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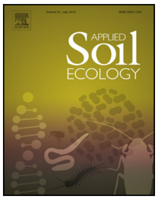

Forest wildfire and grassland prescribed fire effects on soil biogeochemical processes and microbial communities: Two case studies in the semi-arid Southwest

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ABSTRACT

Fire is a natural disturbance that shapes many ecosystems. In semi-arid regions, where high temperatures and low soil moisture limit nutrient cycling and plant growth, fire is critical to supply nutrients and drive vegetation composition. We examined soil chemical and biological properties to assess the short-term impacts of wildfire and prescribed fires on soil functioning in semi-arid regions of Texas. Better understanding of soil organic matter transformation and nutrient cycling processes will aid land managers in predicting ecosystem recovery response post-fire. Soil samples were collected following both prescribed grassland fires in June of 2009 in Lubbock, TX and the April 2012 Livermore Ranch Complex Fire located in the Davis Mountains, TX. Prescribed fire samples (0–2.5 cm) were collected within six h prior to burning and again at 0.5, 24, 48, and 168 h post-fire to experimentally examine short-term influences of fire and fire frequency (1× vs. 2×) on soil carbon dynamics, inorganic nitrogen, and microbial community composition. Wildfire samples (0–5 cm) were collected two and six months following the wildfire. We evaluated the effects of three burn severity levels and sampled under three tree species (*Juniperus deppeana*,*Pinus cembroides*, and *Quercus grisea*). Within 0.5 h of the prescribed fire, CO_2 flux, NH_4^+-N concentration and total microbial biomass (as estimated by total fatty acid methyl esters) increased. A shift in the microbial community from a predominance of fungi to Gram positive bacteria occurred immediately following the fire. Chemical shifts were short lived (decreased within 24 h), but the biotic shift to a dominance of Gram negative bacteria and actinomycetes was measured in samples collected after 168 h. Soil pH and NH_4^+-N concentration increased at two and six months following the wildfire. In contrast, soil organic matter content decreased at two months post wildfire which, in combination of abiotic conditions such as low moisture content (<3.3%), resulted in reduced soil microbial biomass and enzyme activity. Increased soil moisture six months post fire created more favorable conditions for nitrification resulting in increased NO_3^--N concentration (0.8 to 36.1 mg NO_3^--N kg^{-1} soil), particularly following high severity fire. Prescribed fire did not have lasting impacts on soil nutrients, but both prescribed and wildfire resulted in increased NH_4^+-N, shifts in microbial community structure and decreased in microbial biomass. While the increase in nitrogen maybe be beneficial to the plant growth and revegetation, the loss of microbial biomass may have far reaching implications to the overall sustainability of the soils in these systems.

Abbreviations: SOC, soil organic carbon; SOM, soil organic matter; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen.

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1. Introduction

Fire has been a recurrent natural disturbance that shapes terrestrial ecosystem structure (Omi, 2005) and functioning (Johnson et al., 1998; Sampson et al., 1995). Fire patterns, frequency, and behavior are closely related to the interactions between topography, soils, environmental conditions and vegetation composition (Hood and Miller, 2007). A typical fire creates a mosaic pattern leaving areas unburned or burned across a range from low to high severity. In the USA, fire has been used deliberately in grassland ecosystems since the inhabitation of native people on the Great Plains. In these ecosystems, fire aids in the removal of dead litter, stimulates the growth of prairie grasses and suppresses woody species. Fire also is a valuable component of forest regeneration and management. Regardless of the ecosystem, fires typically result in impacts to vegetation structure, composition, dynamics, and biodiversity. The severity of the effect and the rate of recovery depend upon interactions among fire regime (e.g., fire frequency and intensity) and organismal fire response traits (Janzen and Tobin-Janzen, 2008; Keeley 2008).

The combustion of organic material can reduce soil organic matter (SOM) and leave portions of the soil surface bare or covered in ash (Chandler et al., 1983; DeBano et al., 1998). Exposed ground and gaps in the forest canopy alter soil radiative forcing (shifts in both temperature and light), evapotranspiration, and the preferential regrowth of vegetation adapted to respond quickly to these conditions (Cerdá and Robichaud, 2009; Chandler et al., 1983; DeBano et al., 1998; Glenn and Finley, 2009). Incomplete combustion of soil organic matter near the surface and ash inputs influences the soil chemistry by increasing soil pH (Pyne, 2001; Raison, 1979; Viro, 1974) and providing a source of inorganic nutrients (Rau et al., 2008; Rodriguez et al., 2009; Schafer and Mack, 2010) that feed the microbial organisms and stimulates plant regeneration. Soil microorganisms are driving agents which facilitate this regeneration and ecosystem recovery following fire via critical ecosystem processes such as SOM decomposition and nutrient mineralization through the activities of extracellular enzymes. Due to the natural variability within an ecosystem, studies from different fire-prone systems report varying findings of fire effects on different soil properties and also on the time scale required for their restoration (Dangi et al., 2010; Doerr and Cerda, 2005; O'Bryan et al., 2009). In general, soil microbial populations tend to be reduced immediately (90 days) following fire (Andersson et al., 2004; D'Ascoli et al., 2005; Grady and Hart, 2006; Yeager et al., 2005) but quickly recover (Neary et al., 1999). Consequently, combustion, cell death, and denaturation due to increased soil temperatures can also contribute to decreased soil enzymatic activity (Boerner et al., 2005; Fortúrbel et al., 2012; Gutknecht et al., 2010). However, the majority of research has focused on long-term impacts of fires on soil, however it was our intent to examine the immediate, short-term impacts the potential recovery rate in semi-arid systems.

The overall objective of this study was to determine the short-term impacts of fire on soil microbial and biogeochemical processes in semi-arid soils. Soil samples were collected from two independent case studies: (1) a prescribed fire in a native rangeland in Lubbock, TX and (2) the Livermore Ranch Complex Fire in Jeff Davis, TX. These studies allow us to investigate (1) short term fire effects in a relatively homogenous environment and (2) longer term effects across a wider range of soil habitats and microbial communities.

Specific objectives for the prescribed grassland fire were to evaluate short-term (within 7 days) effects and fire frequency (single year vs. two-year summer fires) on soil responses following single-year fires (June 2009) and following two summer fires (June 2008 and 2009) at 0.5, 24, 48, and 168 h after the June 2009 fires. Specific objectives for the forest wildfire were to evaluate the impact of different fire severities on soil chemical and biological properties across a range of fire severities and across three replicated soil environments under three tree species at two and six months post fire. Three different tree species found in all fire regimes and therefore allowing us to conduct appropriate comparisons were targeted in order to examine their potential to influence on microbial community structures stemming from differences in mycorrhizal associations, rooting depths, and effects on soil moisture and pH. In general, we hypothesized that fire would: (1) increase soil moisture, and inorganic N through the deposition of a nutrient-rich ash layer; and (2) reduce SOM, soil microbial biomass, and soil enzyme activity. More specifically, we expected the higher frequency prescribed fires to have fewer impacts on soil properties than the single prescribed fires because of lower fuel loads and because these systems would have adapted to frequent disturbances caused by fire. In the wildfire study, we hypothesized that soil response would be most pronounced in the high burn intensity sites and would differ under the different tree species. These differences may stem from differences in local fire intensities, pre-fire and post-fire soil moisture (evergreen vs. deciduous), rooting depths, and the diversity of microbial communities in relation to different tree species.

