Microbial Ecology

Response of Microbial Community Composition and Function to Soil Climate Change

M.P. Waldrop and M.K. Firestone

Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA

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Abstract

Soil microbial communities mediate critical ecosystem carbon and nutrient cycles. How microbial communities will respond to changes in vegetation and climate, however, are not well understood. We reciprocally transplanted soil cores from under oak canopies and adjacent open grasslands in a California oak–grassland ecosystem to determine how microbial communities respond to changes in the soil environment and the potential consequences for the cycling of carbon. Every 3 months for up to 2 years, we monitored microbial community composition using phospholipid fatty acid analysis (PLFA), microbial biomass, respiration rates, microbial enzyme activities, and the activity of microbial groups by quantifying ^{13}C uptake from a universal substrate (pyruvate) into PLFA biomarkers. Soil in the open grassland experienced higher maximum temperatures and lower soil water content than soil under the oak canopies. Soil microbial communities in soil under oak canopies were more sensitive to environmental change than those in adjacent soil from the open grassland. Oak canopy soil communities changed rapidly when cores were transplanted into the open grassland soil environment, but grassland soil communities did not change when transplanted into the oak canopy environment. Similarly, microbial biomass, enzyme activities, and microbial respiration decreased when microbial communities were transplanted from the oak canopy soils to the grassland environment, but not when the grassland communities were transplanted to the oak canopy environment. These data support the hypothesis that microbial community composition and function is altered when microbes are exposed to new extremes in environmental conditions; that is, environmental conditions outside of their "life history" envelopes.

Correspondence to: M.P. Waldrop at present address: US Geological Survey, 345 Middlefield Road, Menlo Park, CA 94025, USA; E-mail: mwaldrop@usgs.gov

Introduction

In California oak–grassland ecosystems, soil microbial communities are associated with aboveground plant communities, primarily through plant community control of the soil moisture regime [29]. Both the extremes and variability in soil climate can have a dramatic impact on the composition and function of the microbial community [15, 18, 28]. However, studies addressing the sensitivity of the microbial community to environmental change have not presented a consistent pattern. Microbial community composition may shift quickly in response to changes in the environment [2, 7, 8], but changes in microbial community composition may also occur only very slowly or not at all [4, 5, 9, 10, 14, 17]. These contradictory observations have led to inconsistent assumptions about microbial community dynamics in response to climatic and vegetation change [5, 6, 22, 23, 26]. The ways in which microbial communities respond to changes in plant communities and climate will be important factors to understand as plant community distributions continue to change and as regional climate and elevated CO_2 continue to alter patterns of precipitation, temperature, and plant productivity.

As microbial communities are presented with new environmental conditions, shifts in community composition may occur as different sets of organisms outcompete others for available resources in the new environment. If microorganisms respond to changes in soil C dynamics resulting from changes in plant communities, then shifts in microbial community composition may occur slowly, as new carbon replaces old [21–23, 26].

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To study the effects of changing soil environmental conditions on microbial community composition and function, we measured the microbial community response to a reciprocal transplant of soil cores between oak canopies and open grasslands in the Mediterranean climate of northern California. California grassland soils located under oak canopies and in the open are known to vary substantially in nutrient cycling and soil organic matter content but to be essentially identical in terms of mineralogy and parent material. Oak canopy soils may receive six times as much oak litter and 10% more herbaceous litter than surrounding open grasslands, and decomposition rates of both oak and herbaceous litter are faster under oak canopies [19, 20]. In addition, the annual temperature regimes and soil water content differ substantially between undercanopy and open soils [20]. Based on previous work [19], we expected the microbial communities indigenous to these two soils to be substantially different; in addition, we expected the community composition and activity of the transplanted soils to change toward that of their new environment. That is, over a period of 2 years, we expected the transplanted grassland community to become compositionally and functionally similar to the original oak soil community and the transplanted oak community to become more similar to the grassland soil microbial community.

