SOIL Discuss., 2, 923–953, 2015
www.soil-discuss.net/2/923/2015/
doi:10.5194/soild-2-923-2015

SOIL Discussions
Open Access

Burning management in the tallgrass prairie affects root decomposition, soil food web structure and carbon flow

E. A. Shaw[1,2], **K. Denef**[3], **C. Milano de Tomasel**[1,2], **M. F. Cotrufo**[2,4], **and D. H. Wall**[1,2]

[1]Department of Biology, Colorado State University, Fort Collins, CO, USA
[2]Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA
[3]Central Instrument Facility, Department of Chemistry, Colorado State University, Fort Collins, CO, USA
[4]Department of Soil and Crop Sciences, Colorado State University, Fort Collins, CO, USA

Received: 18 August 2015 – Accepted: 20 August 2015 – Published: 10 September 2015

Correspondence to: E. A. Shaw (elizabeth.shaw@colostate.edu)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Root litter decomposition is a major component of carbon (C) cycling in grasslands, where it provides energy and nutrients for soil microbes and fauna. This is especially important in grasslands where fire is a common management practice and removes aboveground litter accumulation. In this study, we investigated whether fire affects root decomposition and C flow through the belowground food web. In a greenhouse experiment, we applied ^{13}C-enriched big bluestem (*Andropogon gerardii*) root litter to intact tallgrass prairie soil cores collected from annually burned (AB) and infrequently burned (IB) treatments at the Konza Prairie Long Term Ecological Research (LTER) site. Incorporation of ^{13}C into microbial phospholipid fatty acids and nematode trophic groups was measured on six occasions during a 180-day decomposition study to determine how C was translocated through the soil food web. Results showed significantly different soil communities between treatments and higher microbial abundance for IB. Root decomposition occurred rapidly and was significantly greater for AB. Microbes and their nematode consumers immediately assimilated root litter C in both treatments. Root litter C was preferentially incorporated in a few groups of microbes and nematodes, but depended on burn treatment: fungi, Gram-negative bacteria, Gram-positive bacteria, and fungivore nematodes for AB and only omnivore nematodes for IB. The overall microbial pool of root litter-derived C significantly increased over time but was not significantly different between burn treatments. The nematode pool of root litter-derived C also significantly increased over time, and was significantly higher for the AB treatment at 35 and 90 days after litter addition. In conclusion, the C flow from root litter to microbes to nematodes is not only measurable, but significant, indicating that higher nematode trophic levels are critical components of C flow during root decomposition which, in turn, is significantly affected by fire management practices. Not only does fire affect the soil community and root decomposition for Konza Prairie LTER soils, but the lower microbial abundance, greater root turnover, and the increased incorporation of root litter C by microbes and nematodes for AB suggests that tallgrass prairie manage-

SOILD

2, 923–953, 2015

ment through annual burning increases root litter-derived C flow through the soil food web.

1 Introduction

Soils contain an immense diversity of soil microorganisms and soil fauna, and are of key importance to terrestrial ecosystems nutrient cycling and carbon (C) storage (Wall et al., 2010; Wall, 2004; Bardgett, 2005; Smith et al., 2015). Understanding the roles of the soil food web in regulating belowground processes of decomposition, nutrient cycling, and C cycling is recognized as a hot topic of research in soil ecology (Bardgett and Cook, 1998; Holtkamp et al., 2011, 2008; Carrillo et al., 2011; Osler and Sommerkorn, 2007; Bardgett et al., 2013; van der Putten et al., 2013). This is especially because we still lack a clear understanding of how soil fauna contribute to these ecosystem processes and the ecosystem services they provide (Nielsen et al., 2011; Carrillo et al., 2011; Brussaard, 1998; Bardgett and Cook, 1998; Smith et al., 2015). Within the soil fauna, nematodes, which can occur at densities of approximately 1 million to 10 million m^{-2} in grasslands (Bardgett et al., 1997; Yeates et al., 1997), are thought to play a fundamental yet poorly understood role in soil C dynamics (Staddon, 2004; Nielsen et al., 2011; Wall et al., 2008; Osler and Sommerkorn, 2007).

Land management practices affect soil and soil biota by altering trophic group and species composition, abundance and biomass (Ferris et al., 2001; Bossio et al., 1998; Bardgett et al., 1996; Reed et al., 2009; Freckman and Ettema, 1993). In tallgrass prairie ecosystems, burning is a common management strategy used to promote growth of warm season grasses (Knapp et al., 1998). Frequent fires can have large effects on plant productivity, plant community composition, and root properties (Kitchen et al., 2009; Knapp et al., 1998), which can significantly alter ecosystem processes such as litter decomposition and C cycling (Ojima et al., 1994; Johnson and Matchett, 2001; Soong and Cotrufo, 2015). Litter decomposition is an important component of belowground C cycling and root litter C provides a major energy source for soil biota

SOILD
2, 923–953, 2015

(Eisenhauer and Reich, 2012). Since fire removes aboveground litter, and enhances root growth and belowground C allocation, root detrital input may be an even more important energy source for decomposer food webs in frequently burned grasslands (Seastedt et al., 1991; O'Lear et al., 1996). Furthermore, root decomposition studies have been highlighted as crucial because root litter is a major source of soil C (Rasse et al., 2005), contributing more than aboveground litter, and very little research has been done on the topic (Schimel and Schaeffer, 2012).

The belowground effects of fire have additional impacts on soil biodiversity and their functions. Burning causes changes in the soil surface energy budget by removing plant litter accumulation (O'Lear et al., 1996; Knapp and Seastedt, 1986). This leads to changes in soil conditions, such as nitrogen (N) content, C content, temperature and moisture, which could impact microbial and faunal activities or change detritivore community composition. Microbial community compositional changes have been reported as a result of fire: for example, fire alters microbial composition by reducing gram-negative and gram-positive bacteria (Docherty et al., 2011) and increasing arbuscular mycorrhizae (Hamman et al., 2007). Also, fire initially impacts the overall abundance of nematodes negatively (Whitford et al., 2014), but this rebounds quickly and certain groups, such as colonizing bacterivore nematodes, respond positively after fire (Jones et al., 2006; Todd, 1996). Such changes in soil community composition have been shown to impact litter decomposition (Verhoef and Brussaard, 1990). While most litter decomposition is ultimately the product of soil fungal and bacterial metabolic activities, soil fauna also play a role in litter decomposition by influencing these microbial activities and altering litter chemical composition (Coleman and Crossley, 1996; Verhoef and Brussaard, 1990; Petersen and Luxton, 1982; Xin et al., 2012; Mamilov, 2000; Coleman and Hendrix, 2000; Carrillo et al., 2011; Swift et al., 1979; Soong et al., 2015). However, little is known about how fire management of grasslands impacts both soil microbial and faunal community function or if frequently burned grasslands' soil communities are more specialized to decompose root litter than unburned soil communities.

SOILD
2, 923–953, 2015

Addition of ^{13}C-enriched plant litter to soil allows tracing litter-derived C into soil microbial and faunal groups during decomposition. This technique has been used to study plant-C utilization by microbial communities in soils by examining ^{13}C incorporation into microbial phospholipid fatty acids (PLFA; e.g., Denef et al., 2009; Rubino et al., 2010; Kohl et al., 2015; Soong et al., 2015). Also, stable isotopes have been useful for studying structures of soil faunal communities (e.g., collembolans, earthworms, enchytraeids, arthropods, gastropods, and nematodes; Chahartaghi et al., 2005; Albers et al., 2006; Goncharov et al., 2014; Crotty et al., 2014; Kudrin et al., 2015). Furthermore, C flow though soil faunal trophic groups can be traced and quantified using ^{13}C (Albers et al., 2006; Pollierer et al., 2007; Elfstrand et al., 2008; Ostle et al., 2007; D'Annibale et al., 2015; Gilbert et al., 2014). However, root turnover and aboveground litter inputs are the main basis for soil faunal trophic groups in the chiefly detrital-based grassland soil food webs (Ostle et al., 2007) and these previous studies often focus only on C from recent photosynthate, ignore some of the most abundant soil fauna groups (e.g., nematodes), and do not consider how differing land management tools, such as fire, might affect C pathways belowground.