2. Materials and methods

2.1. Prescribed fire sites and sample collection

Prescribed fire sites were located on the Natural Resource Management (NRM) Erskine Native Rangeland Research Station, in northwest Lubbock, Texas (33°36′17.52″N, 101°54′07.55″W) at 992 m elevation. The native range site is on approximately 65 hectares and has never been plowed but has been grazed historically (last grazed by cattle in 2002). Dominant soils are Acuff (Fine-loamy, mixed, superactive, thermic Aridic Paleustolls) and Amarillo (Fine-loamy, mixed, superactive, thermic Aridic Paleustalfs). Mean annual precipitation was 475 mm with peak precipitation occurring between May and September. Average daily temperatures ranged from 7.9 °C to 22.9 °C with the coldest temperatures occurring in January (−4.4 °C) and warmest temperatures in July (33.3 °C). Vegetation is typical of short-grass plains common to the Southern Great Plains and include mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*), blue grama (*Bouteloua gracilis* [H.B.K.] Griffiths), buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.), purple threeawn (*Aristida purpurea*), silver bluestem (*Bothriochloa saccharoides* (Sw.) Rydb.), Arizona cottontop (*Digitaria californica* (Benth.) Henr.), sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), and various forbs (Sorenson et al., 2012).

As part of a larger study designed to examine the effects of prescribed fire frequency of a summer burn on the invasive species purple threeawn, a total of 42 plots (4 m × 4 m) were randomly positioned on level terrain within the NRM research station (Sorenson, 2010). Plots were placed in areas of similar soil type, vegetation composition, and vegetative cover. Using a completely randomized design, plots were assigned to one of seven treatments with six reps assigned to each treatment. For the purpose of our study, we examined the short-term effects of prescribed fire in three treatments: control (never burned), June 2009 (burned 1×; S'09) and June 2008 and 2009 (burned 2×, S'08S'09). Samples were collected following the June 2009 fires in four out of the six replicates for each prescribed fire treatment. Eight soil samples to a depth of 2.5 cm were collected within each plot using a hand trowel within 6 h prior to burning (time 0) and then at 0.5, 24, 48, and 168 h after the fire. Because measured soil chemical properties were not expected to change over the short (7 day) sampling period soil samples were collected at all sampling times for the S'09 and S'08S'09 treatment plots but soil samples from the control plots were collected only at time 0. In contrast, small changes in soil temperature can have a more direct effect on soil CO_2 fluxes, thus measurements were done for all treatments. Soils were stored on ice during field collection and immediately transported to the laboratory. Samples were passed through a 4-mm sieve and divided into a subsample stored at 4 °C for subsequent microbial community profiling and into an air-dried subsample for soil chemical analyses (soil total C (TC), total N (TN), NO_3^--N, NH_4^+-N, and pH) (Table 2).

2.2. Wildfire site descriptions and sample collection

In April 2012, two lightning strikes ignited the Livermore Ranch Complex Fire which burned through parts of the Davis Mountains affecting a total area of 5530 ha over approximately 12 days. The Davis Mountains host a nature preserve (13,360 ha) and are located in Jeff Davis County, Texas (30°38′N, 104°10′W). Based on Web Soil Survey and GPS coordinates, soils within the sampled area included Loghouse gravelly loams (Loamy-skeletal, mixed, superactive, mesic Typic Halpustalfs) on slopes of 5–16% and Puerta gravelly silt loams (Clayey-skeletal, smectitic, mesic Alfic Lithic Argiustolls) on slopes of 20–45%. The climate for the region is classified as semi-arid with a mean annual precipitation of 457 mm. Average daily temperatures ranged from 7.8 °C to 25.2 °C with the coldest temperatures in January (0 °C) and warmest temperatures in July (32.6 °C). The ecosystem is characterized as a unique 'Sky Island' woodland and oak savanna with dominate tree species in the area consisting of pinyon pine (*Pinus cembroides*), alligator juniper (*Juniperus deppeana*), gray oak (*Quercus grisea*).

Soil samples were collected (0–5 cm) using a metal hand trowel in June and October 2012 (approximately two and six months post fire, respectively). Three local soil environments were targeted by selecting soil from beneath three different tree species: gray oak, alligator juniper, and pinyon pine. These tree species/environments were replicated over three different fire severities estimated post-burn: unburned, low severity, and high severity (Supplementary Fig. 1). Unburned areas were defined as areas located within the wildfire boundaries that exhibited no signs of charring of litter or vegetation. Low severity areas were those in which litter or grass cover was mostly consumed, but trees remained alive and were not completely defoliated. High severity areas were defined as those in which all ground cover had been consumed (i.e. only a layer of grey/white ash remained) and tree trunks and branches were severely charred and defoliated. Within each burn severity category, 5–9 trees (i.e., replicates) were identified for each of the three tree species (Table 1) while attempting to stratify across the full elevation range of the fire, 1846–2360 m. Eight mineral soil samples were collected with a 1-m radius of each target tree and global positioning system (GPS) data were recorded (latitude, longitude, and elevation). When present, visible ash and litter layer were moved aside prior to sampling. The eight samples were gently mixed together to retrieve one composited sample per tree species and burn severity. Samples were stored on ice in the field and for transport. A total of 57 samples were collected in June 2012 (5–7 replications per species by fire severity). In October 2012, 9 replicates per species by fire severity were sampled with a total of 81 soil samples. Unfortunately, two samples were lost during transport and could not be analyzed. All soil samples were passed through a 2 mm sieve, visible gravel and plant material was removed, and each sample was divided for storage at 4 °C for microbial biomass C and N (MBC and MBN) or air dried for soil chemical (pH, SOM, and inorganic N) and biochemical (three enzyme assays) analyses (Table 2).

Table 1
Number of samples collected for each combination of tree species, *Juniperus deppeana* (*J. deppeana*), *Pinus cembroides* (*P. cembroides*), and *Quercus grisea* (*Q. grisea*), and burn severity collected two and six months after the Livermore Ranch Complex Fire.

Tree species	2 months			6 months		
	Burn severity					
	Unburned	Low	High	Unburned	Low	High
J. deppeana	7	7	7	9	9	9
P. cembroides	7	7	5	9	8	9
Q. grisea	5	7	5	9	9	8

2.3. Prescribed fire soil analyses

2.3.1. Soil chemical analyses

Total N and TC were measured using dry combustion analysis via a TruSpec CN analyzer (LECO®, St. Joseph, Michigan, USA). Soil pH was determined based on a 1:1 soil:water ratio. Inorganic N (NO_3^--N and NH_4^+-N) were measured using a 2*M*KCl extraction (1:10 soil to solution ratio) that was filtered using Whatman No. 42 filter paper and analyzed on a Lachat Flow Injection Analyzer (HACH®, Loveland, Colorado, USA). Volumetric soil moisture and temperature were measured during soil CO_2 flux measurements using an integrated Theta Probe (Dynamax; Houston, TX) and a stainless soil temperature probe, respectively (see details on CO_2 flux measurements below).