Methods

Field Sites. This study was conducted at the University of California Hopland Research and Extension Center, 160 km north of San Francisco. The summers are hot and dry and the winters are cool and wet, typical of Mediterranean ecosystems. The growing season begins in the fall and ends in the spring. Mean annual temperature is 15°C and mean annual precipitation is 940 mm. Grassland soils are typically 7–10°C warmer than oak canopy soils in the summer. Grassland soils are also drier than oak canopy soils in summer, although winter soil moisture contents are similar (Fig. 1). The soils in open grasslands and under oak canopies were upland, sandy clay loams of the Sutherlin soil series, which are classified as mixed, mesic Ultic Haploxeralfs [16]. Textural analysis indicated that the soils contained 23% clay, 25% silt, and 52% sand.

To determine how microbial communities respond to changes in plant communities, we used a reciprocal transplant between oak canopy and grassland soils. In January 2000, we established five 3 × 3 m fenced plots under both blue oak (*Quercus douglasii* H. & A.) canopies and five plots in open grassland sites (primarily *Bromus hordeaceus* and *Avena barbata* grass species). Forty 12.5 × 4.5 cm diameter polycarbonate soil cores were hammered into each plot at ~25-cm intervals. All cores were then pulled from the plot and half of the cores in each plot were randomly chosen and transplanted into the opposite plant community type (oak into grassland and grassland into oak). The second half served as control cores. Soil remained in the original cores at all times. Grass was allowed to grow in all cores in both oak canopy and open grassland plots. Although the polycarbonate walls of the cores were barriers to microbial and faunal movement, immigration and emigration might have occurred through both the open bottom and top of the cores; thus, the potential for microbial movement was similar in all treatments. Gopher disturbance is a common and intrinsic part of this grassland environment [11, 13]. Gopher activity buried some of the cores under 1–5 cm of soil, but Gopher disturbance did not break the cores or alter their position and it similarly impacted both intact and transplanted cores. Cores were open on both ends to drain from the bottom and be exposed to litter inputs from

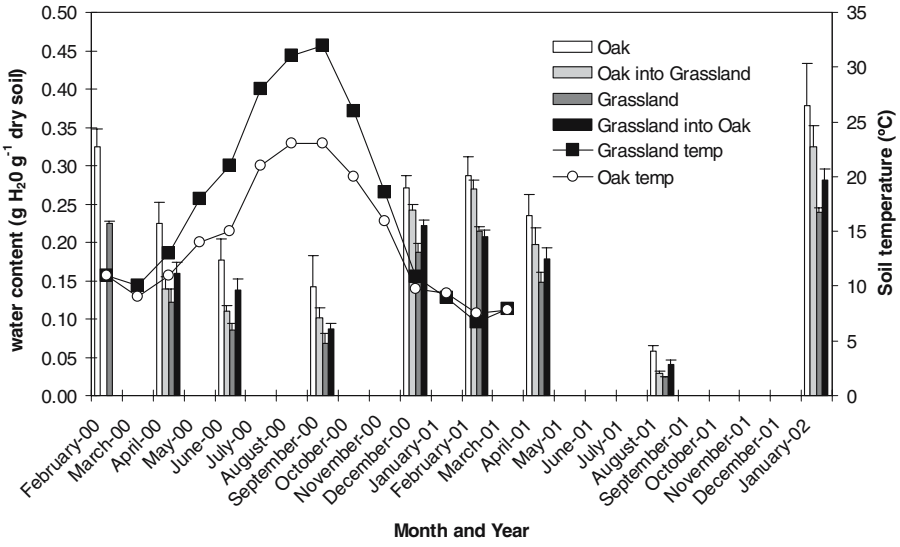

Figure 1. Soil temperature in oak canopy and open grassland soils; soil water content in intact and transplanted oak canopy and open grassland soils. In the oak canopy soil, a water potential value of −0.033 MPa (field capacity) yields a soil water content of 0.33 g H_2O g^{-1} soil and in the open grassland soil, it is 0.24 g H_2O g^{-1} soil.

above. At each sampling interval, approximately every 3 months, two transplanted and two nontransplanted (intact) soil cores were taken from each of the 10 plots, combined, and kept cool (4°C) for several hours until they were brought back to the laboratory. Soil moisture was measured immediately on homogenized soil samples by drying the soil for 24 h at 105°C and recording wet and dry weights. In April 2001, uncored soil was sampled to 12.5 cm and we compared its moisture content with cored soils; moisture content of the uncored soil was not significantly different than the cored soil (data not shown). Methods for measuring soil temperature were presented previously [30]. Soil temperature was measured in two oak canopy plots and two open grassland plots, and was not measured in any intact or transplanted core. The sampling dates were February 1, April 4, June 10, September 25, and December 5, 2000; February 6, April 10, and August 8, 2001; and January 7, 2002. Microbial community composition and biomass were measured at all dates, except February 2001, and functional assays and soil temperature were measured from the beginning of the experiment until February 2001.