This project was designed to trace C from decomposing root litter into components of the soil food web over time for annually (AB) and infrequently burned (IB) prairie soils. Our conceptual approach included the production of a ^{13}C-enriched tallgrass (Big Bluestem, *Andropogon gerardii*) root litter, its incubation in intact AB and IB prairie soil cores in a greenhouse, and quantifying the incorporation of root litter C within the soil food web over time. We hypothesized that: (1) the AB treatment would support a different community composition of microorganisms and nematodes than the IB treatment due to recurrent impacts of fire, (2) root litter mass loss would be greater and occur faster for AB, and (3) root litter would be a more important C source for microorganisms and nematodes from AB prairie, which would thus incorporate root litter-derived C more quickly and in greater amounts than those from IB prairie.

SOILD
2, 923–953, 2015

2 Materials and methods

2.1 Site description and soil collection

Soil samples were taken from historically unplowed tallgrass prairie at the Konza Prairie the Long Term Ecological Research (LTER) station in eastern Kansas, United States (39°05′ N, 96°35′ W). Average monthly temperatures range from −2.7 °C in January to 26.6 °C in July, with 835 mm of total annual precipitation on average. Following a similar sampling design of a concurrent field study by Soong and Cotrufo (2015), we used soils from two fire treatment areas at Konza Prairie LTER: annual spring burn and 20-year burn. Each treatment area is approximately 60 ha and has silty-clay textured Argiustoll soils. The two treatment areas are in close proximity to one another with minimal geological and edaphic differences. The annual spring burn treatment area (labeled SpB by the Konza Prairie LTER) was burned yearly each spring since 1972, and was burned prior to soil collection on 26 April 2011. The annual spring burn treatment area had soil pH 6.2. The 20-year burn treatment area (labeled 20B by the Konza Prairie LTER) was last burned by an unprescribed wildfire on 5 April 1991; previously, a prescribed burn occurred on 3 May 1975. The 20-year burn treatment had soil pH 6.1. For specific soil characterization data for these sites including %C, %N, pyrogenic organic C content and bulk density see Soong and Cotrufo (2015). Soil from the annual spring burn treatment area will be referred to as annually burned (AB) and the 20-year burn as infrequently burned (IB) for the remainder of this paper.

Soil cores (10 cm deep × 10 cm diameter) were extracted from upland soil of the two fire treatment areas on 14 June 2011. Sampling was spread out within each of these areas to capture site variability. Specifically, cores were taken every 3 m in a 24 m × 18 m grid for a total of 48 soil cores from each treatment area. For both treatment areas, soil cores were taken beneath the dominant grass, *Andropogon gerardii*. These soil cores were extracted by driving PVC collars (10 cm diameter) in to a depth of 10 cm soil, and carefully digging out the collars while preserving soil core structure. The soil cores, or mesocosms, intact in PVC collars, were packed into sterile plastic bags in the field, kept

SOILD
2, 923–953, 2015

in coolers with ice packs, and transported to greenhouses at Colorado State University (CSU), Fort Collins, CO, USA for the decomposition experiment. Every effort was made to minimize disturbance to the soil.

Field temperature and moisture were measured at time of soil collection for both AB and IB soils. Soil temperature was recorded in the field and daily during the greenhouse incubation using a temperature probe coupled to a PP system (PP-system, SRC-1). Initial soil moisture was determined by gravimetric water content (GWC) by subtracting the oven-dry weight of soil (105 °C) from the field moist weight. All soil pots were weighed and %GWC was estimated based on initial field levels. Soil moisture was maintained daily at 20 % GWC by weighing the cores every other day and adding deionized water as needed to bring up soil moisture levels.

2.2 Production of ^{13}C-enriched root litter

Prior to experiment setup, *Andropogon gerardii* was grown from rhizomes in soil-free potting mix for one growing season in a continuous labeling chamber at 4 atom% ^{13}C-CO_2 atmosphere, fertilized weekly for 21 weeks with a ^{15}N-KNO_3 solution (7 atom%) (Soong et al., 2014). After the growing season, plants were harvested and roots were separated from shoots. Roots were then washed, air-dried and a sub-sample analyzed for %C, %N, and ^{13}C and ^{15}N enrichment by an Elemental Analyzer (EA; Carlo Erba NA 1500) connected to a continuous flow Isotope Ratio Mass Spectrometer (IRMS; VG Isochrom, Isoprime Inc., Manchester, UK). The root litter had a C and N concentration of 44.37 and 1.49 %, respectively, and an isotopic enrichment of $\delta^{13}C$ 1882.37 ‰ (3.12 atom%) and $\delta^{15}N$ 12147.21 ‰(4.61 atom%).

2.3 Decomposition experiment

Our experimental design consisted of two burn treatments and two litter treatments in a fully factorial design (2 burn treatment ×2 litter treatment × 6 harvests × 4 replicates = 96). Soil cores from AB and IB treatments were incubated inside the PVC collars with

SOILD
2, 923–953, 2015

either of two different litter treatments: control (no litter) or litter addition (^{13}C-enriched root litter). A total of 48 nylon litterbags (8 cm × 8 cm, 1 mm mesh size) were prepared, each containing approximately 1.5 g of the air-dried ^{13}C-enriched root litter and buried in the soil (24 AB and 24 IB) for the litter addition treatment. Subsamples of root litter were dried in an oven at 70 °C for oven-dry mass correction. To minimize disturbance to the soil, each soil core was carefully removed from the PVC collar, sliced in half horizontally (Sanaullah et al., 2010), a litterbag was placed in the center, and the two halves of the core were restored together into the PVC collar. The remaining cores were sliced in half then put back together, with no litterbag added, and established as control treatments. All PVC collars were established on top of sand to allow for drainage and were contained individually in pots to prevent cross contamination. The experiment was conducted in a greenhouse at the Colorado State University Plant Growth Facility.

To assess decomposition and biotic community changes over time, 6 destructive harvests occurred over 180 days, i.e., at 3, 10, 21, 35, 90, and 180 days. At each harvest date, four replicates of each of the four treatments were harvested for analyses of soil, root litter, and biota. Specifically, the litterbag was carefully removed from the soil and set aside, each soil core was removed from the collar, placed into a sterile plastic bag and well-mixed to homogenize soil. Each homogenized soil sample was sub-sampled for PLFA analysis and nematode extraction. The roots were retrieved from the litterbag before drying in an oven at 45 °C for 5 days. Mass loss was assessed by subtracting the remaining mass of roots (oven-dried) from the initial mass of roots (oven-dry mass corrected). All litter samples were then analyzed for %C and ^{13}C as described above for the initial litter material. Only C dynamics are discussed in this study.

2.4 Microbial community

Microbial community structure was assessed by Phospholipid Fatty Acid (PLFA) analysis. Soil sub-samples for PLFA analysis were sieved to 2 mm, with any visibly re-

SOILD
2, 923–953, 2015

maining plant material carefully removed with forceps. The PLFA extraction, quantification and $\delta^{13}C$ analysis methods were based on previous studies (Bossio and Scow, 1995; Denef et al., 2007; Gomez et al., 2014). For all treatments, approximately 6 g soil subsamples from the bulk soil were lyophilized and extracted in duplicate using a modified Bligh–Dyer method (Gomez et al., 2014) at each harvest. Fatty acid methyl ester (FAME) derivatives were analyzed by capillary gas chromatography-combustion-isotope ratio mass spectrometry (GC-C-IRMS) (GC-C/TC DeltaPLUSXP Thermo Scientific) via a GC/C III interface. PLFA identifications were based on the retention times of two standard mixtures, a Supelco FAME mix (47885-U: Supelco 37 component FAME mix, Sigma-Aldrich) and a bacterial acid methyl ester mix (47080-U: BAME mix, Sigma-Aldrich). Representative samples were analyzed by gas chromatography-mass spectrometry (GC-MS; Shimadzu QP-2010SE) and spectral matching was completed using the NIST 2011 mass spectral library (Shimadzu) to identify PLFAs that are not available in standard mixtures,

A number of PLFAs were selected as biomarkers for different microbial groups to investigate the soil microbial community composition (Frostegård and Bååth, 1996; Zelles, 1999). The PLFAs i15:0, a15:0, i16:0, a17:0, i17:0 were selected to estimate the abundance of gram-positive bacteria, and cy17:0, cis16:1n9, 18:1n11, and cy19:0 for gram-negative bacteria. Fungal abundance was based on cis18:1n9 and cis18:2n9,12, and methylated PLFAs 10Me-16:0, 10Me-17:0, and 10Me-18:0 were used as indicators of actinobacteria. The PLFAs 20:4n6 and 20:5n3 were selected to indicate protozoa.

