i>Silphium integrifolium</i>	<i>Desmodium canadense</i> <i>Monarda fistulosa</i> <i>Rosa carolina</i>	<i>Andropogon gerardii</i> <i>Monarda fistulosa</i> <i>Solidago canadensis</i>	<i>Andropogon gerardii</i> <i>Silphium integrifolium</i> <i>Silphium laciniatum</i>	<i>Phalaris arundinacea</i> <i>Pycnanthemum virginianum</i> <i>Veronicastrum virginicum</i>	<i>Carex lacustris</i> <i>Spartina pectinata</i> <i>Typha angustifolia</i>



**Fig. 1.** Map of the study site (indicated with a star on the inset) showing the location of the six experimental plots. The plots are labeled A–F from driest to wettest. The study site is located in the Keith White Prairie on the University of Wisconsin–Green Bay campus in Green Bay, WI, USA (44.5277°N, 87.9264°W).

is common in Northeast Wisconsin, occupying approximately 39% of Brown County (Link et al., 1974). Kewaunee soils are classified as fine, mixed, active, mesic Typic Hapludalfs, and are associated with well drained, upland and slope landscape positions. Manawa soils are classified as fine, mixed, active, mesic Aquollic Hapludalfs, and are associated with somewhat poorly drained, lowland landscape positions. Although the Kewaunee–Manawa complex is formed primarily in clayey glacial till, the surface soils can range from sandy loams to silty clay loams (Link et al., 1974). For the remainder of the manuscript we refer to plots by based on their relative moisture status (labels A–F), ranging from the driest (i.e. A) to the wettest plots (i.e. F), respectively.

## 2.2. Plot surface moisture

We monitored surface volumetric soil water content (0–6 cm) from May through November 2010 with a Delta-T Devices ThetaProbe ML2x time-domain reflectometry (TDR) probe and a Delta-T Devices Theta Meter HH1 (Delta-T Devices Ltd., Cambridge, England). On each sampling date ( $n = 10$ ), we measured soil moisture in six random locations in each plot. We used repeated measures ANOVA to test for soil moisture differences among plots and dates. We use a pseudo- $r^2$  (regression of observed versus model predicted values) to assess the proportion of soil moisture variance explained by our mixed model.

## 2.3. SOC, root biomass, production, and decomposition

Approximately two weeks after plant senescence in 2009 and 2010, we took six soil cores per plot ( $n = 2 \text{ subplot}^{-1} \text{ year}^{-1}$ ) for a total of 12 cores per plot. The cores were 6.2 cm diameter, 40 cm long, and extracted manually with a steel soil coring device (Giddings Machine Company, Windsor, CO., USA). These cores were utilized to estimate plot-specific live fine root biomass ( $\text{g m}^{-2}$ ) for the top 40 cm of the soil profile. In addition, we measured SOC on the 2009 soil cores using a Shimadzu SSM-5000A combustion unit and a TOC-V CSH total organic carbon analyzer (Shimadzu Corp., Kyoto, Japan). Soil samples that effervesced upon acid exposure were pretreated with acid to remove carbonates prior to SOC analysis. Because short-term (<50 years) accrual of SOC has been demonstrated to occur primarily near the soil surface in grassland restorations (e.g., O'Brien et al., 2010; Sanford et al., 2012), we focus on the 0–10 cm depth. In order to correct for differences in bulk density among plots, we use an equivalent soil mass approach (Ellert and Bettany, 1995) with all total SOC values adjusted to the lowest soil mass observed in the 0–10 cm depth (Wander et al., 1998). To this end, we modeled SOC as a function of soil mass in SigmaPlot 11.0 (Systat Software Inc., California, USA) using the equation:

$$y = \alpha(1 - \exp(-bx))$$

where  $y$  is the cumulative SOC at cumulative soil mass  $x$ , and  $a$  and  $b$  are fitted parameters. All model  $r^2$  values were greater than 0.91 ( $P < 0.05$ ), indicating good model fits. We then estimated SOC in all plots at a cumulative soil mass of  $62.15 \text{ kg m}^{-2}$ , which represents the lightest mass of soil observed in the 0–10 cm depth (plot F).