Microbial Respiration and Enzyme Activities. We measured potential microbial respiration on 50-g homogenized and root-free soil samples at 35°C in 1-L mason jars at 60% of water-holding capacity for 2 days after a 2-day preincubation. Carbon dioxide concentrations were determined on a Shimadzu 14A gas chromatograph (GC) with a thermal conductivity detector.

Enzyme activities [β-1,4-glucosidase, α-1,4-glucosidase, cellobiohydrolase, β-xylosidase, *N*-acetyl-glucosaminidase (NAGase), and phosphatase] were assayed using 50 mM methylumbylliferal (MUB) enzyme substrates. Approximately 1 g (wet weight) soil samples were added to 100 mL of 5 mM bicarbonate buffer solution (pH 8.0) and stirred on a stir plate while sampling with a multichannel pipettor. One hundred microliters of the mixture was added to 100 μL of MUB–substrate solution. Assays were conducted on fluorometric microplate in 96-well format. There were eight analytical replicates for each enzyme and four quenching controls for each sample. Four replicate standards from 0 to 2.5 μg MUB were run in tandem for each sample to control for quenching. Plates were read on a Fluorolog 3 spectrofluorometer linked to a Micromax plate reader (ISA Instruments). Excitation was set at 360 nm and emission was measured at 450 nm. Assays were incubated at 27°C for 1–2 hours. Emission was measured at the beginning and end of the incubation and activity was measured as the difference between start and end of fluorescence measurements [25].

Microbial Community Composition and Biomass. Microbial community composition and microbial biomass were quantified using phospholipid fatty acid analysis (PLFA) [31, 32]. We combined the PLFA method with isotopic labeling using a universal substrate, pyruvate, to assess metabolic activities of Gram-positive bacteria, Gram-negative bacteria, fungi, and actinomycetes [1, 3, 26]. We added 1 mL of 10 mg mL^{-1} [^{13}C]pyruvate (99.9‰, Cambridge Isotope Labs) to 10 g of field moist soil; soil samples were immediately incubated at 35°C for 24 h and then frozen at –20°C and subsequently lyophilized. We extracted fatty acids from 5 g of lyophilized soil samples using a methanol/chloroform/phosphate buffer mix. Phospholipid fatty acids were separated from neutral lipids and glycolipids by on a solid phase extraction column using chloroform, acetone, and methanol in sequential washes of the sample. Phospholipids were then transesterified using methanolic potassium hydroxide and heat [31]. Final phospholipid samples were analyzed first for PLFA abundance and nomenclature, and second for isotope ratios of PLFAs. PLFA abundance and nomenclature was measured using a Hewlett Packard 6890 GC with a 25 m × 0.2 mm × 0.33 μm Ultra 2, 5% phenylmethylpolysiloxane column (Hewlett Packard) using H_2 as the carrier, N_2 as the make-up gas, and air to support the flame. The GC analyzed a 1-μL injection with a 1:100 split, at an initial temperature of 170°C, ramped to 260°C at 2°C min^{-1} at a constant flow rate of 0.4 mL min^{-1}, with a rapid increase to 310°C for 2 min at the end of each run to bake out the column. Peaks were identified using bacterial fatty acid standards and MIDI peak identification software (MIDI, Inc., Newark, DE). Only PLFA biomarkers with >1% abundance were used in subsequent analysis. Biomarker abundances were transformed to mol% values and used in principal components analysis (PCA; JMP software, SAS Institute) to assess microbial community composition. Microbial biomass was calculated by summing the total moles of extracted PLFAs. Extraction efficiencies were determined to be >90% by adding fatty acid standards to soil before extraction.