The abundance of individual PLFAs was calculated (ng g^{-1} soil) and used as a proxy for microbial biomass. Changes in the microbial community composition were evaluated based on relative PLFA abundance data, which were calculated as in Gomez et al. (2014).

2.5 Nematode community

For both AB and IB treatments, soil nematodes were extracted from each soil sample by a modified Baermann funnel method in deionized water after Hooper (1970). A

SOILD
2, 923–953, 2015

subsample of 100 g of soil was placed onto the Baermann funnels and an aliquot of water and nematodes removed daily for 3 days.

Nematodes were counted, identified, and sorted using an inverted microscope (Olympus CKX41, 200X magnification) into five different trophic groups (bacterivore, fungivore, plant parasite, omnivore, and predator), based on Yeates et al. (1993), and trophic groups sorted into separate microcentrifuge tubes (0.5 mL). For elemental and isotopic analysis 75 individuals from each trophic group were then handpicked using an eyelash (Superfine eyelash with handle, Ted Pella, Inc., Prod no. 113) under a dissecting microscope (Olympus SZX10, 30X magnification), and transferred to a pre-weighed tin capsule (8 × 5 mm, Elemental Microanalysis BN/170056) containing 120 µL of deionized water. The tin capsules containing the different nematode trophic groups were desiccated for 3 days, weighed again to obtain final sample weights, and then prepared for analysis. The tin capsules containing nematode samples were analyzed for %C and ^{13}C using a CE-1110 EA coupled via Conflo II interface to an IRMS (ThermoFinnigan Delta Plus).

The absolute abundance of individual nematode groups was calculated (number nematodes kg^{-1} dry soil). Changes in the nematode community composition were evaluated based on relative nematode abundance data, which were calculated by dividing the absolute abundance of a nematode group by the sum of the absolute abundance of all nematode groups.

2.6 Data analyses

The isotope ratios are reported in terms of $\delta^{13}C$ (‰) values (Brenna et al., 1997), i.e.:

$$\delta^{13}C\ (‰) = (R_{sample} - R_{standard})/(R_{standard}) \times 10^3 \quad (1)$$

where R_{sample} is the $^{13}C/^{12}C$ ratio of the sample and $R_{standard}$ refers to the reference standard, Pee Dee Belemnite.

SOILD
2, 923–953, 2015

The proportion of root-litter carbon incorporated into nematode and microbial tissue (f_R) was calculated by a two-source mixing model with:

$$f_R = (\delta_{BioR} - \delta_{BioC})/(\delta_R - \delta_{BioC}) \quad (2)$$

δ_{BioR} and δ_{BioC} refer to the $\delta^{13}C$ signature of a group in the root litter-addition and the corresponding control, respectively, and δ_R to the $\delta^{13}C$ signature of the initial root litter.

The amount of root-derived C incorporated into individual PLFAs and nematode groups was calculated by multiplying the f-value by the absolute PLFA or nematode concentration (per g soil) for each individual PLFA or nematode group. The relative incorporation within each microbial group was calculated:

$$\text{PLFA-C}_{\text{root-derived/group}} = (\Sigma\text{PLFA-C}_{\text{group}} \times 100)/\Sigma\text{PLFA-C}_{\text{root-derived all}} \quad (3)$$

The effects of time, soil burning treatment, and litter addition on microbial PLFA abundance, nematode densities, and microbial and nematode incorporation of root litter derived ^{13}C were analyzed by Analysis of Variance (ANOVA) methods using a generalization of the general linear model (GLM) in the Proc Mixed procedure. Statistical analyses were completed with SAS 9.3 (SAS Institute Inc., Cary, North Carolina). Data were analyzed using a three factor model, where y = time + soil + litter addition. Time, soil, and litter addition were treated as categorical variables. Data were tested to meet assumptions of normality and residuals were log transformed to achieve normality if necessary. Significance was accepted at a level of probability (P) of < 0.05.

A distance-based redundancy analysis (dbRDA) was used to evaluate differences in microbial and nematode community composition among fire and litter treatments. The dbRDA is a multivariate approach that is widely accepted and used for ecological studies to evaluate multispecies responses to several factors (Legendre and Anderson, 1999). For our dbRDAs, PLFA and nematode relative abundance data (mol% of each identified PLFA or nematode group) were used in two dbRDA models. A distance matrix was calculated for each community using the Bray-Curtis measure to model the

SOILD
2, 923–953, 2015

species matrix. A principal coordinate analysis was performed on the distance matrix and the resulting eigenvalues were applied to a redundancy analysis. Ordination plots were drawn with ellipsoids (representing a 95 % confidence interval) around the multivariate community groups. The dbRDA and subsequent drawing of ordination plots were performed using R (R Core Team, Vienna, Austria).

3 Results

3.1 Effects of burning and root litter addition on the soil community

Burn treatment had a significant effect on soil community. The dbRDA revealed that soil microbial and nematode community compositions were significantly different (Fig. 1). PLFA abundance for AB was significantly lower than IB treatment ($P < 0.05$; Fig. 2). Specifically, there were lower proportions of PLFA biomarkers for gram-positive bacteria and fungi for AB (Fig. 2). Total nematode abundance did not differ between the AB and IB treatment, but community structure was significantly different (Figs. 3 and 1b). In particular, bacterivore nematodes were more abundance for AB, while plant parasitic nematodes were more abundant for IB (Fig. 3).

With the addition of root litter to the soil, microbial and nematode communities were changed (Fig. 1). The dbRDA revealed that the microbial community structure became slightly more similar with root litter addition between the two burn treatments, yet biomarkers for fungi and gram-negative bacteria still significantly separated them (Fig. 1a). Specifically, after litter addition, gram-negative bacteria, gram-positive bacteria, actinobacteria, and protozoa increased in abundance for the IB treatment, but there were no significant changes in microbial abundance for any functional group for the AB treatment (Fig. 2).

Neither AB nor IB nematode communities were significantly different with the addition of root litter, but there was a general shift in the community (Fig. 1b). The shift in the litter-addition communities was largely driven by bacterivore nematodes (Fig. 1b),

SOILD
2, 923–953, 2015

and the abundance of bacterivore nematodes significantly increased with root litter addition for both treatments (Fig. 3). There were significant differences in communities from each burning treatment; while the differences for the AB soil were driven by fungivores and plant parasitic nematodes, the IB soil community was influenced by omnivore and predator nematodes (Fig. 1b). The abundance data generally reaffirmed these changes. For example, fungivore nematodes were significantly more abundant for AB than IB at 90 days; conversely, omnivore nematodes were significantly more abundant for IB at 180 days (Fig. 3). There were no significant differences in abundance of plant parasitic or predator nematodes between AB and IB after litter addition.

3.2 Effects of burning on root decomposition and root-C dynamics

Significantly more root litter mass was lost for the AB treatment ($P = 0.028$). Decomposition occurred rapidly (> 30 % mass loss) in the first 10 days and progressed slowly for the remainder of the experiment. By day 180, the percent of root litter mass remaining for the AB and IB treatment was 53.0 ± 2.3 and 57.9 ± 2.2 %, respectively, and likewise, more root litter C was lost from the AB treatment ($P = 0.03$). Both time and burn treatment had significant effects on the root litter C pool dynamics (Fig. 4a).