To estimate annual belowground production, we used a series of root ingrowth cores (Jordan and Escalante, 1980). Briefly, we employed 6.9 cm diameter, 50 cm long (40 cm belowground) mesh ingrowth cores over the course of three time periods ( $n = 6 \text{ plot}^{-1} \text{ time}^{-1}$ ): November 2009–April 2010, April 2010–July 2010, and July 2010–November 2010. At the beginning of each time period, we extracted six soil cores per plot ( $n = 2 \text{ subplot}^{-1}$ ), inserted root ingrowth cores, and filled the cores with serially sieved, root-free soil. At the end of each time period, we extracted each core by cutting the soil around the edge and pulling the entire core out of the ground. Although the root ingrowth method is generally viewed as a conservative estimator of root production (Hendricks et al., 2006), the method is effective at capturing differences among treatments within a study (Milchunas, 2009).

We selected a subset of three plots (hereafter referred to as decay plots) to study fine root decomposition (reported as percent mass loss) using a modified intact decay core technique (Dornbush et al., 2002). In short, we removed eighteen ( $n = 6 \text{ subplot}^{-1}$ ) cores that were 4.9 cm diameter and 50 cm long (40 cm belowground) from each plot in mid-December 2009. The cores were inserted



into PVC tubes affixed with fine mesh on the bottom in order to prevent root growth into the core. Decay cores were placed under heat lamps for two weeks to kill live surface rhizomes and corms and then reinserted into the ground in late December 2009. We immediately removed nine cores per plot ( $n = 3$  subplot $^{-1}$ ) for estimates of initial fine root biomass, and subsequently removed the nine remaining cores per plot ( $n = 3$  subplot $^{-1}$ ) from each plot in late December 2010.

Following field harvest, all cores (biomass, ingrowth, and decay) were divided into 10 cm sections and then stored at  $-18^{\circ}\text{C}$  until they could be further processed. Following the methods of Dornbush et al. (2002), roots were gently washed with deionized water onto a  $500\text{ }\mu\text{m}$  sieve to separate roots from soil. Roots were sorted into three size classes ( $\leq 1\text{ mm}$ ,  $1\text{--}2\text{ mm}$ ,  $>2\text{ mm}$ ) and classified into live and dead categories based on color, elasticity, and state of the stele (Hayes and Seastedt, 1987). Roots were oven dried at  $65^{\circ}\text{C}$  for 48 h and weighed. Consistent with a common classification of fine roots (Hendricks et al., 1993), we report only  $\leq 2\text{ mm}$  (fine) roots, which are highly dynamic (Taylor et al., 2013) and thus play a major role in SOC dynamics. In addition, we report only live roots, except for decay cores where all roots are dead. Roots from decay cores are reported and analyzed on an ash-free dry-weight basis.

#### 2.4. Plant community composition

Plant surveys were conducted at identical locations in June and October of 2011. Sample locations were determined by randomly placing a  $1 \times 1\text{ m}$  quadrat within each subplot ( $n = 3$  quadrats plot $^{-1}$ ). We recorded all species rooted within quadrats, and visually estimated the three most abundant species based on their standing biomass. Finally, we harvested aboveground biomass using  $0.5\text{ m}^2$  quadrats ( $n = 2$  subplot $^{-1}$ ,  $6$  plot $^{-1}$ ) in late August 2011 to determine ANPP and the relative abundance of graminoids and forbs on a  $65^{\circ}\text{C}$  dry-weight basis.

#### 2.5. Calculations and statistical analyses

We took averages of cores within each subplot ( $n = 2$  subplot $^{-1}$  year $^{-1}$  for biomass cores,  $n = 2$  subplot $^{-1}$  time $^{-1}$  for ingrowth cores,  $n = 3$  subplot $^{-1}$  time $^{-1}$  for decay cores) to create three estimates plot $^{-1}$  time period $^{-1}$  for each root parameter. Estimates of root biomass, production, and decay were thus calculated at the subplot level ( $n = 3$  plot $^{-1}$ ). We calculated annual fine root ( $\leq 2\text{ mm}$  diameter) production as the summation of the three ingrowth periods. We calculated annual decomposition as the percentage of fine root mass lost after one year. We tested for differences in fine root biomass, production, and decomposition (collectively referred to as root parameters) among plots using individual ANOVAs for each root parameter, with plot as a class variable and the root parameter as the response variable. For root biomass, we included year as a random effect to account for potential differences among the two sampling years (2009 or 2010). We evaluated changes in each root parameter across the soil moisture gradient using regressions between growing season average soil moisture ( $n = 1$  plot $^{-1}$ ) and the plot average root parameters ( $n = 1$  plot $^{-1}$ ). Similarly, we used linear regression to test whether species richness, graminoid biomass, ANPP, and surface SOC were related to soil moisture.