We measured isotope ratios of microbial PLFA markers (^{13}C-PLFA) on the same samples as above using a Europa (PDZ Europa, Sandbach, Cheshire, UK) Orchid

Table 1. Characteristics of oak canopy and open grassland soils

	C (g kg^{-1})	*N* (g kg^{-1})	*C/N*	*pH*	*Available P* (μg P g^{-1})	*Water-holding capacity* (g g^{-1})
Oak canopy	36 ± 3^a	2.4 ± 0.1^a	14.6 ± 0.5^a	5.44 ± 0.03^a	40.1 ± 1.8^a	0.67 ± 0.07^a
Grassland	12 ± 1^b	1.2 ± 0.1^b	10.1 ± 0.5^b	5.18 ± 0.01^b	10.2 ± 0.3^b	0.35 ± 0.35^b

Values are means ± SE. Letters denote differences between soils (n = 3–5). Data are from Waldrop and Firestone [30].

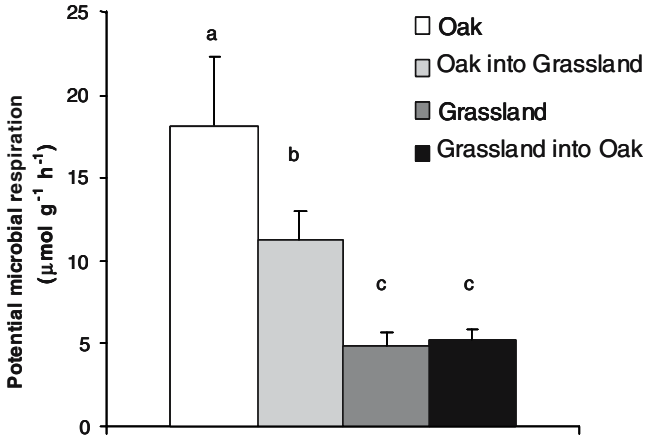

Figure 2. Potential microbial respiration in intact and transplanted grassland and oak canopy soils. ANOVA revealed that respiration decreased when the oak canopy soils were transplanted into the open grassland environment but not when the grassland soils were transplanted into the oak canopy environment ($p < 0.0001$). *Bars* are means with standard errors ($n = 30$) of samples taken at six regular intervals over 1 year. Means with different *letters* are significantly different ($p < 0.05$).

II interface between a Hewlett Packard (Agilent) 6890 GC and a Europa 20–20 Geo IRMS. The GC column was a HP5 (DB5), 5% phenylmethylpolysiloxane (30 m × 320 μm) with 0.25 film thickness. Metabolic profiles of microbial PLFAs were calculated as the amount of [^{13}C]pyruvate incorporated into the PLFA and grouped into Gram-positive and Gram-negative bacteria, fungi, and actinomycete clades [32]. Saturated PLFAs (16:0, 18:0) were not included in any microbial guilds because of their nonspecificity to any microbial group. ^{13}C-PLFA profiles were calculated by quantifying the total amount of ^{13}C incorporated into each PLFA, normalizing those data to the total amount of ^{13}C taken up into all PLFAs, and performing PCA on the normalized data.

Statistical Analysis. To test whether transplantation affected microbial community composition and function, we used an analysis of variance (ANOVA) with "soil" (oak and grassland), "transplant" (intact and transplanted treatment), and sampling date as the independent variables (Statistix, Analytical Software). Significant effects from ANOVA were followed by least significant difference *post hoc* tests. The seasonal dynamics of microbial community composition and function from intact cores were analyzed and discussed in a previous article [30]. In this article, our primary aim was to understand the effect of transplantation on soil communities. Only interactions that included a significant "transplant" effect were included and discussed. The level of statistical significance was $p < 0.05$. All microbial and process data were collected for year 1, but only microbial community composition data were collected for year 2.

Results

Soil Climate and Microbial Activity. During the summer months, open grassland soils were warmer and drier than the oak canopy soils. In the winter, soil temperatures were generally similar between the two soils (Fig. 1), but soil moisture was still higher in the oak canopy soils. Soil summer temperatures reached a maximum of 33°C in the open grassland and 24°C under the oak canopy. We did not independently measure soil temperature within intact and transplanted cores, but we assume that transplanting soils from the oak canopy to the open grassland increased the temperature experienced by soil organisms, and transplanting the grassland soil into the oak canopy environment decreased soil temperature over the summer months. We observed a significant soil × transplant × time interaction for soil moisture ($p = 0.0001$). Transplanting soil from the open grassland to the oak canopy significantly increased soil moisture during June 2000, although soil moisture was generally higher in transplanted cores on all dates. Soils transplanted into the open grassland from the oak canopy environment had reduced soil moisture