2.3.2. Soil biological analyses

Soil microbial community structure for the prescribed fire soil was evaluated using ester-linked fatty acid methyl ester (EL-FAMEs) profiling as described by Schutter and Dick (2000). Briefly, ester-linked fatty acids were extracted from 3 g of freeze-dried soil sample using a mild alkaline methanolysis. Samples containing isolated FAMEs were evaporated under N_2 using a sample concentrator (DB-3, Dri Block®, Techne, UK) at 35 °C for about 20 min. Extracted FAMEs were re-dissolved with 200 μL of hexane—methyl *tert*-butyl ether (MTBE) and 30 μL of an internal standard (0.01 M methylnonadecanoate in 1:1 hexane—MTBE). Samples were transferred to a 250 μL glass insert in a GC vial and analyzed on a Agilent 6890 N gas chromatograph equipped with a flame ionization detector and a fused silica capillary column (25 m × 0.32 mm × 0.25 μm) using ultra high purity hydrogen as the carrier gas. The temperature program was ramped from 170 to 250 °C at 5 °C min^{-1} followed by a ramp to 300 °C for 2 min to clear the column. The FAMEs were identified, and their relative peak areas (percentage) were determined using TSBA6 aerobe program provided by MIDI (Microbial ID, Inc., Newark, DE). The FAMEs are described by the number of C atoms, followed by a colon, the number of double bonds and then by the position of the first

Table 2
Soil analyses conducted for prescribed and wildfire case studies conducted in semiarid west Texas.

Analysis	Prescribed fire	Wildfire
Soil organic matter		X
Total N and C	X	
Inorganic N (NO_3^--N and NH_4^+-N)	X	X
pH	X	X
Soil temperature	X	
Soil moisture	X	X
CO_2 flux	X	
EL-FAMEs	X	
Microbial biomass C and N		X
β-glucosidase		X
L-asparaginase		X
N-acetyl-β-D-glucosaminadase		X

double bond from the methyl (ω) end of the molecule. Additional notations were used for Methyl (Me), *cis* (*c*) and *trans* (*t*) isomers, and iso (*i*) and anteiso (*a*) branched FAMEs. Selected FAMEs were used a microbial biomarkers using previous research (Zelles, 1999). Identified bacterial groups included Gram-positive (GM+) bacteria (*i*15:0, *a*15:0, *i*17:0, and *a*17:0), Gram-negative (GM-) bacteria (cy7:0, cy19:0), and actinomycetes (10Me 16:0). Fungal groups included saprophytic fungi (18:1ω9c, 18:2ω6c) and arbuscular mycorrhizal fungi (AMF) (16:1ω5c). Using the 19:0 internal standard, absolute amounts of FAMEs (nmol g^{-1}) were calculated (Zelles, 1996) and used to calculate relative abundance (mol%) for each microbial group. Total bacteria was calculated based on GM+, GM−, and actinomycete biomarkers (listed above); while total fungi was calculated using the saprophytic and AMF fungal biomarkers (listed above). The fungal/bacteria ratio was calculated by dividing the total fungi by the total bacteria.

For the prescribed fire treatments, soil respiration was determined in situ from soil CO_2 flux measurements using a Li-Cor LI-8100 and 20 cm survey chamber (LI-COR®, Lincoln, Nebraska, USA). Two PVC collars (11 cm tall by 20 cm diameter) were installed a minimum of 24 h prior to the June 2009 prescribed burns in each plot and remained throughout the 168 h study to minimize soil disturbance. Collar replacement occurred only once when damage was extensive enough to interfere with CO_2 flux measurements. Soil temperature and volumetric soil moisture were simultaneously measured at the time of flux measurement using a soil temperature probe and Theta Probe (Dynamax; Houston, TX) interfaced with the LI-COR. Baseline soil CO_2 measurements in control and treated plots were collected 6 h prior to the prescribed fire event. Following the fire, CO_2 flux was measured at 0.5, 24, 48, and 168 h post-fire at approximately the same time of each day (i.e., early afternoon).

2.4. Wildfire soil analyses

2.4.1. Soil chemical analyses

For the wildfire samples, SOM was determined using the dry combustion analysis by first drying samples at 60 °C to remove any moisture before being placed in a muffle furnace at 450 °C for 4 h. Organic matter was calculated on a percent loss-on-ignition basis. Inorganic N (NO_3^--N and NH_4^+-N) was analyzed using the methods described in section 2.3.1. Soil pH was determined based on a 1:2.5 soil:water ratio. Gravimetric water content was measured in wildfire samples by drying subsamples at 60 °C for 48 h.

2.4.2. Soil biological analyses

Soil microbial properties assessed for the wildfire samples included microbial biomass carbon (MBC) and nitrogen (MBN) and the activity of three enzymes involved in C and N cycling. Soil MBC and MBN were determined using the chloroform fumigation extraction method (Brooks et al., 1985; Vance et al., 1987). Briefly, three replicates of 15 g of field moist (oven-dried equivalent) soil was placed into three 125 mL bottles. Two lab replicates were fumigated for 24 h by placing 100 mL of ethanol-free chloroform in a vacuum desiccator and applying vacuum until the chloroform boiled. The third replicate was not fumigated and served as the control. Following fumigation, 75 mL of 0.5 M potassium sulfate was added to all bottles, shaken for one hour, centrifuged for one minute at 1800 rpm, and passed through a Whatman No. 42 filter. The filtrate was analyzed via a Shimadzu Model TOC/VCPH-TN analyzer (Shimadzu, Japan). Concentrations from non-fumigated samples were subtracted from fumigated samples with a K_{EC} of 0.45 for C (Wu et al., 1990) and a K_{EN} of 0.54 for N (Jenkinson, 1988) applied to calculate MBC and MBN, respectively.

The three enzyme assays involved in C and N cycling were conducted to determine potential activities for β-glucosidase (conversion of cellulose to glucose) and L-asparaginase (conversion of asparagine to NH_4^+) as described by Tabatabai (1994) and *N*-acetyl-β-D-glucosaminadase (conversion of glucosamine to amino sugar) as described by Parham and Deng (2000). Based on the adaptations as described by Bandick and Dick (1999), no toluene was used for any of the assays and soil quantities were decreased from 1 g to 0.25 g for the β-glucosidase and *N*-acetyl-β-D-glucosaminadase assays to minimize the extraction of dissolved organics (common in forested ecosystems and fire-affected soils) which interfered with the development of the yellow color produced by *p*-nitrophenol. Each sample was duplicated with one control in which the substrate was added following incubation. The NH_4^+-N released from the L-asparaginase assay was measured using steam distillation on a FOSS Kjeltec 2200 distillation apparatus (FOSS Analytical AB, Sweden).

2.5. Statistical analyses

2.5.1. Prescribed fire

The experimental design included repeated measures (time of sample collection) for a completely randomized design with fire frequency (1× vs. 2×) as the main effect. Mean fuel load in the 1× burn plots was 6720 kg/ha (59,994 lbs/ac). We did not sample fuel loads for 2× burn plots although we assume it is less because plots only had one year to grow fuels since the last prescribed fire. All statistical analysis was done using R (R Core Team, 2014) with significances determined using an $\alpha = 0.05$ unless otherwise stated. Samples collected at time zero were compared to determine if there were any pre-existing differences between each treatment. Because soil samples from control plots were not collected following fires, determination of differences over time (repeated measures) was done between samples collected from S'09 and S'08S'09 plots only. However, changes in CO_2 flux rates, soil temperature, and moisture were measured in all three treatments such that comparison across all treatments was possible. Soil microbial community composition was evaluated using distance-based (Bray distance) redundancy analysis of all FAMEs analyzed via the *capscale* function from the *vegan* package (Oksanen et al., 2015). Ordination was used to visualize this analysis with greater distance between two points indicating greater dissimilarities. Vectors were added using the *envfit* function such that those selected had the maximum correlation with environmental variables.