Vertical distributions of root biomass and production were modeled in SigmaPlot 11.0 (Systat Software Inc., California, USA) using an asymptotic equation (Gale and Grigal, 1987; Jackson et al., 1996):

$$y = 1 - \beta^d$$

where  $y$  is the cumulative proportion of total roots to a given depth ( $d$ ), and  $\beta$  is an estimated coefficient that is indicative of the relative

shallowness of root distribution. For both biomass and production,  $\beta$  values closer to 1.0 indicate a larger proportion of biomass or production that occurred deeper in the soil profile. We calculated  $\beta$  coefficients at the subplot level for root biomass and production. The asymptotic model showed excellent agreement with fine root data, resulting in average  $r^2$  values of 0.96 and 0.96 for root biomass and production distribution models, respectively. We tested for significant differences in relative rooting distributions among plots using an ANOVA with plot as a class variable, and  $\beta$  as the response variable. For biomass distributions, we included a random term to account for potential differences among the two years that data was collected. To test the hypothesis that relative root distributions are related to surface soil moisture,  $\beta$  coefficients were regressed against plot level surface moisture.

To test for species turnover among plots, we analyzed quadrat-level species occurrences using a multi-response permutation procedure (MRPP) with Jaccard distance. To present the species occurrences for visual interpretation and quantitative analysis, we utilized non-metric multidimensional scaling (NMDS) with Jaccard distance and varimax rotation. To evaluate the relationship between soil moisture and species turnover, we used a MANCOVA with soil moisture as the independent variable and the NMDS axes as the dependent variables. MRPP and NMDS procedures were performed in PC-ORD 6.0 (MjM Software, Gleneden Beach, OR, USA) while other statistical procedures were performed in SAS 9.2 (SAS Institute, Cary, NC, USA).