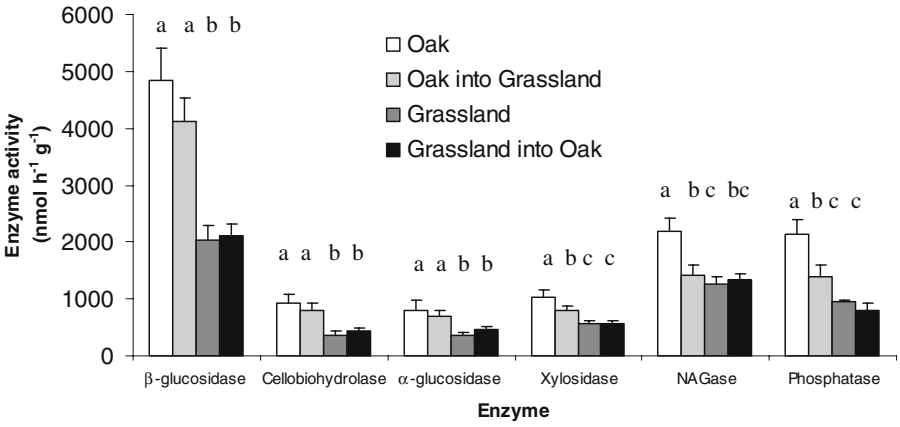

Figure 3. Soil enzyme activities in intact and transplanted grassland and oak canopy soils. ANOVA revealed a transplant effect when the oak canopy soil was transplanted into the open grassland soil for the enzymes xylosidase ($p < 0.0001$), NAGase ($p < 0.0001$), and phosphatase ($p < 0.0001$). β-glucosidase, cellobiohydrolase, and α-glucosidase enzyme activities were unaffected by the transplant treatment. Different *letters* denote statistically significant differences among means. Samples were taken at six time points from February 2000 to February 2001.

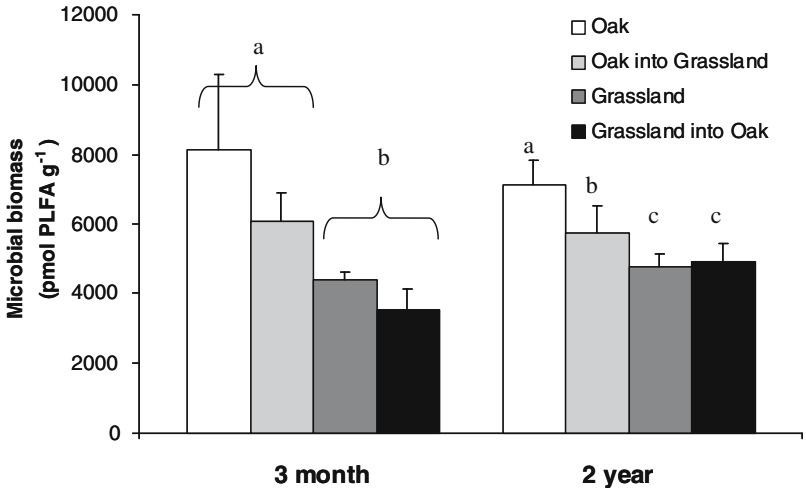

Figure 4. Microbial biomass in intact and transplanted grassland and oak canopy soils. Microbial biomass decreased when the oak canopy soils were transplanted into the grassland environment but not when the grassland soils were transplanted into the oak canopy environment (soil × transplant interaction; $p = 0.0002$). *Letters* indicate statistically significant differences. Microbial biomass tended to be reduced immediately after the oak canopy soil was transplanted into the grassland environment (3 months), but the decrease was not statistically significant; thus, *letters* indicate a difference among soils at each time point.

contents only in April 2000, although soil moisture content always tended to be lower in transplanted cores (Fig. 1). The transplantation treatment never resulted in transplanted cores maintaining the same moisture content as the environment into which they were transplanted, partly reflecting the different water retention characteristics of the two soils (Fig. 1; Table 1). Despite this fact, transplanting altered the soil temperature and soil moisture regime experienced by the soil microorganisms.

