

Microbial community responses in forest mineral soil to compaction, organic matter removal, and vegetation control¹

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Abstract: We tested three disturbance hypotheses in young conifer plantations: H₁: soil compaction and removal of surface organic matter produces sustained changes in microbial community size, activity, and structure in mineral soil; H₂: microbial community characteristics in mineral soil are linked to the recovery of plant diversity; and H₃: community responses are strongly modified by regional climate. Microbial biomass, respiration, carbon utilization, and phospholipid fatty acids were compared at two subtropical installations and one Mediterranean-type climate installation of the North American Long-Term Soil Productivity study. Treatments included combinations of compaction (none vs. severe), organic matter removal (none vs. complete), and weed control (none vs. complete), plus an uncut reference stand. Weed control resulted in the only consistent decline or shift in microbial indices at the subtropical sites. At the Mediterranean-type climate site, overstory harvesting resulted in declines in microbial biomass, respiration, and fungal phospholipid fatty acids that far outweighed the effects of the soil disturbance treatments. Severe compaction had no effect on community size or activity at any site. Microbial communities were generally tolerant of postharvest soil disturbance, leading to a rejection of the experimental hypotheses, with the exception of a link between microorganisms and recovery of plant diversity (H₂) at the subtropical sites.

Résumé : Les auteurs ont testé trois hypothèses ayant trait aux perturbations dans de jeunes plantations de conifères : H₁ : la compaction du sol et l'enlèvement des résidus organiques de surface entraînent des changements persistants dans la structure, l'activité et la taille de la communauté microbienne dans le sol minéral; H₂ : les caractéristiques de la communauté microbienne dans le sol minéral sont reliées au rétablissement de la diversité végétale; H₃ : les réactions de la communauté microbienne sont fortement influencées par le climat régional. La biomasse, la respiration, l'utilisation du carbone et les acides gras phospholipidiques microbiens ont été comparés dans deux stations au climat subtropical et une station au climat méditerranéen du programme nord-américain de productivité des sols à long terme. Les traitements incluaient des combinaisons de compaction du sol (aucune vs sévère), d'enlèvement des résidus organiques (aucun vs complet) et de maîtrise de la végétation (aucune vs complète), en plus d'un peuplement non coupé comme témoin. La maîtrise de la végétation est le seul traitement qui a entraîné une diminution ou un changement constant des indices microbiens dans les stations subtropicales. Dans la station au climat méditerranéen, la récolte de l'étage dominant a entraîné une diminution de la biomasse microbienne, de la respiration et des acides gras phospholipidiques fongiques qui était de loin plus importante que les effets des traitements de perturbation du sol. La compaction sévère du sol n'a eu aucun effet sur l'activité ou la taille des communautés microbiennes dans aucun des sites. Les communautés microbiennes étaient généralement tolérantes aux perturbations du sol qui suivaient la récolte, entraînant le rejet des hypothèses expérimentales à l'exception d'un lien entre les microorganismes et le rétablissement de la diversité végétale (H₂) dans les stations subtropicales.

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Introduction

Genetic diversity is a trademark of most soil microbial communities. Bacteria alone account for several thousand distinct genomes in a single gram of soil (Torsvik et al. 1990). Theoretical studies indicate that spatial isolation of microbial species within the soil matrix and extensive heterogeneity of organic material are responsible for the abundance and, at first glance, redundancy, of microbial diversity (Zhou et al. 2002). The ecological benefit of maintaining such a high level of soil organism diversity is clear: genetic diversity is the precursor to physiological versatility. Indeed, there are few naturally occurring compounds that cannot be degraded or utilized by microorganisms, and there are few environmental conditions, including extremes in temperature, moisture, pH, or contaminants, that exclude microorganisms (Madsen 1996).

Rich diversity also engenders chaos and clouds our understanding of community responses to disturbance. That microbial communities respond to disturbance with seeming disorder and unpredictability is an ongoing challenge to many ecologists (Wardle and Giller 1996). In theory, no other natural community reacts as rapidly as microorganisms to fluctuations in habitat conditions. In practice, however, microbial community responses in forest ecosystems range from low resilience, as seen by long-term community changes following relatively innocuous practices such as low-severity prescribed burning (Fritze et al. 1993; DeLuca and Zouhar 2000), to high resilience or even complete tolerance following intensive forest management (Edmonds et al. 2000; Busse et al. 2001b; Siira-Pietikäinen et al. 2001).