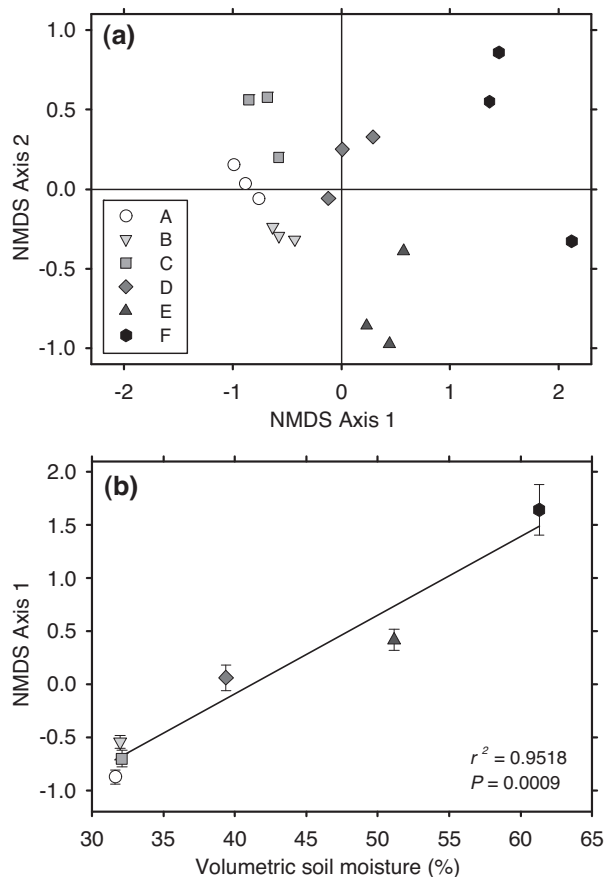
### 3. Results

#### 3.1. Plot surface soil moisture

Growing season average surface soil moisture ranged from 31.6 to 61.3% among plots, although all three of the upland plots (A–C) all had consistently lower soil moisture (Table 1). Average soil moisture in lowland plots (D–F) ranged widely from 39.4 to 61.3%, potentially reflecting differences in plot slopes and drainage (Table 1). In contrast, there were minimal temporal trends in soil moisture during the growing season, with surface soil moisture remaining relatively stable between May and October, except for a brief decline in August (data not shown). The temporal stability of soil moisture likely reflected the relatively consistent precipitation that occurred throughout our study (data not shown). These trends were supported by statistical comparisons, with surface soil moisture varying significantly by plot ( $F_{5,30} = 606.01$ ;  $P < 0.0001$ ), date ( $F_{9,266} = 20.78$ ;  $P < 0.0001$ ), and their interaction ( $F_{45,266} = 2.70$ ;  $P < 0.0001$ ). However, the interaction term accounted for less than 4% of the explained variability, whereas plot and date accounted for approximately 91% and 5% of the explained variability, respectively. Based on these findings, we conclude that average growing season (May through October) soil moisture was an appropriate independent metric to evaluate belowground responses among plots.

#### 3.2. Effect of landscape-level soil moisture differences on species composition and soil organic carbon

In total, 77 different species were identified across all plots (data not shown). Mean species richness among plots ranged from 10 to 19.7 species  $\text{m}^{-2}$  (Table 1), but was not significantly related to growing season average soil moisture ( $r^2 = 0.41$ ;  $P > 0.16$ ; Table 1). Species composition differed significantly among plots (MRPP,  $A = 0.35$ ;  $P < 0.05$ ) and was most similar among upland plots (Fig. 2a). Soil moisture was a strong predictor of axis 1 and 2 NMDS coordinates (Wilks' Lambda,  $F = 46.4$ ;  $P < 0.01$ ), although soil moisture was most strongly related to axis 1 ( $r^2 = 0.95$ ;  $P < 0.001$ ; Fig. 2b). Within-plot variability of species occurrence increased

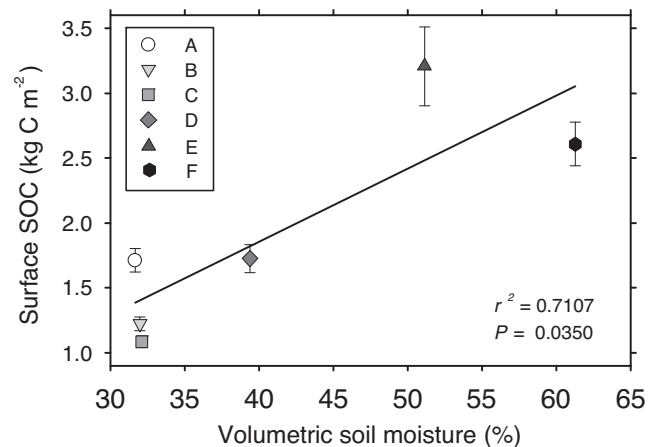


**Fig. 2.** (a) Non-metric multidimensional (NMDS) scaling ordination of species occurrence in a restored tallgrass prairie in Northeast Wisconsin. Species occurrence differed significantly among plots (MRPP,  $A = 0.35$ ;  $P < 0.05$ ). (b) Average growing season surface soil moisture plotted against NMDS axis 1. Error bars are  $\pm$  one standard error.

with increasing plot soil moisture, with most of the variability occurring in axis 2. Graminoid biomass ranged from 5 to 95% of total aboveground biomass, and was marginally related to soil moisture ( $r^2 = 0.62$ ;  $P = 0.062$ ; Table 1). However, ANPP was relatively consistent among plots (Table 1) and did not vary as a function of soil moisture ( $r^2 = 0.07$ ;  $P > 0.61$ ). Surface SOC concentrations ranged from 1.8 to 5.1% (Table 1), and mass-equivalent SOC stocks were positively related to surface soil moisture ( $r^2 = 0.71$ ;  $P < 0.04$ ; Fig. 3).