2.5.2. Livermore Ranch Complex Wildfire

For wildfire samples, the experimental design was completely randomized as a 3 × 3 factorial. Samples collected two and six months post-fire were analyzed separately because not all trees samples two months post-fire were re-sampled at six months. Analysis of homoscedasticity and variance (ANOVA) were performed using R (R Core Team, 2014) with burn severity (unburned, low, and high) and tree species (pine, juniper, oak) as the main effects. When ANOVA's indicated that burn severity, tree species, or the interaction between severity and species was significant (*p-value* less than 0.05 unless otherwise stated), treatment comparisons were conducted using mean separation.

3. Results & discussion

3.1. Prescribed fire minimally affected soil chemical properties but altered microbial community composition

Soil pH (average = 7.5 ± 0.05), TC (28 ± 0.8 g kg^{-1}) and TN (2.2 ± 0.06 g kg^{-1}) were not affect by prescribed fire frequency at any sampling time following the June 2009 prescribed fires. Soil respiration (CO_2 flux), a measurement of soil microbial activity, was only different in the 1x summer fires at 0.5 h (Fig. 1), suggesting an immediate increase in microbial activity in response to influx of ash material (Bååth et al., 1995). All flux measurements had decreased to pre-fire levels and were not significantly different from each other by 24 h post fire (average = 144 mg CO_2-C m^{-2} h^{-1}). Soil moisture was low (average of 8%), and neither soil moisture nor temperature were significantly affected by the prescribed fires. Although soil temperatures were not measured during the prescribed fire, peak canopy temperatures (133 °C in 2× burned plots and 269 °C in 1× burned plots), suggested low to moderate severity fires. While these temperatures can result in hydrophobic tendencies, the rate at which these plots burned (<2 min) would not have exposed the soil surface to sufficient temperature extremes. Likewise, no response in soil chemical properties were reported following long-term fire used for oat stubble removal in eastern Kansas (Biederbeck et al., 1980) and in a native grass dominated site in southeast Arizona (Biggs et al., 2005). As soil temperature and moisture were not influenced by fire frequency, observed changes are likely the response of deposition of material and shifts in the vegetation community.

Soil inorganic N often increases typically follow fire events (Biederbeck et al., 1980; Hulbert, 1988; Ojima et al., 1994) but some studies report reduced inorganic N concentrations (Biggs et al., 2005; Blair, 1994). Following the prescribed fire described here, soil NH_4^+-N increased 241% relative pre-burn samples immediately following the fire before decreasing by 33% within 24 h post-fire (Fig. 2). Concentrations remained at levels 118% greater than those measured pre-fire for up to 7 days. More NH_4^+-N was released in the 1x fires (June '09-270% increase) compared to the 2x plots burned in both summers (June '08 and '09-216% increase), however levels in the burned plots had decreased to similar concentrations by 168 h post-fire. Soil NO_3^--N (average 5.2 mg kg^{-1}) was not affected by the fires suggesting that nitrification was not a significant process within our sampling timeframe, which is further supported by the low moisture conditions. Ojima et al. (1994) attributed this decrease of NO_3^--N to inputs of lower quality plant residues and increases in N immobilization. An examination of annually burned tall grass prairie in eastern Kansas found that ammonium-N (NH_4^+-N) contributed the most to the inorganic N pool in annually burned sites; while nitrate-N (NO_3^--N) was highest in unburned plots (Turner et al., 1997). In our study, concentrations in previously burned sites, 2× plots, were not statistically different pre-fire than those measured in the control soils indicating this effect was not persistent for up to one year following a fire event.

Despite minor impacts on most soil chemical properties, the soil microbial community was sensitive to fire. By collecting samples immediately following the prescribed fire, it was possible to observe shifts in total biomass and microbial community structure not often observed in soils effected by fire. Averaged across both fire treatments, soil microbial biomass (as estimated by total FAME content) increased 41% within 0.5 h post fire (Table 3). Total FAME concentration then decreased by 22% within 48 h of the fire and decreased by 51% within 168 h, similar to long-term decreases observed in forest fire studies (Bååth et al., 1995). In general, biomarkers for bacteria were more sensitive than fungal biomass (FAME biomarkers for AMF and saprophytic fungi) within the first 48 h post fire and were the major contributors to the reduced microbial biomass. Relative to pre-fire levels, AMF and saprophytic fungal biomarkers were reduced at 168 h by 48% and 60%, respectively. These results contradict other studies that found bacteria to be more resilient to fire than fungi in the short-term (Dangi et al., 2010; Hart et al., 2005; Pietikäinen and Fritze, 1995). While shifts in microbial communities have been attributed to pH (Frostegård et al., 1993) and ash deposition, this was less evident when soils were exposed to fire (Bååth et al., 1995) and, thus, unlikely in this case where pH did not change. This decrease in the overall fungal population may reflect the shift in or loss of the plant community (Hart et al., 2005) on which these organisms depends. This loss of vegetation, which not only serves as a substrate for microbial processes but also as a host to many soil organisms, is thus a significant driver of the shifts of the microbial community.

The microbial community composition as evaluated by multivariate analysis of the relative abundance (mol%) of all FAME biomarkers was impacted significantly by time following fire and between treatments ($p < 0.0001$; Fig. 3). In general, the microbial community shifted from a greater relative abundance of fungal biomarkers prior to the fire to a community dominated by GM+

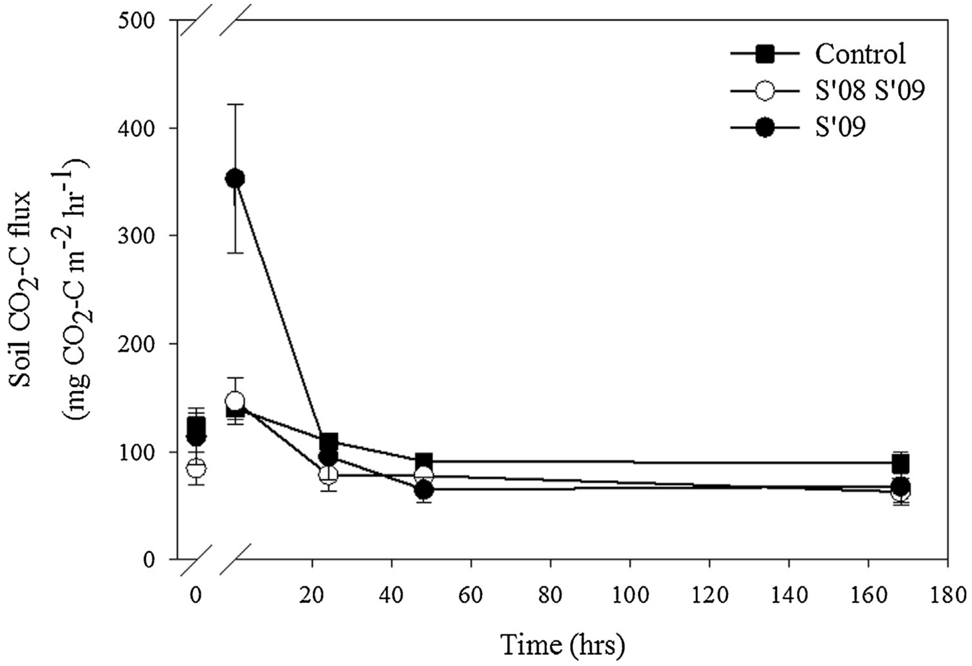

Fig. 1. Carbon dioxide (CO_2) flux measured following June 2009 prescribed fire at 0 h (h) pre- and 0.5, 24, 48, and 168 h post-fire.