3.3 Effects of burning on soil community utilization of root-C

Soil biota (both microbial PLFA biomarkers and nematodes) assimilated root litter ^{13}C for both AB and IB. Microbial and nematode groups utilized root litter C immediately after root litter addition and throughout the experiment for both treatments. However, this C was translocated differently through the soil communities for AB and IB treatments (Fig. 5). Plant parasitic nematodes did not have a significant amount of root litter C incorporated into their biomass in either treatment. Higher trophic levels (omnivore and predator nematodes) began to have root litter C incorporated into their biomass by 21 days, and this increased by the final harvest (Fig. 5).

SOILD
2, 923–953, 2015

The microbial biomarkers assimilation of root litter C increased significantly over time for both treatments (Fig. 4b). Despite higher total PLFA concentration in the infrequent burn treatment, the microbial pool of root litter C was not different between treatments. While there was generally more root litter derived C in the PLFAs initially (days 3, 10, 21) for IB and a lag in root litter C uptake for AB (Fig. 4b), the effect of burn treatment and the interaction of burn treatment and time was not significant for this pool of C. Also, the flow of C through the different groups of the microbial community was similar for each burn treatment (Fig. 5). In general, gram-negative bacteria dominated the C uptake initially (days 3 to 21) and this shifted to gram-positive dominance by 35 days for both burn treatments (Fig. 5). Fungal use of root litter C differed slightly for the burn treatments, with fungi from the AB treatment increasing in root litter C over time (Fig. 5c and d). Protozoa also differed between treatments, with earlier incorporation (35 vs. 90 days) for the IB treatment vs. the AB treatment.

The nematodes' assimilation of root litter C also increased significantly over time for both treatments (Fig. 4c). While the burn treatment alone was not significant, the interaction of time and burn treatment was highly significant for the nematode C pool. At day 35 and 90, the nematode root litter-derived C pool was significantly higher for AB than the IB treatment (Fig. 4c). The flow of C through the nematode community also differed somewhat (Fig. 5a and b). For both treatments bacteria and, correspondingly, bacterivore nematodes played a dominant role in root litter C utilization for both AB and IB soils (Fig. 5). Bacterivore nematodes dominated the nematode community in abundance and incorporated the greatest amount of root litter C overall; however, the other trophic groups differed between burning treatment. For the IB treatment, omnivore and predator nematodes utilized a significant portion of root litter C by 35 days after litter addition, but not for AB. For the AB treatment, fungivore nematodes significantly incorporated root litter C from day 3, but not for the IB treatment.

When we looked at the proportions of root litter C incorporated into individual group's biomass, there were differences between burn treatments. Overall, fungivore nematodes, saprotrophic fungi (cis-18:2n9,12), gram-negative bacteria (18:1n11), and gram-

SOILD
2, 923–953, 2015

positive bacteria (a17:0 and i16:0) incorporated significantly more root litter C for the AB treatment than the IB treatment (Table 1). Only omnivore nematodes incorporated more root litter C for the IB treatment.

4 Discussion

4.1 Effects of burning management on the soil community

Burning management practices have significant impacts on the belowground community including soil microbes and soil nematodes. We found that both soil microbial and nematode community structure differed with long-term burn treatments (Fig. 1), with the AB treatment showing reduced microbial biomass (via PLFA methods), decreased gram-positive bacteria and fungi, and higher proportions of bacterivore nematodes. These findings support our first hypothesis, that different burn treatments would house different soil communities, and confirmed previous observations. In particular, Todd (1996) showed that bacterivore nematodes respond positively to frequent fire while predator nematodes do not. Jones et al. (2006) later corroborated that study via molecular methods. Additionally, fire has been shown to reduce overall microbial biomass and specifically affects Gram-negative and gram-positive bacteria and fungi (Docherty et al., 2011; Ajwa et al., 1999). Such differences in the soil communities have implications for ecosystem function, such as impacts to organic matter decomposition (Verhoef and Brussaard, 1990).

4.2 Effects of burning management on root decomposition and root-C dynamics

Our results showed a difference in root litter mass loss between burn frequency treatments, confirming our second hypothesis. With significantly higher mass loss for the AB treatment, our results were in agreement with the observed higher aboveground litter respiration in the AB as compared to the IB site (Soong and Cotrufo, 2015). Yet,

SOILD
2, 923–953, 2015

in a root decomposition study by Reed et al. (2009) there were no significant main effects of burning management on root decomposition; however, low precipitation may have masked the effects of burning on decomposition for that study. Other studies have compared belowground decomposition (Reed et al., 2005, 2009; O'Lear et al., 1996) in areas of contrasting burning treatments. These studies have shown that wood decomposed significantly faster in annually burned tallgrass prairie compared to unburned prairie (Reed et al., 2005; O'Lear et al., 1996). Such differences in decomposition between burning treatments could be to be due to the indirect effects of burning on the soil community composition or to the direct effects on soil conditions (i.e., heat, moisture), which would impact decomposition processes (O'Lear et al., 1996). For instance, relative to unburned tallgrass prairie soils, a history of frequent burning can cause a buildup of non-decomposable pyrogenic material in the soil, promote N limitation forcing microbes to scavenge for N before beginning decomposition, thus altering C cycling (Johnson and Matchett, 2001; Soong and Cotrufo, 2015).

4.3 Effects of burning on soil community utilization of root-C

Corroborating part of our third hypothesis, we found that, overall, a significantly higher amount of ^{13}C was incorporated into the total soil community for AB, indicating greater utilization of root litter C in this more frequently burned soil. In particular, fungivore nematodes and specific biomarkers for fungi, gram-negative bacteria, and Gram-positive bacteria had a significantly higher proportion of their biomass composed of root litter C, suggesting that root litter C was a more important C source for the AB soil food web. Additionally, despite significantly lower microbial abundance for the AB treatment, there was no difference in the amount of root litter derived C in the total microbial pool between AB and IB treatment. Other studies have found similar results. Instead, our study supports the hypothesis that decomposition is strongly affected by decomposer community composition instead of the abundance (Wickings et al., 2012). In other words, distinct decomposer communities (such as the significantly different AB and IB communities) could have differing metabolic or functional capabilities. Perhaps because

SOILD
2, 923–953, 2015

the AB community is subjected to greater inputs of root litter due to the environmental changes cause by frequent fire, that community decomposes the root litter faster and incorporates a greater proportion of the root litter C into biomass because the biota are predisposed to take advantage of this C source. This may also indicate different mechanisms such as higher microbial turnover or increased microbial grazing by nematodes during decomposition of roots for the AB treatment.

We also hypothesized that root-C would be incorporated more quickly for AB. Yet despite the overall greater incorporation of root-C by AB, the root litter derived microbial-C and nematode-C pools both took up C immediately and changed over time of decomposition for both treatments (Fig. 4b and c). There was a slight lag in microbial uptake of root litter C for AB, but not for IB (Fig. 4b). This lag likely corresponds to the time microbes needed to scavenge N from the N-limited AB soil before commencing root decomposition (Manzoni et al., 2012). Yet through time, evidence exists for greater cycling of root litter C to the higher trophic levels of the AB food web. The root litter derived nematode-C pool was significantly higher in the AB treatment at 35 and 90 days after root addition. This accumulation of C in the higher nematode trophic levels indicates a greater or faster flow of root litter C from the microbes to their nematode consumers. Others have suggested that most energy from detritus flows to microbes and only a negligible amount of energy flows to the higher trophic levels of the soil food web (Setala, 2005). Our study opposes this view, as we show that in 1 g of soil, the nematodes can hold as much as half of litter derived-C as microbes in the same amount of soil (Fig. 4b and c).

5 Conclusions

Our results provide evidence that burning management affects decomposition processes and add a temporal dynamic of C flow through the soil food web. We have shown that decomposing roots are an important C-source for microbes and nematodes in this tallgrass prairie soil. ^{13}C originating from root litter was traced into different ne-

SOILD
2, 923–953, 2015

matode trophic groups, indicating that they had utilized root-derived C by feeding on bacteria, fungi, protozoa, other nematodes, or other soil organisms. Our study shows that not only does fire affect the soil community composition and root mass loss for Konza Prairie LTER soils, but the lower microbial abundance, greater root turnover, and the increased incorporation of root litter C by fungi, gram-negative bacteria, Gram-positive bacteria, and fungivore nematodes for AB indicates greater root litter-derived C flow through the soil food web for AB. Until now, nematodes' contribution to root litter decomposition was inconclusive, but we have shown that nematodes incorporate a significant amount of root litter C across trophic levels and this differs by fire treatment. Thus, both microbial and higher nematode trophic levels are critical components of C flow during root decomposition, which, in turn, is significantly affected by fire management practices.