### 3.3. Effect of landscape-level soil moisture differences on fine root dynamics

Total fine root ( $\leq 2$  mm) biomass in the top 40 cm of soil ranged from 427 to 853  $\text{g m}^{-2}$ , and differed significantly among plots ( $F_{5,12} = 3.20$ ;  $P < 0.002$ ). However, in contrast to our expectations, differences in total fine root biomass across the landscape were not significantly related to surface soil moisture ( $P > 0.69$ ; Fig. 4a). Fine root production also differed significantly among plots ( $F_{5,12} = 5.61$ ;  $P < 0.007$ ), ranging from 251 to 524  $\text{g m}^{-2} \text{ year}^{-1}$  to a depth of 40 cm, but were again unrelated to plot average growing-season soil moisture levels ( $P > 0.76$ ; Fig. 4b). Average fine root decomposition differed significantly among plots ( $F_{2,6} = 5.33$ ;  $P < 0.05$ ) ranging from 28 to 61%  $\text{year}^{-1}$ . In agreement with our hypothesis, root decomposition decreased with increasing soil moisture, although the trend was only marginally significant ( $P = 0.061$ ; Fig. 4c). Thus, despite significant differences in total fine root biomass, production, and decomposition among plots, only



**Fig. 3.** Relationship between surface (0–6 cm) growing season (May–November) soil moisture and surface horizon soil organic carbon stocks in a Wisconsin tallgrass prairie. Soil organic carbon stocks are reported on a soil mass-equivalent basis adjusted to the 0–10 cm soil mass of plot F, which had the lowest surface soil mass. Error bars are  $\pm$  one standard error.

differences in decomposition were related to differences in surface soil moisture.

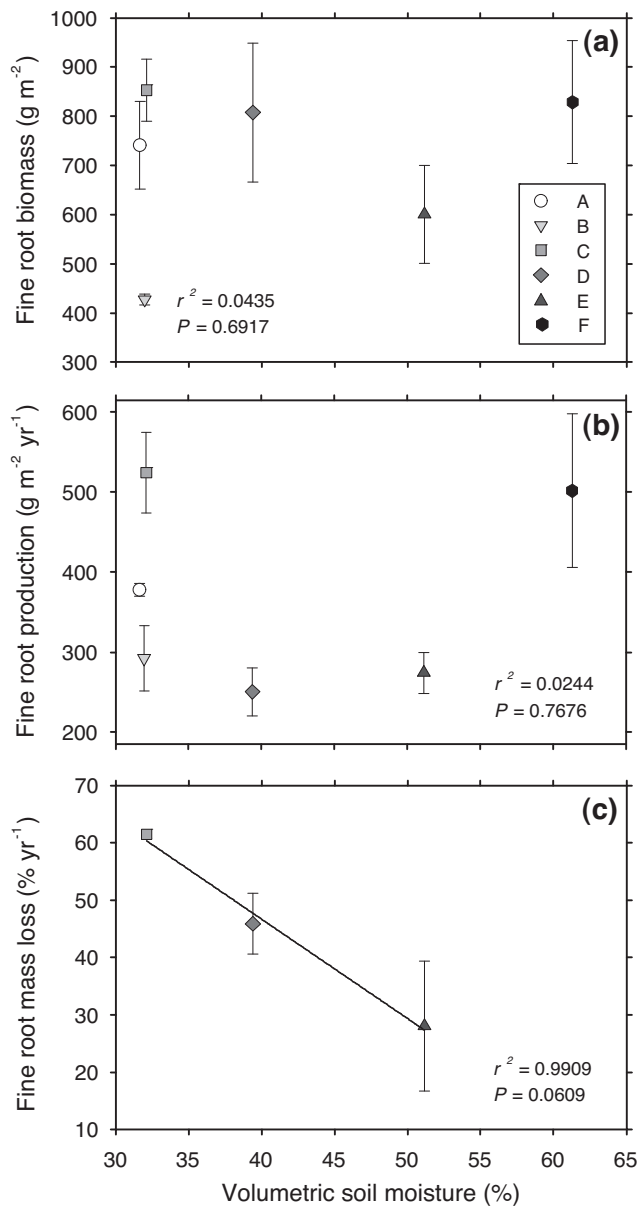
### 3.4. Effect of landscape-level soil moisture differences on root vertical distributions