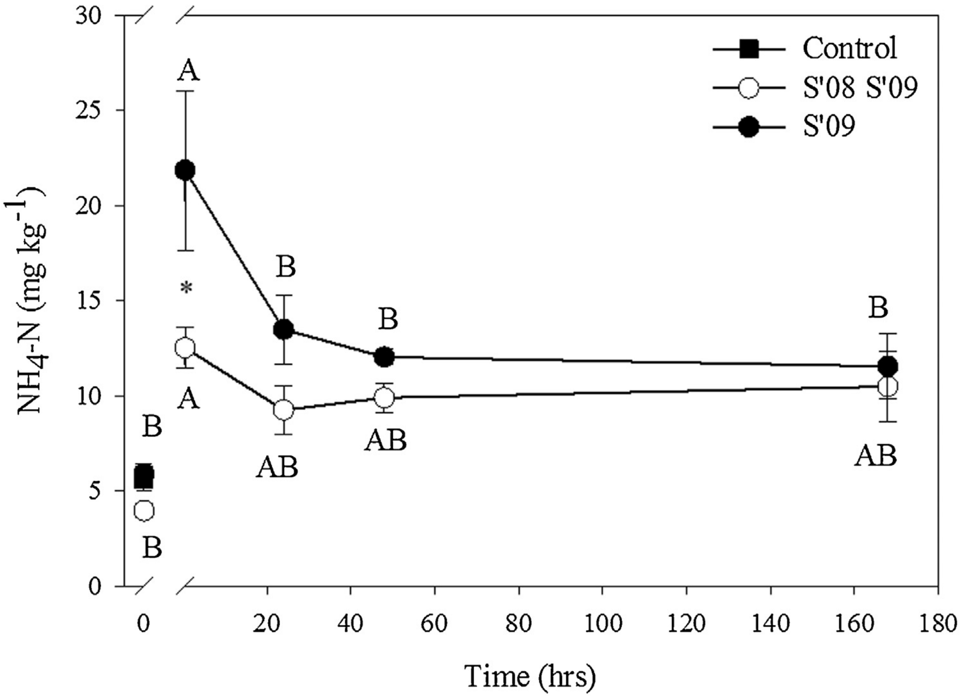

Fig. 2. Soil NH_4^+-N concentration measured following the June 2009 prescribed fire at 0 h (h) pre- and 0.5, 24, 48, and 168 h post-fire. Different upper case letters indicate significant difference ($\alpha = 0.05$) over time for each fire treatment. Significant differences between fire treatments at a given time are indicated using '*'.

bacteria between 0.5 and 48 h post fire to a community characterized by greater relative abundance of GM− bacteria (Fig. 4), actinomycetes and the 18:1ω9c biomarker (often used as a fungal biomarker) by 168 h post fire (Fig. 3a). The increased GM+ bacteria population (Fig. 4) is likely the result of increased inputs of nutrient poor surface material (primarily charred vegetation and ash). Following their boost in growth and subsequent die off, they may then become a readily decomposable source of material for the GM- bacteria population. The samples from 2× plots were more dissimilar to the pre-fire samples than the 1× plots, which experienced a single fire (Fig. 3b). Although not significant, fungal biomarkers tended to be greater in soils post-fire in 1× plots than in 2× plots which tended towards greater bacterial biomarkers. The similarity of the microbial community structure prior to the 2009 fire in samples collected from all three treatments (i.e. soils never burned vs. those burned 1 year previously) suggests that microbial communities under these lower severity fires are resistance to disturbance (Dangi et al., 2010) and may recover in shorter time periods.

3.2. Effects of wildfire on soil properties

No differences due to tree species were measured, except for one soil property, indicating that responses represent general patterns over the sampling area despite soil heterogeneity and tree species. The effects of fire on soil properties and processes begin at the soil surface with the combustion of organic matter. In general, SOM decreases following fire and losses increase with increasing fire severity (Chandler et al., 1983; Fynn et al., 2003; Gonzalez-Perez et al., 2004). Samples were not collected from the litter layer where most of organic matter losses would have been expected but instead were collected just below this layer in the mineral soil horizon. At two months, SOM was significantly lower (p-value = 0.054) in low severity burn ($30.2 \pm 5.0\,\mathrm{g\,kg^{-1}}$) than in the unburned ($45.0 \pm 4.7\,\mathrm{g\,kg^{-1}}$) but neither treatment was significantly different from high severity burn ($33.2 \pm 3.2\,\mathrm{g\,kg^{-1}}$). At six months, SOM was lowest in high severity ($24.7 \pm 1.8\,\mathrm{g\,kg^{-1}}$) than in unburned or low severity (average = $27.0 \pm 3.4\,\mathrm{g\,kg^{-1}}$). These results coupled with the observed presence of an ash layer as one of the criteria for designation as a high severity burn, suggested that organic matter was consumed above ground but temperatures did not reach high enough levels to consume organic matter in the mineral soil horizon. The unburned soils had the lowest pH, and soil pH increased with increasing burn severity at the two months post-fire sampling (Table 4). This pH response is consistent with other fire ecology research and is likely the result of chemical components with high base content accumulating in the ash layer and then percolating into the soil (Andersson et al.,

Table 3
Absolute abundance ($\mathrm{nmol\,g^{-1}}$) of fatty acid methyl ester (FAMEs) biomarkers for samples collected following prescribed fire in June 2009. Data reported as average (standard error).

Time (h)	Total FAMEs	Gram positive bacteria	Gram negative bacteria	Actinomycetes	Protozoa	Total bacteria	Arbuscular mycorrhizal fungi	Total fungi
	$\mathrm{nmol\,g^{-1}}$							
0	120.4 (10.3) B	19.1 (1.8) C	22.3 (2.7) B	8.3 (1.0) BC	0.9 (0.2) A	49.7 (5.5) B	5.8 (0.9) A	20.2 (1.2) AB
0.5	169.5 (6.9) A	31.6 (0.8) A	32.7 (1.4) A	11.4 (0.5) A	0.9 (0.2) A	75.7 (2.5) A	7.2 (0.7) A	23.8 (1.5) A
24	137.1 (5.5) B	25.0 (1.1) B	26.1 (1.1) AB	9.6 (0.5) AB	0.6 (0.1) A	60.7 (2.7) B	6.0 (0.4) A	20.4 (1.5) AB
48	128.8 (3.8) B	24.2 (0.7) B	24.5 (0.9) B	9.3 (0.5) AB	0.8 (0.1) A	58.1 (2.1) B	5.5 (0.6) A	17.8 (0.5) B
168	82.5 (8.4) C	12.0 (1.2) D	17.8 (1.8) B	6.5 (0.6) C	0.6 (0.1) A	36.3 (3.6) C	3.3 (0.5) B	12.9 (1.3) C

Different uppercase letters indicates significant differences at $\alpha = 0.05$ between time of collection.