Variation in site abiotic factors (climate, soil development, disturbance intensity, soil physical and chemical properties) and biotic conditions (forest type, growth rates, vegetation recovery, community composition) contribute to our imperfect understanding of disturbance effects. One approach to surmount this obstacle is through large-scale ecosystem studies that compare disturbance gradients across diverse climates, forest types, and soils. We selected the North American Long-Term Soil Productivity (LTSP) study as a vehicle to test microbial responses to disturbance for this reason. The LTSP study has a common treatment design replicated at multiple sites across North America (Powers et al. 2005). Our objective was to compare community size, activity, and structure in differing climatic zones at a minimum of 5 years after standardized disruption of soil porosity, organic matter (OM), and understory vegetation. By doing so we hoped to identify key abiotic and biotic drivers that regulate microbial response to disturbance.

Materials and methods

Study sites and treatment design

Three LTSP installations were selected for our study: two (North Carolina, Louisiana) in the subtropical zone of the southeastern United States and the third in the Mediterranean-type climate of California (Fleming et al. 2006; Powers et al. 2005). The subtropical sites have cool winters, warm summers, and consistent year-round rainfall, while the California site has cold winters and warm, moisture-limiting summers. Annual precipitation is relatively similar between sites (North Carolina, 136 cm; Louisiana, 147 cm; California, 165 cm) despite large differences in seasonal precipitation patterns. Mean annual temperature is 17 °C at the North Carolina site, 19 °C at the Louisiana site, and 11 °C at the California site. The North Carolina installation (Lynchburg, Goldsboro) was established in 1990 at the Croatan National Forest, approximately 190 km southeast of Raleigh on the Lower Coastal Plain of North Carolina; the Louisiana installation (Glenmora, Mayhew, Metcalf) was established in 1992–1993 at the Kisatchie National Forest in central Louisiana, approximately 48 km north of Alexandria; and replicate blocks of the California installation (Boldgett, Brandy, Lowell) were established in 1994–1995 at the Tahoe National Forest and the University of California, Blodgett Experimental Forest, in the central Sierra Nevada Mountains, approximately 130 km east of Sacramento.

Forest types are loblolly pine (*Pinus taeda* L.) at the North Carolina and Louisiana installations and mixed conifer (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. – *Pinus ponderosa* Dougl. ex P. & C. Laws. – *Pseudotsuga menziesii* (Mirb.) Franco) at the California installation. Soil textures are loamy sand in North Carolina, sandy loam in Louisiana, and loam in California. Replicate blocks at each installation have similar soil type, plant community, precipitation, and elevation.

Each LTSP installation has three blocks of 18 treatments arranged in a split-plot experimental design. The whole plot is a 3 × 3 factorial combination of compaction (C_0 , none; C_1 , intermediate; C_2 , severe) and aboveground OM removal (OM_0 , bole only; OM_1 , whole tree; OM_2 , whole tree plus forest floor removal). The subplot compares two weed-control treatments (none or complete). Multiple passes with heavy machinery (equipment type varied by LTSP installation) were used to compact soils. The goal of the C_2 treatment was to increase soil bulk density to 80% of the density level needed to restrict root penetration (Powers et al. 2005). Weed control was accomplished by repeated applications of glyphosate (Accord), imazapyr (Arsenal), triclopyr (Garlon), or sulfometuron methyl (Oust) in combination with manual cutting of resprouting or germinating vegetation. We selected eight treatment combinations for our study: compaction (C_0 vs. C_2), surface OM removal (OM_0 vs. OM_2), and weed control (none vs. complete).

Sample collection and analyses

Composite samples (combined from 10 subsamples) from each plot were randomly collected from the surface 15 cm of mineral soil in September 2000 and May 2001, 10 years posttreatment in North Carolina, 8 years posttreatment in Louisiana, and 6 years posttreatment in California. Three composite samples were also collected from adjoining uncut reference stands at the North Carolina and California sites to assess the general effects of harvesting. No suitable reference stand was available at the Louisiana installation.

All samples were analyzed within 48 h of collection at our laboratory facility in Redding, California (samples from North Carolina and Louisiana were shipped by overnight mail). The only exception was for spring 2001 samples from Louisiana, which were stored at 4 °C for 72 h prior to overnight shipment to the Redding lab. All samples were sieved (2 mm) prior to analysis, with the exception of the fall 2000 samples from North Carolina. Excessive soil moisture prevented sieving of these samples. Instead, we removed large organic particles and rock fragments by hand sorting. Subsamples (~25 g) were frozen at –20 °C for phospholipid fatty acid (PLFA) analysis immediately following sieving or hand sorting. Both microbial biomass and soil respiration were determined using 25 g (dry-mass equivalent) samples. Microbial biomass was measured by substrate-induced respiration (Anderson and Domsch 1978), with glucose applied at 5 mg·(g soil)⁻¹. Soil respiration was measured using an infrared gas analyzer (LI-COR 6200; LI-COR, Lincoln, Nebraska) following a 3–5 h incubation period. Soil OM content was determined by loss on ignition (400 °C for 24 h) and converted to total carbon by dividing by 1.9 (Nelson and Sommers 1996).