We sampled soil respiration at six time points from February 2000 to February 2001, and temporal dynamics of respiration have been previously reported [30]. Potential soil respiration rates were higher in the oak canopy soils compared with the open grassland soils and decreased when the oak canopy soil was transplanted into the grassland environment (soil × transplant interaction, $p = 0.039$; Fig. 2). Despite differences in soil temperature and moisture in the field, potential soil respiration rates were not significantly different between the intact grassland soils and the transplanted grassland soils (Fig. 2).

Soil β-glucosidase and cellobiohydrolase (enzymes that degrade cellulose) and α-glucosidase (an enzyme that degrades starch) activities were unaffected by the transplant treatment of either the oak or grassland soil. However, xylosidase, NAGase, and phosphatase enzyme activities were all significantly reduced when the oak canopy soil was transplanted into the open grassland soil (soil × transplant interaction, $p < 0.0001$; Fig. 3). Xylosidase degrades hemicellulose, NAGase degrades chitin and N-acetylglucosamine-containing polymers, and phosphatase releases inorganic phosphate from organic bound forms. In the grassland soil transplanted into the oak canopy environment, there was no significant effect of transplantation on soil enzyme activities (Fig. 3).

Microbial Biomass and Community Composition. Transplantation reduced microbial biomass in the oak canopy soil that was moved into the grassland environment, but did not affect microbial biomass of the grassland soil placed into the oak canopy environment (soil × transplant interaction; $p = 0.0002$; Fig. 4). Although microbial biomass was reduced by as much as 25% in 3 months after transplantation, this rapid reduction was not statistically significant (Fig. 4). Transplantation altered microbial community composition when the oak canopy soil was transplanted into the grassland environment (PLFA principal component 1,

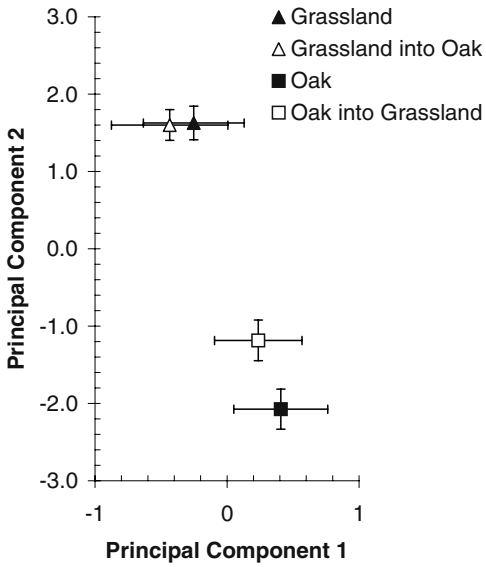

Figure 5. Microbial community composition in intact and transplanted grassland and oak canopy soils. PLFA principal component 1 incorporated 23% of the variability and PLFA principal component 2 incorporated 22% of the variability in the PLFA data set. Transplantation altered microbial community composition of the oak canopy community when it was transferred to the grassland environment, but transplantation did not affect the composition of grassland soil community (soil × transplant interaction; $p = 0.0013$, $n = 30$). Values represent means (±1 SE) of data from April 2000 to January of 2002.

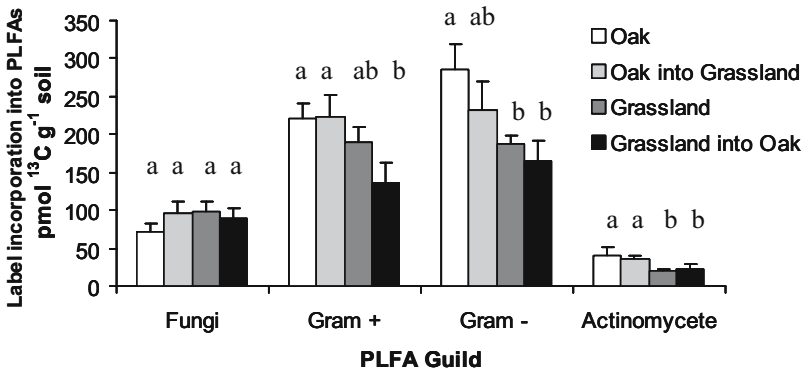

Figure 6. Incorporation of ^{13}C label into PLFA guilds. Activity was calculated as the total uptake of ^{13}C-labeled pyruvate into PLFAs over a 24-h period. Values are means ± SE (n = 7–16).