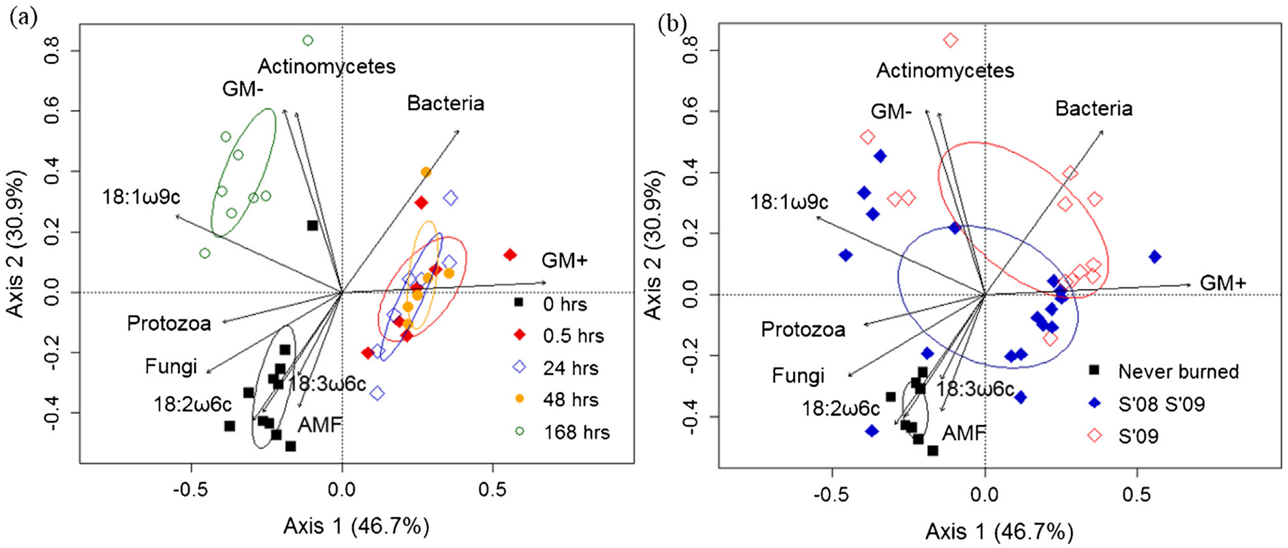

Fig. 3. Ordination plots for relative abundance (mol%) of FAME profiles in samples collected following the June 2009 prescribed fire. Ellipses indicate one standard error around the centroid for each group based on either time of sample collection following the fire event (a) or frequency of fire (b). Arrows indicate vectors that have the maximum correlation with environmental variables. (GM+: Gram positive bacteria; GM−: Gram negative bacteria; AMF: arbuscular mycorrhizal bacteria).

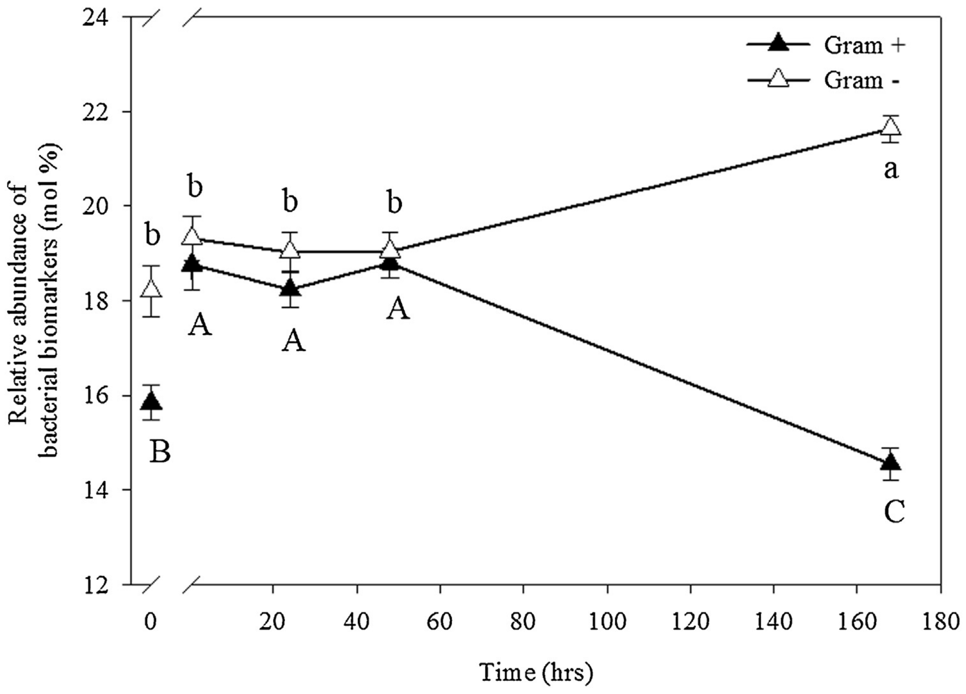

Fig. 4. Relative abundance of Gram positive (Gram +) and Gram negative (Gram −) bacterial biomarkers averaged across both treatments. Different upper case letters indicate significant difference (α = 0.05) over time for Gram positive bacteria. Different lower case letters indicate significant differences (α = 0.05) over time for Gram negative bacteria.

2004; Bååth et al., 1995; Grady & Hart, 2006; Knicker et al., 2006; Ponder et al., 2009; Úbeda et al., 2005). This is especially likely when soil moisture and precipitation are low and cations are not leached or washed away (Chandler et al., 1983), as was the case for the two months post-fire sampling. Just prior to the six months sampling, a few minor rain events occurred (32 mm as recorded by the nearby Fort Davis weather station), thus stimulating microbial processing and leaching of dissolved alkaline compounds into the mineral horizon or potential off-site transportation via erosion.

Interactions between aboveground and belowground responses to fire drive the structure and functionality of ecosystems, including soil microbial communities, and C and nutrient cycling while creating heterogeneous soil patterns. These interactions also play an important role in ecosystem restoration as responses of one ecosystem component to a disturbance like fire could influence the response of another component (Kardol and Wardle, 2010). Depending on fire intensity and frequency, fire can also lead to losses of important plant nutrients to the atmosphere as gaseous compounds (Sampson et al., 1995). Nitrogen, for example, is considered to be sensitive to fire because volatilization occurs at temperatures around 200 °C, which is much lower than the volatilization temperature of moderately sensitive nutrients like potassium and phosphorus (volatilize at 774 °C) or relatively insensitive nutrients like magnesium and calcium (volatilize at

Table 4
Average chemical and microbial properties collected under different burn severities two and six months after the Livermore Ranch Complex Fire. Standard error found in parenthesis.

	Fire severity	Gravimetric water content (%)	pH	Ammonia-N (mg NH_4^+-N kg^{-1})	Nitrate-N (mg NO_3^--N kg^{-1})	Microbial biomass C (g kg^{-1})	Microbial biomass N (g kg^{-1})	β-glucosidase (mg *p*-nitrophenol kg^{-1} h^{-1})
2 Months	Unburned	3.3 (0.5) A	6.9 (0.1) B	27.6 (10.5) B	2.9 (0.4) A	1227.3 (130.9) A	59.6 (9.8) A	545.7 (51.1) A
	Low	2.1 (0.4) B	7.1 (0.1) AB	23.1 (4.4) B	1.2 (0.2) B	1123.7 (232.4) A	53.3 (11.6) A	321.3 (38.2) B
	High	1.3 (0.1) B	7.4 (0.1) A	75.5 (7.5) A	0.8 (0.1) B	859.0 (127.8) A	47.9 (11.0) A	215.5 (31.6) C
6 Months	Unburned	25.7 (2.3) a	6.8 (0.1) b	5.8 (0.7) b	7.2 (1.3) b	1124.4 (77.2) a	132.4 (11.9) a	347.5 (30.2) a
	Low	22.0 (1.8) ab	7.5 (0.1) a	9.3 (1.7) b	9.1 (1.6) b	876.9 (74.4) b	97.5 (11.3) ab	207.9 (29.0) b
	High	19.1 (1.3) b	7.3 (0.1) a	36.0 (5.7) a	36.1 (5.2) a	760.2 (82.3) b	75.9 (14.6) b	118.3 (16.5) c

Different uppercase letters indicates significant differences at $\alpha = 0.05$ between fire severities at 2 months post-fire. Different lowercase letters indicate significant differences between fire severities at 6 months post-fire.