Acknowledgements. This project was funded by the National Science Foundation under grant no. 0918482. We are grateful to the Konza Prairie LTER site for making this research possible. We thank the Wall Lab, especially K. Ivanovich and E. Bernier, for assistance with work in the field and laboratory. We thank the staff of the Colorado State University's EcoCore Analytical Facility (http://ecocore.nrel.colostate.edu/) and Kansas State University's Stable Isotope Mass Spectrometry Laboratory (http://www.k-state.edu/simsl/SIMSL_Home.html) for their support with analyses.

References

Ajwa, H., Dell, C., and Rice, C.: Changes in enzyme activities and microbial biomass of tallgrass prairie soil as related to burning and nitrogen fertilization, Soil Biol. Biochemistry, 31, 769–777, 1999.

Albers, D., Schaefer, M., and Scheu, S.: Incorporation of plant carbon into the soil animal food web of an arable system, Ecology, 87, 235–245, 2006.

Bardgett, R. D.: The Biology of Soil: A Community and Ecosystem Approach, Oxford University Press, New York, 2005.

SOILD

2, 923–953, 2015

Bardgett, R. D. and Cook, R.: Functional aspects of soil animal diversity in agricultural grasslands, Appl. Soil Ecol., 10, 263–276, 1998.
Bardgett, R. D., Hobbs, P. J., and Frostegard, A.: Changes in soil fungal:bacterial biomass ratios following reductions in the intensity of management of an upland grassland, Biol. Fert. Soils, 22, 261–264, 1996.
Bardgett, R. D., Leemans, D. K., Cook, R., and Hobbs, P. J.: Seasonality of soil biota of grazed and ungrazed hill grasslands, Soil Biol. Biochemistry, 29, 1285–1294, 1997.
Bardgett, R. D., Manning, P., Morriën, E., De Vries, F. T., and van der Putten, W.: Hierarchical responses of plant-soil interactions to climate change: consequences for the global carbon cycle, J. Ecology, 101, 334–343, doi:10.1111/1365-2745.12043, 2013.
Bossio, D. A. and Scow, K. M.: Impact of carbon and flooding on the metabolic diversity of microbial communities in soils, Appl. Environ. Microbiol., 61, 4043–4050, 1995.
Bossio, D. A., Scow, K. M., Gunapala, N., and Graham, K. J.: Determinants of soil microbial communities: Effects of agricultural management, season, and soil type on phospholipid fatty acid profiles, Microb. Ecology, 36, 1–12, 1998.
Brenna, J. T., Corso, T. N., Tobias, H. J., and Caimi, R. J.: High-precision continuous-flow isotope ratio mass spectrometry, Mass Spectrom. Rev., 16, 227–258, 1997.
Brussaard, L.: Soil fauna, guilds, functional groups and ecosystem processes, Appl. Soil Ecology, 9, 123–135, 1998.
Carrillo, Y., Ball, B. A., Bradford, M. A., Jordan, C. F., and Molina, M.: Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil, Soil Biol. Biochemistry, 43, 1440–1449, doi:10.1016/j.soilbio.2011.03.011, 2011.
Chahartaghi, M., Langel, R., Scheu, S., and Ruess, L.: Feeding guilds in Collembola based on nitrogen stable isotope ratios, Soil Biol. Biochemistry, 37, 1718–1725, doi:10.1016/j.soilbio.2005.02.006, 2005.
Coleman, D. C. and Crossley, D. A.: Fundamentals of Soil Ecology, Academic Press, New York, 1996.
Coleman, D. C. and Hendrix, P. F.: Invertebrates as Webmasters in Ecosystems, CAB International Press, New York, 2000.
Coleman, K. and Jenkinson, D. S.: RothC-26.3 – A model for the turnover of carbon in soil, in: Evaluation of Soil Organic Matter Models Using Existing Long-Term Datasets, edited by: Powlson, D. S., Smith, P., and Smith, J. U., Springer, Verlag, Heidelberg, 237–246, 1996.

SOILD
2, 923–953, 2015

Crotty, F. V., Blackshaw, R. P., Adl, S. M., Inger, R., and Murray, P. J.: Divergence of feeding channels within the soil food web determined by ecosystem type, Ecol. Evol., 4, 1–13, doi:10.1002/ece3.905, 2014.

D'Annibale, A., Larsen, T., Sechi, V., Cortet, J., Strandberg, B., Vincze, É., Filser, J., Audisio, P. A., and Krogh, P. H.: Influence of elevated CO_2 and GM barley on a soil mesofauna community in a mesocosm test system, Soil Biol. Biochemistry, 84, 127–136, doi:10.1016/j.soilbio.2015.02.009, 2015.

Denef, K., Bubenheim, H., Lenhart, K., Vermeulen, J., Van Cleemput, O., Boeckx, P., and Müller, C.: Community shifts and carbon translocation within metabolically-active rhizosphere microorganisms in grasslands under elevated CO_2, Biogeosciences, 4, 769–779, doi:10.5194/bg-4-769-2007, 2007.

Denef, K., Roobroeck, D., Manimel Wadu, M. C. W., Lootens, P., and Boeckx, P.: Microbial community composition and rhizodeposit-carbon assimilation in differently managed temperate grassland soils, Soil Biol. Biochemistry, 41, 144–153, doi:10.1016/j.soilbio.2008.10.008, 2009.

Docherty, K. M., Balser, T. C., Bohannan, B. J. M., and Gutknecht, J. L. M.: Soil microbial responses to fire and interacting global change factors in a California annual grassland, Biogeochemistry, 109, 63–83, doi:10.1007/s10533-011-9654-3, 2011.

Eisenhauer, N. and Reich, P. B.: Above- and below-ground plant inputs both fuel soil food webs, Soil Biol. Biochemistry, 45, 156–160, doi:10.1016/j.soilbio.2011.10.019, 2012.

Elfstrand, S., Lagerlöf, J., Hedlund, K., and Mårtensson, A.: Carbon routes from decomposing plant residues and living roots into soil food webs assessed with 13C labelling, Soil Biol. Biochemistry, 40, 2530–2539, doi:10.1016/j.soilbio.2008.06.013, 2008.

Ferris, H., Bongers, T., and de Goede, R. G. M.: A framework for soil food web diagnostics: extension of the nematode faunal analysis concept, Appl. Soil Ecol., 18, 13–29, 2001.

Freckman, D. W. and Ettema, C. H.: Assessing nematode communities in agroecosystems of varying human intervention, Agriculture, Ecosyst. Environ., 45, 239–261, 1993.

Frostegård, A. and Bååth, E.: The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil, Biol. Fert. Soils, 22, 59–65, 1996.

Gilbert, K. J., Fahey, T. J., Maerz, J. C., Sherman, R. E., Bohlen, P., Dombroskie, J. J., Groffman, P. M., and Yavitt, J. B.: Exploring carbon flow through the root channel in a temperate forest soil food web, Soil Biol. Biochemistry, 76, 45–52, doi:10.1016/j.soilbio.2014.05.005, 2014.