Beta ( $\beta$ ) coefficients for fine root biomass, which reflect the vertical partitioning of roots within the soil profile, ranged from 0.885 to 0.933 and differed significantly among plots ( $F_{5,12} = 6.89$ ;  $P < 0.005$ ). Fine root biomass distributions trended towards shallower distributions (i.e. lower  $\beta$  values) in plots with greater surface moisture (Fig. 5a). However, in contrast to our hypothesis the overall relationship between soil moisture and root biomass distribution was not significant ( $P > 0.16$ ; Fig. 5a). Overall,  $\beta$  coefficients calculated for fine root production were similar to those calculated for fine root biomass, ranging from 0.901 to 0.942, and also differed significantly among plots ( $F_{5,12} = 8.1$ ;  $P < 0.002$ ). Root production distributions were also generally shallower in wetter plots, but the trend was again non-significant ( $P > 0.34$ ; Fig. 5b). Root production distributions were positively correlated with root biomass distributions ( $P < 0.006$ ).

## 4. Discussion

### 4.1. Landscape-level relationship between soil moisture and SOC stocks

Although SOC was highly variable across our study site, we found a strong, positive relationship between soil moisture and surface SOC stocks (Fig. 3), supporting expectations that wet landscape positions have high soil organic carbon sequestration potentials (Euliss et al., 2006). Our findings are in agreement with Lane and BassiriRad (2005) who previously documented that soil moisture explained a substantial amount of the spatial heterogeneity of SOC within restored and native Illinois prairies. Although we did not directly measure carbon accrual rates, our results are also in agreement with O'Brien et al. (2010), who demonstrated that surface SOC accrual rates in restored Illinois prairies were related to long-term soil moisture status. While it has been suggested that increased productivity, decreased decomposition, or a combination of the two factors may be responsible for greater soil carbon storage in wet prairie locations (Lane and BassiriRad, 2005; O'Brien et al., 2010),

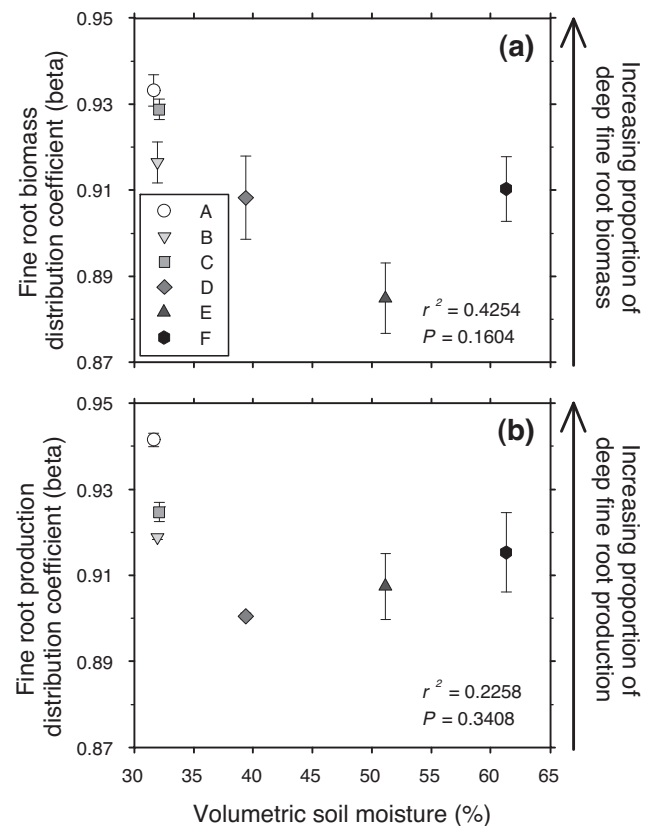


**Fig. 4.** Growing season (May–November) soil moisture content versus (a) live fine root biomass, (b) annual fine root production, and (c) annual fine root decomposition (reported as percent mass loss) in a restored tallgrass prairie. Fine roots were defined as  $\leq 2$  mm, and all analyses are to a depth of 40 cm. Plots differed significantly in fine root biomass, production, and decomposition ( $\alpha = 0.05$ ). Error bars are  $\pm$  one standard error. Error bars for plot C in (c) are smaller than the symbol and thus are not visible.

to our knowledge this question has not yet been addressed in an integrated manner.