>1000 °C) (DeBano et al., 1998; Johnson et al., 2008; Sampson et al., 1995). The amount of N lost during a fire is directly proportional to the amount of organic matter combusted (DeBano et al., 1998). Two months post burn, NH_4^+-N was greatest and NO_3^--N was lowest in high severity burns (Table 4). High NH_4^+ -N concentrations in the surface soil layer in the high severity burns persisted six months post fire despite 52% decrease in the NH_4^+-N pool and increase in the NO_3^--N pool (from 0.8 mg kg^{-1} at 2-months post burn to 36 mg kg^{-1} at six months post burn). This shift may be in response to nitrification, however because of the differences in sampling locations between the two sampling times, this interpretation of nitrification potential rates must be made with caution. Although there was a significant fire severity by tree species interaction for NO_3^--N at six months post wildfire (*p*-value = 0.0142), only soil beneath oaks in high severity areas had greater NO_3^--N concentrations than that beneath the pine and juniper under high severity (Fig. 5). Within each tree species, the high severity burn NO_3^--N content (average 36.1 mg kg^{-1}) was greater than both the unburned and low severity burn sites (overall average 8.1 mg kg^{-1}). The increased inorganic N concentration following the Livermore Ranch Complex Fire reported here has important implications for ecosystem recovery because N is the most limiting nutrient for most plant growth. In these semi-arid woodlands, recycling of N following fire may help with regeneration of vegetation and ecosystem recovery (Christensen, 1973; Neary et al., 2003). The duration of increased soil N levels will depend upon numerous factors including soil temperature and moisture, and the nutrient turnover by the microbial community which in turn will influence the rate of re-vegetation. Soil NH_4^+-N levels returned to unburned levels two months after a wildfire in a *Pinus canariensis* forest ecosystem (Rodriguez et al., 2009). Higher NH_4^+-N levels in burned soils were also found by Schafer and Mack (2010) with higher levels remaining for 20 days following the fire. Soil NH_4^+-N levels were lower six months post fire than in the samples collected only 2 months after the fire event but remained over 400% greater than in unburned areas. The decline in NH_4^+-N levels by 63% over time was partially offset by the increase in soil nitrate-N levels as ammonium is converted to nitrate by the

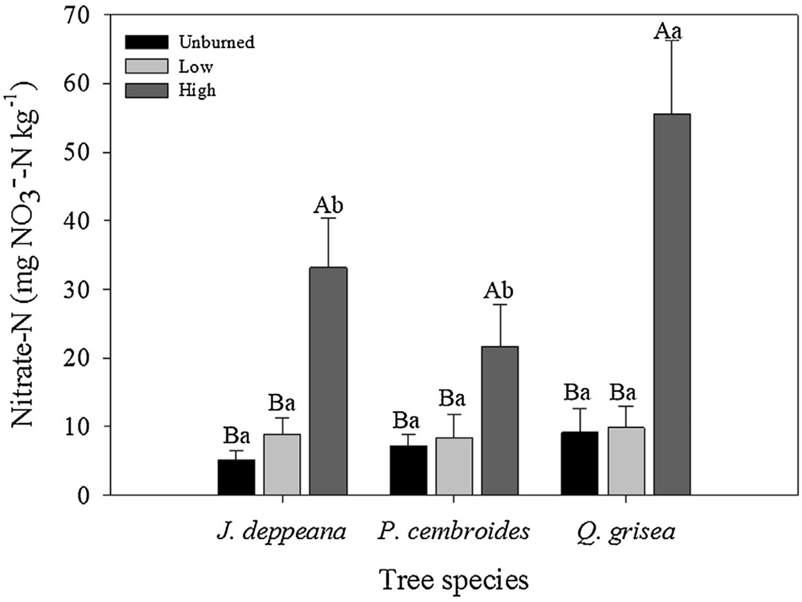

Fig. 5. Nitrate-N concentrations in samples collected six months after the Livermore Ranch Complex Fire. Samples were identified based on burn severity and specific tree species *Juniperus deppeana* (*J. deppeana*), *Pinus cembroides* (*P. cembroides*), and *Quercus grisea* (*Q. grisea*). Different uppercase letters indicate significant difference ($\alpha = 0.05$) between burn severity within each tree species. Different lowercase letters indicates significant difference between tree species within the same burn severity.

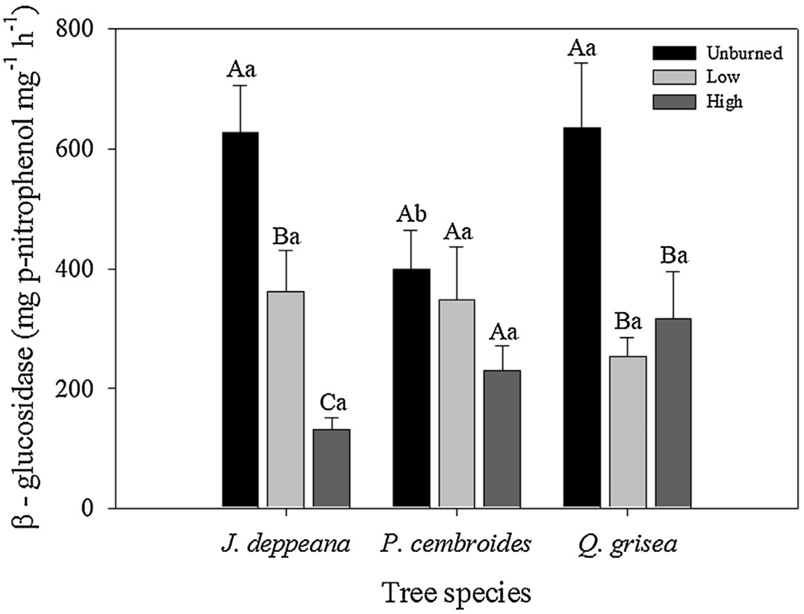

Fig. 6. β-glucosidase concentrations in samples collected two months after the Livermore Ranch Complex Fire. Samples were identified based on burn severity and specific tree species *Juniperus deppeana* (*J. deppeana*), *Pinus cembroides* (*P. cembroides*), and *Quercus grisea* (*Q. grisea*). Different uppercase letters indicate significant difference ($\alpha = 0.05$) between burn severity within each tree species. Different lowercase letters indicates significant difference between tree species within the same burn severity.

processing of the microbial community (e.g., nitrification), assimilated by the microbial biomass by the (100% increase) in MBN, and increased uptake by plants to aide in revegetation (Maathuis, 2009). Six months post-fire increased soil moisture, partial recovery of the microbial biomass and a surplus of ammonium would create ideal conditions for nitrification to proceed.