SOILD
2, 923–953, 2015

Gomez, J. D., Denef, K., Stewart, C. E., Zheng, J., and Cotrufo, M. F.: Biochar addition rate influences soil microbial abundance and activity in temperate soils, European J. Soil Sci., 65, 28–39, doi:10.1111/ejss.12097, 2014.
Goncharov, A. A., Khramova, E. Y., and Tiunov, A. V.: Spatial variations in the trophic structure of soil animal communities in boreal forests of Pechora-Ilych Nature Reserve, Eurasian Soil Sci., 47, 441–448, doi:10.1134/s106422931405007x, 2014.
Hamman, S. T., Burke, I. C., and Stromberger, M. E.: Relationships between microbial community structure and soil environmental conditions in a recently burned system, Soil Biol. Biochemistry, 39, 1703–1711, doi:10.1016/j.soilbio.2007.01.018, 2007.
Holtkamp, R., Kardol, P., van der Wal, A., Dekker, S. C., van der Putten, W. H., and de Ruiter, P. C.: Soil food web structure during ecosystem development after land abandonment, Appl. Soil Ecol., 39, 23–34, doi:10.1016/j.apsoil.2007.11.002, 2008.
Holtkamp, R., van der Wal, A., Kardol, P., van der Putten, W. H., de Ruiter, P. C., and Dekker, S. C.: Modelling C and N mineralisation in soil food webs during secondary succession on ex-arable land, Soil Biol. Biochemistry, 43, 251–260, doi:10.1016/j.soilbio.2010.10.004, 2011.
Hooper, D. J.: Extraction of free-living stages from soil, in: Laboratory methods for work with plant and soil nematodes, 6th ed., edited by: Southey, J. F., Ministery of Agriculture, Fisheries and Food, London, 5–30, 1970.
Johnson, L. C. and Matchett, J. R.: Fire and grazing regulate belowground processes in tall-grass prairie, Ecology, 82, 3377–3389, 2001.
Jones, K. L., Todd, T. C., Wall-Beam, J. L., Coolon, J. D., Blair, J. M., and Herman, M. A.: Molecular approach for assessing responses of microbial-feeding nematodes to burning and chronic nitrogen enrichment in a native grassland, Molecular Ecology, 15, 2601–2609, doi:10.1111/j.1365-294X.2006.02971.x, 2006.
Kitchen, D. J., Blair, J. M., and Callaham, M.: Annual fire and mowing alter biomass, depth distribution, and C and N content of roots and soil in tallgrass prairie, Plant Soil, 323, 235–247, 2009.
Knapp, A. K. and Seastedt, T. R.: Detritus accumulation limits productivity of tallgrass prairie, Bioscience, 36, 662–668, 1986.
Knapp, A. K., Briggs, J. M., Hartnett, D. C., and Collins, S. L.: Grassland Dynamics: Longterm Ecological Research in Tallgrass Prairie, Oxford University Press, New York, 1998.
Kohl, L., Laganière, J., Edwards, K. A., Billings, S. A., Morrill, P. L., Van Biesen, G., and Ziegler, S. E.: Distinct fungal and bacterial δ13C signatures as potential drivers of increasing δ13C of

SOILD
2, 923–953, 2015

soil organic matter with depth, Biogeochemistry, 124, 13–26, doi:10.1007/s10533-015-0107-2, 2015.
Kudrin, A. A., Tsurikov, S. M., and Tiunov, A. V.: Trophic position of microbivorous and predatory soil nematodes in a boreal forest as indicated by stable isotope analysis, Soil Biol. Biochemistry, 86, 193–200, doi:10.1016/j.soilbio.2015.03.017, 2015.
Legendre, P. and Anderson, M. J.: Distance-Based Redundancy Analysis: Testing Multispecies Responses in Multifactorial Ecological Experiments, Ecological Monogr., 69, 1–24, 1999.
Li, X., Han, S., Guo, Z., Shao, D., and Xin, L.: Changes in soil microbial biomass carbon and enzyme activities under elevated CO2 affect fine root decomposition processes in a Mongolian oak ecosystem, Soil Biol. Biochemistry, 42, 1101–1107, doi:10.1016/j.soilbio.2010.03.007, 2010.
Mamilov, A. S.: Regulation of the biomass and activity of soil microorganisms by microfauna, Microbiology, 69, 612–621, 2000.
Manzoni, S., Taylor, P., Richter, A., Porporato, A., and Agren, G. I.: Environmental and stoichiometric controls on microbial carbon-use efficiency in soils, The New Phytologist, 196, 79–91, doi:10.1111/j.1469-8137.2012.04225.x, 2012.
Nielsen, U. N., Ayres, E., Wall, D. H., and Bardgett, R. D.: Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships, European J. Soil Sci., 62, 105–116, doi:10.1111/j.1365-2389.2010.01314.x, 2011.
Ojima, D. S., Schimel, D. S., Parton, W. J., and Owensby, C. E.: Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie, Biogeochemistry, 24, 67–84, 1994.
O'Lear, H. A., Seastedt, T. R., Briggs, J. M., Blair, J. M., and Ramundo, R. A.: Fire and topographic effects on decomposition rates and N dynamics of buried wood in tallgrass prairie, Soil Biol. Biochemistry, 28, 323–329, 1996.
Osler, G. H. R. and Sommerkorn, M.: Toward a complete soil C and N cycle: Incorporating the soil fauna, Ecology, 88, 1611–1621, 2007.
Ostle, N., Briones, M. J. I., Ineson, P., Cole, L., Staddon, P., and Sleep, D.: Isotopic detection of recent photosynthate carbon flow into grassland rhizosphere fauna, Soil Biol. Biochemistry, 39, 768-777, doi:10.1016/j.soilbio.2006.09.025, 2007.
Parton, W. J., Hartman, M., Ojima, D., and Schimel, D.: DAYCENT and its land surface submodel: description and testing, Global Planet. Change, 19, 35–48, doi:10.1016/S0921-8181(98)00040-X, 1998.

SOILD
2, 923–953, 2015

Petersen, H. and Luxton, M.: A comparative analysis of soil fauna populations and their role in decomposition processes, Oikos, 39, 288–388, 1982.
Pollierer, M. M., Langel, R., Korner, C., Maraun, M., and Scheu, S.: The underestimated importance of belowground carbon input for forest soil animal food webs, Ecology Lett., 10, 729–736, doi:10.1111/j.1461-0248.2007.01064.x, 2007.
Rasse, D. P., Rumpel, C., and Dignac, M.-F.: Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation, Plant Soil, 269, 341–356, doi:10.1007/s11104-004-0907-y, 2005.
Reed, H. E., Seastedt, T. R., and Blair, J. M.: Ecological consequences of C4 grass invasion of a C4 grassland: a dilemma for managment, Ecol. Appl., 15, 1560–1569, 2005.
Reed, H. E., Blair, J. M., Wall, D. H., and Seastedt, T. R.: Impacts of management legacies on litter decomposition in response to reduced precipitation in a tallgrass prairie, Appl. Soil Ecol., 42, 79–85, doi:10.1016/j.apsoil.2009.01.009, 2009.
Rubino, M., Dungait, J. A. J., Evershed, R. P., Bertolini, T., De Angelis, P., D'Onofrio, A., Lagomarsino, A., Lubritto, C., Merola, A., Terrasi, F., and Cotrufo, M. F.: Carbon input belowground is the major C flux contributing to leaf litter mass loss: Evidences from a (13)C labelled-leaf litter experiment, Soil Biol. Biochem., 42, 1009–1016, doi:10.1016/j.soilbio.2010.02.018, 2010.
Sanaullah, M., Chabbi, A., Leifeld, J., Bardoux, G., Billou, D., and Rumpel, C.: Decomposition and stabilization of root litter in top- and subsoil horizons: what is the difference?, Plant Soil, 338, 127–141, doi:10.1007/s11104-010-0554-4, 2010.
Schimel, J. and Schaeffer, S.: Microbial control over carbon cycling in soil, Front. Microbiol., 3, 348, 2012.
Seastedt, T. R., Briggs, J. M., and Gibson, D. J.: Controls of nitrogen limitation in tallgrass prairie, Oecologia, 87, 72–79, 1991.
Setala, H.: Does Biological Complexity Relate to Functional Attributes of Soil Food Webs?, in: Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development and Environmental Change, edited by: de Ruiter, P., Volters, V., and Moore, J., Theoretical Ecology Series, Academic Press, Amsterdam, 308–320, 2005.
Smith, P., Cotrufo, M. F., Rumpel, C., Paustian, K., Kuikman, P. J., Elliott, J. A., McDowell, R., Griffiths, R. I., Asakawa, S., Bustamante, M., House, J. I., Sobocká, J., Harper, R., Pan, G., West, P. C., Gerber, J. S., Clark, J. M., Adhya, T., Scholes, R. J., and Scholes, M. C.: Biogeochemical cycles and biodiversity as key drivers of ecosystem services provided by soils, SOIL Discuss., 2, 537–586, doi:10.5194/soild-2-537-2015, 2015.