#### 4.2. Landscape-level relationship between soil moisture and live fine roots

Live fine root biomass (e.g., Tufekcioglu et al., 2003; Dahlman and Kucera, 1965) and production (e.g., Johnson and Matchett, 2001) were within the range reported from other temperate grasslands. These root parameters, as well as their vertical distributions, differed significantly among plots, but in contrast to our expectations, differences were unrelated to surface soil moisture. Nippert et al. (2012) reported similar findings for root biomass and biomass distributions in upland and lowland locations in Kansas tallgrass prairie. However, these results contrast with several grassland



**Fig. 5.** Average surface soil moisture versus (a) fine root biomass distribution coefficients and (b) fine root production distribution coefficients. Beta coefficients were calculated based on 10 cm increments to a depth of 40 cm. Error bars are  $\pm$  one standard error.

studies reporting increased root biomass (Hayes and Seastedt, 1987; Fiala et al., 2009) and production (Fiala et al., 2009; Bai et al., 2010) following short-term increases in soil water availability, and global-scale patterns reporting deeper root distributions in drier ecosystems (Schenk and Jackson, 2002). Irrespectively, we found no significant trend in fine root biomass, production, or their vertical distributions across our soil moisture gradient, refuting our expectation that root biomass and production would vary with landscape-level differences in soil moisture.

Several potential explanations could account for the apparent lack of a response by root systems to landscape-level differences in soil moisture that we report. First, the wet growing season of our study year may have moderated root responses to soil moisture differences among our plots, as soil moisture in even our driest plots averaged  $>30\%$ . Singh et al. (1998), who also failed to find significant changes in root distributions across a soil moisture gradient in shortgrass steppe, hypothesized that a high frequency of small precipitation events could provide sufficient surface water to meet plant demands, thereby reducing the need for deeper roots. In agreement, Nippert and Knapp (2007) observed that tallgrass prairie functional groups differing in root distributions all preferentially utilized surface moisture when water was not limiting. In our study, the wettest plots remained flooded or close to saturation throughout the experiment, and roots in these plots likely experienced notably different stresses (e.g., oxygen limitation) than roots in our drier plots (Huang and Johnson, 1995). Thus, while it seems clear that our plots exposed live roots to notably different soil moisture conditions, it remains unclear as to how our results might have differed should the study have occurred in a drier year, when soil moisture differences among plots might have been more extreme.

Second, we hypothesize that in this study strong species turnover in response to landscape-scale soil moisture differences may have moderated the effects of soil water on root systems. Whereas short-term water manipulations that constrain species composition seemingly emphasize plant physiological responses to soil moisture (Fiala et al., 2009), long-term differences in soil moisture are associated with concomitant changes in species assemblages (Silvertown et al., 1999; Yang et al., 2011; this study), thus emphasizing ecosystem responses to soil moisture. In support, our findings agree with regional-scale studies reporting non-significant relationships between precipitation and root biomass (Zhou et al., 2009) or root production (McCulley et al., 2005) where grassland plant communities differed from wet to dry regions. Furthermore, trends toward shallower rooting distributions in our wetter plots were disrupted by the wettest plots (i.e. plot F for biomass and E and F for production), which tended to have relatively deep root distributions (Fig. 5). Plot F in particular, which was flooded or nearly saturated throughout the duration of the experiment, was dominated by *Carex lacustris*, a wetland sedge known to produce aerenchyma across more than 90% of its root length under saturated conditions (Bedford et al., 1991). Hence, roots in our wettest plot may have been tolerant of soil anaerobiosis, thereby allowing for deeper root distributions. These results indicate that species turnover may work to equalize root dynamics across both landscapes (this study) and regions (McCulley et al., 2005). A lack of a clear trend between soil moisture and root distributions, coupled with species turnover in response to soil moisture suggests that heterogeneity in root biomass, production, and their distributions in our mesic prairies seem to have varied more as a function of species composition (e.g., Weaver, 1958; Dornbush and Wilsey, 2010) than soil moisture content.