Soil moisture is a key driver influencing soil microbial biomass and microbial activity. Extremely low soil moisture levels (average 2.2%; Table 4) reported two months post-fire are likely the main factor for the lack of burn effect on soil microbial biomass for this sampling. However, even during this dry period, there was a trend of reduced soil microbial biomass with increasing fire severity, as expected from the literature (Andersson et al., 2004; D'Ascoli et al., 2005; Grady and Hart, 2006; Prieto-Fernández et al., 1998; Yeager et al., 2005). However, soil microbial biomass remained unaltered by a prescribed fire in a South African grassland (Fynn et al., 2003) and in another study, soil MBN increased immediately after a fire

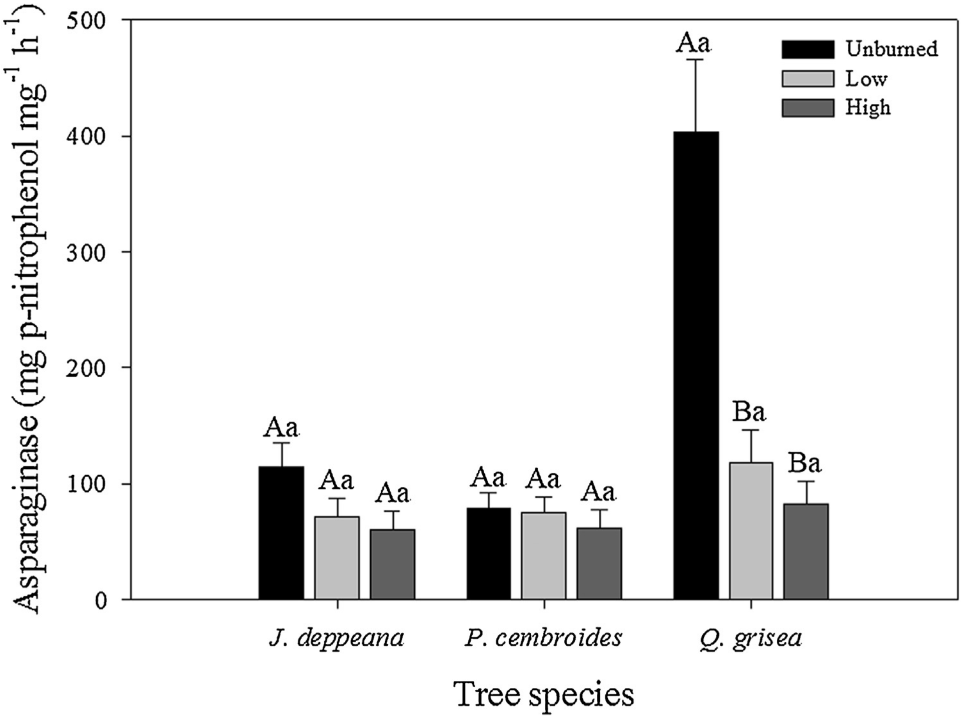

Fig. 7. L-aparaginase concentrations in samples collected two months after the Livermore Ranch Complex Fire. Samples were identified based on burn severity and specific tree species *Juniperus deppeana* (*J. deppeana*), *Pinus cembroides* (*P. cembroides*), and *Quercus grisea* (*Q. grisea*). Different uppercase letters indicate significant difference ($\alpha = 0.05$) between burn severity within each tree species. Different lowercase letters indicates significant difference between tree species within the same burn severity.

but decreased within the first month post-fire (Wilson et al., 2002). Sampling at six months followed a wetting pattern (Table 4) which would stimulate microbial activity with differential responses due to fire severity. Soil MBC was 27% lower in burned sites (averaged across both severities) compared to unburned soil and soil MBN also was reduced by 43% in the high severity burn.

Our β-glucosidase activity results also support reduced soil microbial biomass. Two months post burn, β-glucosidase was significantly higher in the unburned juniper and oak sites relative to the low severity and high severity burn sites (Fig. 6 and Table 4). Six months post burn, the main effect of burn severity persisted and β-glucosidase decreased with increasing severity (Table 4). In contrast, MBN was 54% higher in unburned soils, relative to that measured in high severity soils (Table 4). Although fungal and bacterial biomass was not assessed in the wildfire study, the ratio of MBC to MBN can be an indication of fungal vs. bacterial dominated systems (Campbell et al., 1991). In general, a wide ratio indicates fungal dominated populations. The ratios of MBC:MBN were 18:1 (std. error = 2.1) in the high severity fire and 21:1 (std. error = 1.5) in both the unburned and low severity sites (data not shown). Although not significant, this reduction in MBC:MBN in the high severity fire may be an early indication of reduced fungal biomass, similar to the microbial community shifts measured in the previously discussed prescribed fire study and in Hamman et al. (2007). At six months post fire, when soil moisture conditions increased, there was a substantial decline in this ratio (average 9:1), which supports our hypothesis that there was a shift to bacterial populations primed to take advantage of the release of dissolved nutrients (e.g., increased nitrification).

A reduction in soil L-asparaginase activity (an enzyme involved in N cycling) and β-glucosidase followed lower soil microbial biomass and higher nutrient availability at burned areas (Fig. 7). Gutknecht et al. (2010) attribute the decrease in enzyme activity to an 'initial pulse response' associated with increased nutrient availability following fire. The abundance of nutrients from ash depositions could explain low activities of β-glucosidase and L-asparaginase at the high severity fires for both sampling times. Decreased enzyme activity in fire-affected soils was also found in other studies conducted in shrubland, grassland and forest ecosystems (Boerner et al., 2005; Boerner et al., 2006; Boerner et al., 2008; Fortúrbel et al., 2012; Gutknecht et al., 2010).

4. Summary

With the exception of soil NH_4^+-N concentrations immediately following the prescribed fires, soil chemical properties were not affected by prescribed burning. However, increased NH_4^+-N concentrations persisted up to six months post wildfire. Soil moisture may have contributed to less than ideal conditions for microbial activity for both the prescribed fire and samples collected two months post-wildfire. Microbial biomass and CO_2 fluxes increased 0.5 h post-fire before decreasing to (CO_2 fluxes) or below (microbial biomass) pre-fire levels 168 h post- prescribed fire. Soil microbial community structure shifts were measured following a procession from predominantly fungal communities to Gram positive bacteria up to 48 h post-prescribed fire before a dominance of Gram negative bacteria and actinomycetes was measured 168 h post fire.

The Livermore Ranch Complex Fire had a similar impact with decreased microbial biomass and enzymatic activity up to six months post-fire. As fire was historically part of the semi-arid grassland ecosystem, our results which showed no long-term impacts on soil chemical properties related to C and N cycling suggest that the ecosystem can take advantage of abundant nutrient availability and recover from fire events. That implies that the use of prescribed fire for management purposes of weedy species within a natural woodland ecosystem is a valid approach to ecosystem management. However, as evidenced by the delay in increased NO_3^--N following the Livermore Ranch Complex wildfire, when conditions more favorable for microbial activity (i.e. increased soil moisture) are achieved, there may be long-term impacts requiring further study. Overall, while prescribed and wildfire resulted in increased NH_4^+-N, shifts in microbial community structure and decreased in microbial biomass, prescribed fire did not have lasting impacts on soil nutrients.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2015.10.023.

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