SOILD
2, 923–953, 2015

Soong, J. L. and Cotrufo, M. F.: Annual burning of a tallgrass prairie inhibits C and N cycling in soil, increasing recalcitrant pyrogenic organic matter storage while reducing N availability, Global Change Biol., 6, 2321–2333, doi:10.1111/gcb.12832, 2015.
Soong, J. L., Reuss, D., Pinney, C., Boyack, T., Haddix, M. L., Stewart, C. E., and Cotrufo, M. F.: Design and Operation of a Continuous 13C and 15N Labeling Chamber for Uniform or Differential, Metabolic and Structural, Plant Isotope Labeling, J. Vis. Experiments: JoVE, 83, 51117, doi:10.3791/51117, 2014.
Soong, J. L., Vandegehuchte, M. L., Horton, A. J., Nielsen, U. N., Denef, K., Shaw, E. A., Milano de Tomasel, C., Parton, W., Wall, D. H., and Cotrufo, M. F.: Soil microarthropods support ecosystem productivity and soil C accrual: evidence from a litter decomposition study in the tallgrass prairie, Soil Biol. Biochemistry, in review, 2015.
Staddon, P. L.: Carbon isotopes in functional soil ecology, Trends Ecol. Evol., 19, 148–154, doi:10.1016/j.tree.2003.12.003, 2004.
Swift, M. J., Heal, O. W., and Anderson, J. M.: Decomposition in Terrestrial Ecosystems, Studies in Ecology, edited by: Anderson, D. J., Greig-Smith, P., and Pitelka, F. A., University of California Press, Berkeley, 1979.
Todd, T. C.: Effects of management practices on nematode community structure in tallgrass prairie, Appl. Soil Ecol., 3, 235–246, 1996.
van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van de Voorde, T. F. J., Wardle, D. A., and Hutchings, M.: Plant-soil feedbacks: the past, the present and future challenges, J. Ecol., 101, 265–276, doi:10.1111/1365-2745.12054, 2013.
Verhoef, H. A. and Brussaard, L.: Decomposition and nitrogen mineralization in natural and agroecosystems – the contribution of soil animals, Biogeochemistry, 11, 175–211, 1990.
Wall, D. H.: Sustaining Biodiversity and Ecosystem Services in Soils and Sediments, Island Press, Washington, 2004.
Wall, D. H., Bradford, M. A., St. John, M. G., Trofymow, J. A., Behan-Pelletier, V., Bignell, D. E., Dangerfield, J. M., Parton, W. J., Rusek, J., Voigt, W., Wolters, V., Gardel, H. Z., Ayuke, F. O., Bashford, R., Beljakova, O. I., Bohlen, P. J., Brauman, A., Flemming, S., Henschel, J. R., Johnson, D. L., Jones, T. H., Kovarova, M., Kranabetter, J. M., Kutny, L. E. S., Lin, K.-C., Maryati, M., Masse, D., Pokarzhevskii, A., Rahman, H., Sabar, M. G., Salamon, J.-A., Swift, M. J., Varela, A., Vasconcelos, H. L., White, D. O. N., and Zou, X.: Global decomposi-

SOILD
2, 923–953, 2015

tion experiment shows soil animal impacts on decomposition are climate-dependent, Global Change Biol., 14, 2661–2677, doi:10.1111/j.1365-2486.2008.01672.x, 2008.
Wall, D. H., Bardgett, R. D., and Kelly, E. F.: Biodiversity in the dark, Nature Geosci., 3, 296–298, doi:10.1111/j.1365-2699.2010.02281.x, 2010.
Wardle, D. A., Yeates, G. W., Nicholson, K. S., Bonner, K. I., and Watson, R. N.: Response of soil microbial biomass dynamics, activity and plant litter decomposition to agricultural intensification over a seven-year period, Soil Biol. Biochemistry, 31, 1707–1720, 1999.
Whitford, W. G., Pen-Mouratov, S., and Steinberger, Y.: The effects of prescribed fire on soil nematodes in an arid juniper savanna, Open J. Ecol., 04, 66–75, doi:10.4236/oje.2014.42009, 2014.
Wickings, K., Grandy, A. S., Reed, S. C., and Cleveland, C. C.: The origin of litter chemical complexity during decomposition, Ecol. Lett., 15, 1180–1188, doi:10.1111/j.1461-0248.2012.01837.x, 2012.
Xin, W. D., Yin, X. Q., and Song, B.: Contribution of soil fauna to litter decomposition in Songnen sandy lands in northeastern China, J. Arid Environ., 77, 90–95, doi:10.1016/j.jaridenv.2011.10.001, 2012.
Yeates, G. W., Bongers, T., de Goede, R. G. M., Freckman, D. W., and Georgieva, S. S.: Feeding habits in soil nematode families and genera – an outline for soil ecologists, J. Nematology, 25, 315–331, 1993.
Yeates, G. W., Bardgett, R. D., Cook, R., Hobbs, P. J., Bowling, P. J., and Potter, J. F.: Faunal and microbial diversity in three Welsh grassland soils under conventional and organic management regimes, J. Appl. Ecol., 34, 453–470, 1997.
Zelles, L.: Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review, Biol. Fert. Soils, 29, 111–129, 1999.

SOILD
2, 923–953, 2015

Table 1. Overall mean relative contribution (f) of root litter C to PLFA-C and nematode-C with (standard errors), $n = 18$. The relative contribution of root litter C was calculated only for the PLFA biomarkers and nematode trophic groups from root litter addition samples that were significantly different in $d^{13}C$ from the control. Bold font indicates a significantly higher f-value for a burn treatment.

Functional group	PLFA Biomarker	Freq. burn mean f-root litter × 100	Infreq. burn mean f-root litter ×100
Fungi SAP	cis-C18:1n9	0.4 (0.14)	0.3 (0.05)
	cis-C18:2n9,12	**1.6 (0.37)**	1.1 (0.15)
Gram−	cis-C16:1n9	0.6 (0.11)	0.3 (0.07)
	C17:0cy	0.6 (0.09)	0.4 (0.10)
	C18:1n11	**0.7 (0.10)**	0.4 (0.06)
	C19:0cy	0.1 (0.06)	0.1 (0.03)
Gram+	aC15:0	0.4 (0.08)	0.3 (0.05)
	aC17:0	**0.3 (0.06)**	0.1 (0.03)
	iC15:0	0.3 (0.12)	0.2 (0.05)
	iC16:0	**0.4 (0.08)**	0.2 (0.05)
Actinobacteria	10Me-C16:0	0.3 (0.08)	0.1 (0.04)
	10Me-C17:0	0.2 (0.07)	0.1 (0.03)
	10Me-C18:0	0.3 (0.08)	0.3 (0.06)
	Trophic group		
Nematodes	Bacterivore	8.2 (1.4)	6.4 (1.4)
	Fungivore	**7.5 (1.8)**	ns
	Omnivore	0.5 (0.2)	**1.7 (0.7)**
	Predator	0.5 (0.3)	0.4 (0.2)

SOILD
2, 923–953, 2015

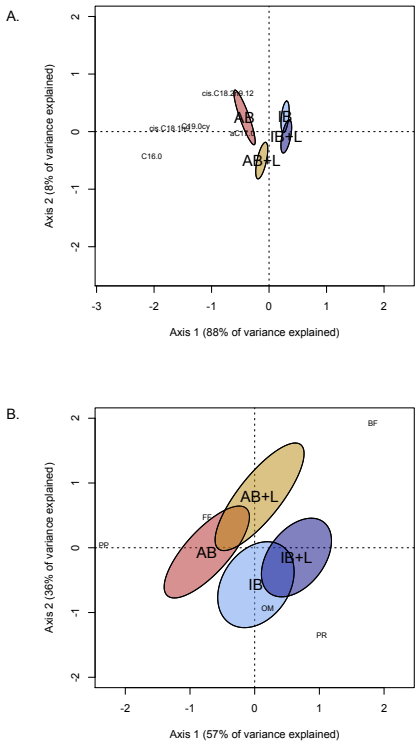

Figure 1. Community structure plots depicted from results of the distance-based redundancy analysis performed on relative abundance of PLFA biomarkers **(a)** and on nematode trophic groups **(b)**; Groups with top species scores are plotted along with ellipsoids. Ellipsoids represent 95 % confidence intervals. The first and second capscales are depicted by Axis 1 and Axis 2, respectively. Percentage of variance explained by each capscale is indicated. Treatments are indicated by: AB = annually burned, IB = infrequently burned, and +L = litter addition. For nematode trophic groups: BF = Bacterivore, FF = Fungivore, OM = Omnivore, PP = Plant Parasite, and PR = Predator.