Finally, factors other than soil moisture and species diversity appeared important in controlling root heterogeneity in our mesic grasslands. For example, two plots (C and F) that were located within the same historic field, but differed dramatically in soil moisture and species composition (Table 1), had root production rates that were nearly double that of the other four plots (Fig. 4b). These plots were both burned in spring of the previous growing season, resulting in reduced litter layers and seemingly increased root production (Knapp and Seastedt, 1986; Johnson and Matchett, 2001). Thus, while our study documented significant heterogeneity in fine root biomass and production among our plots, we found no evidence that differences in soil moisture accounted for this observed heterogeneity. Combined, these findings indicate that the positive correlations between SOC and surface soil moisture in mesic grasslands (e.g., Lane and BassiriRad, 2005; this study) are unlikely driven by landscape-level differences in fine root biomass or production. However, we caution that this conclusion may hold true only for grasslands with significant species turnover along soil moisture gradients.

#### 4.3. Landscape-level relationship between soil moisture and root decomposition

In agreement with our expectations, average fine root decomposition was reduced relative to our driest plot by 25 and 54% in our moderate and wet plots, respectively (Fig. 4c). These findings support those of Neckles and Neill (1994) and Conn and Day (1997), who found reduced root decomposition under wet, anoxic soil conditions in prairie marsh and coastal swale grasslands, respectively. However, in moisture limited systems, root (Bontti et al., 2009) and litter (Murphy et al., 1998; McCulley et al., 2005; Bontti et al., 2009) decomposition often increase with increasing water availability. This dichotomous response of decomposition to soil moisture illustrates the importance of considering the range of soil moisture conditions being evaluated, even within a given biome

(e.g., temperate grassland). Although initial root chemistry and subsequent decomposition rates (Silver and Miya, 2001) are known to vary by species (Vivanco and Austin, 2006; Raich et al., 2009), the effects of species richness, evenness, and functional identity on decomposition are less clear (Wardle et al., 1999; Dickson and Wilsey, 2009; McLaren and Turkington, 2010). We acknowledge that species turnover among our plots may have influenced root tissue chemistry, and thus our evaluation of the effect of soil moisture on root decomposition is likely confounded with changes in root chemistry. Nonetheless, the effect of soil moisture on root decomposition is in agreement with other studies in water-saturated soils (e.g., Neckles and Neill, 1994), indicating longer root litter residence time in wet topographic locations. The simultaneous consistency of fine root inputs and fine root biomass, coupled with reductions in organic matter outputs via decomposition in wetter soils suggests that seasonally saturated, low-lying landscape positions have the greatest potential for SOC storage in our and similar mesic grasslands.

## 5. Conclusions

Our results indicate that significant reductions in fine root decomposition (i.e. increases in root litter residence time) with increasing soil moisture was the principle plant-related factor likely responsible for the greater SOC observed in seasonally saturated areas at our study site. Thus, the spatial heterogeneity of SOC in our perennial grassland appears largely explained by soil moisture mediated differences in decomposition, not soil moisture mediated differences in root inputs. In contrast to root decomposition, fine root biomass, production, and their vertical distributions in the top 40 cm of the soil profile were unrelated to surface soil moisture, which we suggest resulted from high species turnover in response to different soil moisture regimes. In practice, maximizing grassland root and soil C storage across landscapes appears to be most readily accomplished by establishing diverse species assemblages, where community composition can shift in response to changes in environmental resources, or by the targeted planting of different species or cultivars based on soil moisture conditions. This conclusion has important implications for the potential for carbon storage by monoculture, biofuel grassland plantings, such as switchgrass (*Panicum virgatum* L.). For example, Ontl et al. (2013) reported reduced switchgrass root production in floodplains relative to drier landscape positions, while Barney et al. (2009) found that both upland and lowland switchgrass cultivars produced less root biomass when grown in either drought or flooded conditions. If root production by monocultures is reduced under either wet or dry soil conditions, then we also expect reduced organic matter inputs in monocultures relative to grasslands with spatially heterogeneous species assemblages, when averaged across the landscape. This conclusion requires greater attention considering the growing interest in the planting of monoculture grasslands for biofuel production, and may further emphasize the need for greater trait-based considerations by selective breeding programs.

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