not significant; PLFA principal component 2 soil × transplant interaction, $p = 0.0013$; Fig. 5); however, microbial community composition was not changed when the grassland soil community was transplanted into the oak soil. Microbial PLFAs 18:0 (a general biomarker) and 10Me18:0 (actinomycete marker) increased in relative abundance and i15:0 (a Gram-positive marker), 18:2ω6c (a fungal marker), and 16:1ω7c (a Gram-negative marker) decreased in relative abundance when the oak community was transplanted into the grassland environment. Microbial community composition of the transplanted oak community became more similar to the grassland community in principal component space, although it was still significantly different than the grassland community (Fig. 5).

We used an isotope labeling technique to determine the activity of different microbial groups in soil. The incorporation of ^{13}C label into Gram-negative, Gram-positive, and actinomycete PLFA guilds was higher in the oak canopy soil than the open grassland soil, but incorporation of label into the fungal biomarkers was not significantly different between the oak canopy and grassland soils (Fig. 6). Transplantation of the soil community from either soil did not affect the uptake of [^{13}C]pyruvate into any of the PLFA guilds (Fig. 6). PCA of the ^{13}C-PLFA data showed that although the first principal component differed between the oak and grassland communities, there was no transplant effect (data not shown).

Discussion

Reciprocal transplantation of soils between oak canopy and grassland soils provided a useful approach to experimentally test the microbial community response to a change in soil climate regime. Transplantation altered the environmental conditions experienced by the soil microorganisms but it could not exactly replicate the new environment if only because the water-holding capacities of the two soils differed. Transplantation led to significant changes in microbial community composition, microbial biomass, and microbial community function in the oak canopy soil community; however, there was no detectable change in the grassland microbial community for up to 2 years. Signs of change in the transplanted oak soil community began to occur within 3 months of being transplanted into the grassland environment. Interestingly, the oak canopy soil community shifted to a soil community that was more similar to the open grassland community, as shown by changes in principal component space.

We had previously shown that the distinct microbial communities in this ecosystem are associated with overstory plant communities [30]; here, we wanted to assess the response of microbial communities to changes in soil climate and new litter inputs. Although we allowed for aboveground litter inputs from the new plant community to occur in transplanted soil cores, this was likely not a significant source of new carbon to the microbial community for the first year. To the degree that the grasses growing in the cores shifted toward the ambient plant community during year 2, the quality and quantity of plant carbon inputs would have begun to change. However, changes in temperature and moisture began to occur immediately after transplantation and thus were likely the primary drivers of changes in microbial community composition and function.

The response of soil microbial community composition to changing plant communities, and resulting soil temperature, moisture, and C quality, has been found to be very rapid in some studies [2, 7, 8] and very slow in others [4, 5, 9, 10, 14, 17]. The shift in the oak soil microbial community that occurred rapidly following transplantation is likely due to the lower soil water content and higher soil temperatures present in the open grassland, as significant changes in soil C inputs occurred on a longer time scale. In contrast, the microbial community composition of the grassland soil did not change after being transplanted into the oak environment, although significant increases in soil water content and decreases in soil temperature occurred. Changes in soil microbial community composition seem to be related to the magnitude and range of changes in the soil temperature and moisture experienced in the new soil climate. Oak soils transplanted into the grassland environment experi-

enced a greater magnitude of change in soil moisture compared with grassland soils transplanted into the oak environment. This does not explain why the oak canopy soil community changed more rapidly than the grassland soil community transplanted into the oak environment. At lower soil water contents, the change in soil water potential (energetic availability of water) per unit change in water content is greater than at higher soil water contents. Thus, whereas the change in water content was greater as the wetter oak soil dried down in the grassland environment, the changes in soil water potential experienced by the two soils undergoing transplant may have been quite similar. The grassland soil community was largely unaffected by transplantation, although it also experienced large changes in soil moisture as early as 4 months into the study.