SOILD
2, 923–953, 2015

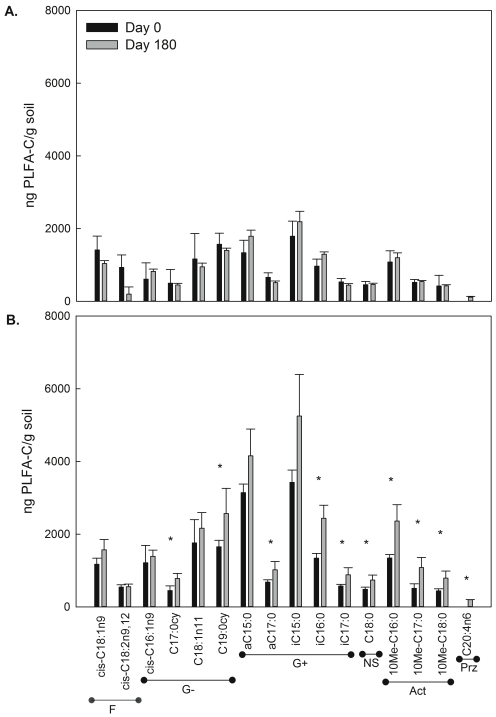

Figure 2. Abundances of PLFA biomarkers for the annual burn **(a)** and infrequent burn **(b)** treatments with litter addition for the day 0 and final 180 day harvest. Data are averages ($n = 3$) with standard error bars. Asterisks (*) indicate significant differences in abundance ($P < 0.05$) between day 0 and 180 for a particular biomarker. For PLFA groups: F = fungi, G+ = gram-positive bacteria, G− = gram-negative bacteria, NS = non-specific bacteria, Act = Actinobacteria, Prz = protozoa.

SOILD
2, 923–953, 2015

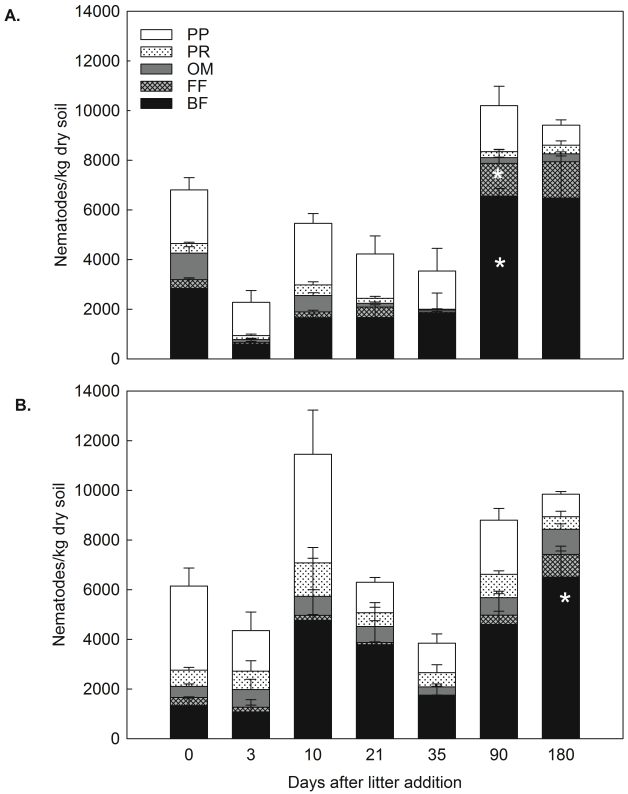

Figure 3. Change in nematode trophic group abundance (#Nematodes/kg dry soil) over time for both **(a)** annual burn and **(b)** infrequent burn treatments with litter addition. Day 0 indicates the initial densities of nematode trophic groups before the greenhouse incubation with root litter addition. White asterisks (*) indicate significantly higher abundance of a particular trophic group between burn treatments (n = 3). For nematode trophic groups: BF = Bacterivore, FF = Fungivore OM = Omnivore, PP = Plant Parasite, and PR = Predator.

SOILD
2, 923–953, 2015

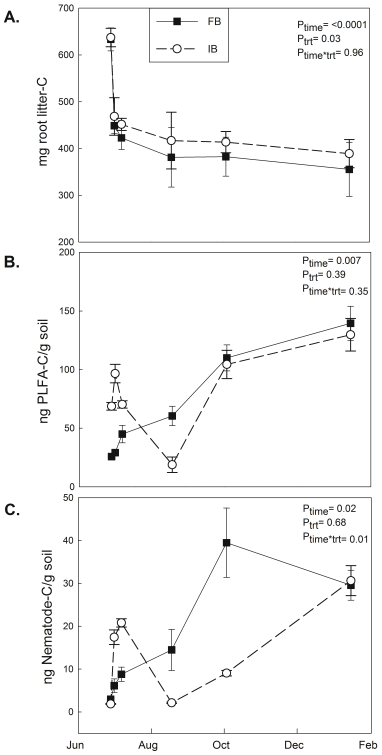

Figure 4. Root litter C dynamics during incubation for the annual burn and infrequent burn treatments. Data are averages with standard error bars. The root litter carbon **(a)**, root litter derived carbon incorporated in microbial phospholipid fatty acids (PLFA) **(b)**, and root litter derived carbon **(c)** incorporated in nematodes are reported.

SOILD
2, 923–953, 2015

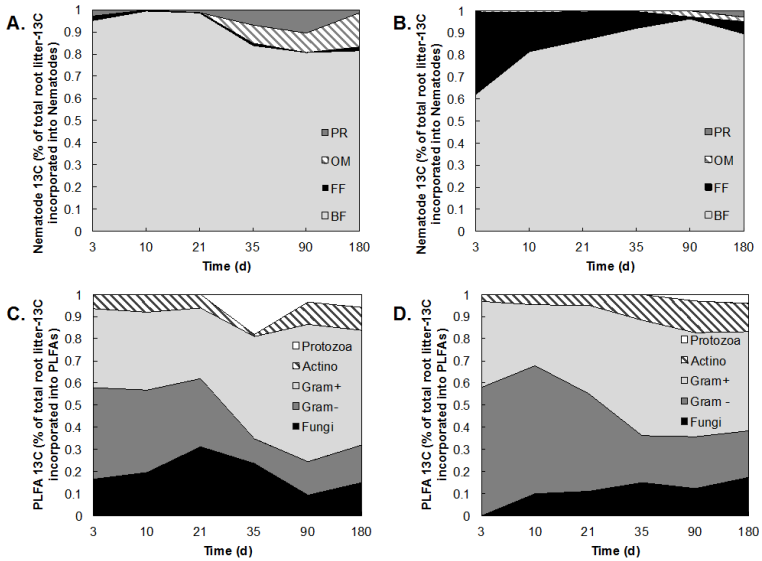

Figure 5. Root litter C incorporation into microbial PLFAs and nematode trophic groups. Panels **(a)** and **(c)** are infrequent burn treatment and **(b)** and **(d)** are annual burn treatment. Panels **(a)** and **(b)** show the percentage of total litter-derived C (^{13}C) incorporated into the total nematode signature quantified at each time point, and panels **(c)** and **(d)** show the percentage of total litter-derived C (^{13}C) incorporated into the total PLFA signature at each time point.

SOILD
2, 923–953, 2015