Changes in microbial community composition and function in a new soil climate may be predicated upon whether the forcing variables (e.g., temperature and moisture) are outside the "life history" of the microbial community. Microbial communities should be acclimated to the local environmental conditions that they repeatedly experience. New environmental conditions outside of the annually experienced life history of the microbial community may force changes in community composition and function [4, 15, 18, 24]. This concept may help to explain why microbial communities change in response to altered environments in some studies but not in others. The grassland soil microbial community experiences the range of oak canopy soil conditions within a single yearly cycle, but the oak canopy community does not regularly experience temperatures as warm or springtime soil moisture as dry as that occurring in the open grassland environment. Thus, when the oak soil community was transplanted into an environment with temperature and moisture regimes to which it was not acclimated, the microbial community began to rapidly change, with nearly simultaneous reductions in microbial biomass, enzyme activities, and respiration rates. When the grassland soil was transplanted into the oak soil environment, community composition and C cycling activities did not change measurably for 2 years. The grass soil microbial community remained in an environment that had a similar range of soil temperature and moisture, despite summer soil temperatures and soil moisture contents that were clearly different between grassland intact and transplanted soils.

If microbial communities are acclimated to local environmental conditions, then changes in climate have the potential to alter ecosystem processes in ways that are not simply predicted from abiotic variables. Many studies have shown that variation in the sensitivity of microbial communities to changes in climate affect soil processes [4, 12, 15, 18, 24, 27, 28]. For example, Stark and Firestone [28] found that nitrifiers in California open grasslands had different temperature response optima and curves that those from undercanopy soils. Gulledge and Schimel [18] showed that methane oxidizers in upland Alaskan soils were adapted to the local moisture regime and that changes in soil moisture, either positively or negatively, would decrease methane consumption. Cavigelli and Robertson [12] found that denitrifiers had a differential sensitivity to moisture stress, which constrained N_2 production. In another study, the functioning of the litter decomposing community Alaskan taiga soils was affected by the history of moisture stress, and thus the historical exposure of the microbial community to water fluctuations had an important effect on decomposition [27]. In a study that compared oak canopy and grassland soils in a location in central California, Fierer and Schimel [15] showed that oak soil communities were more sensitive to extremes in soil moisture than was the open grassland community. We believe this occurs because the oak soil community normally does not experience the extremes in temperature that the grassland experiences. These studies then support the hypothesis that microbial communities are acclimated to their indigenous environment and therefore may be sensitive to climatic change that is not regularly experienced by the indigenous community.

The temperature response of a soil microbial community exposed to a new condition for only a short period of time will not be predictive of the long-term temperature response curves of that community. Whereas some studies have found that microbial community composition is not affected by small changes (1–4°C) in soil temperature [5, 22], it is possible that microbial communities from less variable environments are more sensitive to environmental change than are those from more variable environments. Temperature and moisture are clearly important controls on microbial community composition, but they are certainly not the only drivers; soil carbon quantity and quality must also play a role. In previous research on this site [30], we determined that substrate availability is not as important as climate in predicting microbial community composition. However, as the quality and quantity of plant carbon available to the soil microbial communities in the transplanted soils continue to change, and as faunal immigration and emigration continue, larger changes in soil community composition would be expected to occur.

The ^{13}C-PLFA technique allowed us to quantify the activity of microbial guilds and determine whether the members of the microbial community that were utilizing the substrate pyruvate differed between soil types and in response to the transplant treatment. Although there were differences in the incorporation of label into Gram-negative, Gram-positive, and actinomycete guilds between oak canopy and grassland soils, there was no effect of the transplant treatment. This may underscore the limited sensitivity of grouping PLFA biomarkers into

guilds to detect members of the soil community that are being affected by the transplant treatment. Also, PCA of the ^{13}C-PLFA data was not sensitive to the transplantation treatment. ^{13}C-PLFA data tend to be less sensitive to environmental change than simply using PLFA without label incorporation [30]. The ^{13}C-PLFA technique has potential to link microbial community composition to function, but the carbon compound used (if any) and the way in which the data are calculated and interpreted need to be carefully considered.

In conclusion, microbial communities in oak canopy soils that experience lower variability in soil climate are more sensitive to changing soil climate than are microbial communities in open grassland soils that regularly experiences extremes in soil temperature and water content. Sensitivity to change may be dependent on the historical exposure of the microbial community to a range of environmental conditions. Changes in microbial community composition, when they did occur, were associated with decreases in microbial biomass, enzyme activities, and microbial respiration. Because microbial communities are the catalysts of soil processes, understanding soil processes under conditions of change require an improved understanding of the factors that affect microbial community composition.

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