Carbon utilization was measured using BIOLOG GN plates (BIOLOG, Hayward, California) by methods adapted from Garland and Mills (1991). Soil inoculum was prepared by mixing 3 g of soil (dry-mass equivalent) in 27 mL of sterilized

0.15 mol/L NaCl on an orbital shaker for 10 min. Following 10 min of settling, the supernatant was diluted 15-fold in saline, and a 0.15 mL aliquot was added to each of the 95 wells. Preliminary experiments indicated no differences in carbon utilization when either sterile saline or water was used as the diluent. BIOLOG plates were incubated in the dark at 28 °C for 72 h, and metabolic potential (optical density at 590 nm) was measured three times per day. Average well color development of all 95 wells was corrected by subtracting the optical density of the control well. Microtiter wells with optical densities greater than 0.2 were considered positive for determining BIOLOG richness.

A subset of five treatments was selected for PLFA analysis: (1) bole-only harvest (OM_0); (2) OM_0 plus severe compaction; (3) OM_0 plus weed control; (4) complete OM removal (OM_2); and (5) reference stand. Total soil lipids were extracted using a method similar to that of Frostegård et al. (1993). Soil (3 g) was extracted with chloroform – methanol – 0.15 mol/L citrate buffer (pH 4.0) (1:1:0.8). Lipids were fractionated on silicic acid columns (J and W, Folsom, California) into neutral lipids, glycolipids, and phospholipids, as described by the manufacturer. Only the phospholipid fraction was retained for methylation. Fatty acid methyl esters (FAME) were produced using 4% sulfuric acid in methanol (Selivonchick and Roots 1977). Mixtures were transesterified at 95 °C for 1 h. This procedure has been shown to prevent bond migration while giving equivalent yields of FAMES (Selivonchick and Roots 1977).

Individual FAMES were identified using a Varian 3800 gas chromatograph with a Hewlett-Packard 5973 mass-selective detector (Agilent, Palo Alto, California) coupled to a HP-6890 engine. The capillary column was an HP-5 (30 m × 0.25 mm), with helium as the carrier gas and a temperature program as described by Frostegård et al. (1993). Total quantity ($ng \cdot (g \text{ soil})^{-1}$) of individual FAME was determined using methyl nonadecanoate as an internal standard.

Statistical analyses

Analysis of variance using the PROC GLM procedure for split-plot design (SAS 2000) was used to test treatment effects on microbial biomass, respiration, total carbon, microbial carbon / total carbon, metabolic quotient (respiration/biomass), and carbon utilization. Each LTSP installation was analyzed separately. The reference stands in California and North Carolina were not included in the analysis, since they were not randomized in the original LTSP experimental design; instead, means and standard errors are presented. Differences in PLFA community structure were compared visually by principal components analysis (PCA) using the Proc Princomp procedure (SAS 2000). A covariance matrix was used in the analysis to account for the common units (mole percent) of the data set. Tukey's studentized range test was used for treatment separation of individual bacterial PLFA (15:0; 17:0; 10Me 16:0; 10Me 18:0; i15:0; a15:0; i16:0; i17:0; a17:0; cy 17:0; cy 19:0).

Results

Microbial community size and activity

Site differences

Microbial characteristics varied considerably among the three sites. Mean microbial biomass (substrate-induced

respiration) for the eight treatment combinations was $371 \text{ mg} \cdot \text{kg}^{-1}$ at the California site compared to $202 \text{ mg} \cdot \text{kg}^{-1}$ for North Carolina and $261 \text{ mg} \cdot \text{kg}^{-1}$ for Louisiana. Soil respiration was also greatest at the California site: $134 \mu\text{mol} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ compared to $114 \mu\text{mol} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ for North Carolina site and $63 \mu\text{mol} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ for Louisiana. Variation between sites was partially attributed to differences in soil carbon content (California, $100 \text{ g} \cdot \text{kg}^{-1}$; North Carolina, $24 \text{ g} \cdot \text{kg}^{-1}$; Louisiana, $15 \text{ g} \cdot \text{kg}^{-1}$). Normalizing microbial biomass based on total soil carbon (microbial carbon / total carbon), in turn, resulted in California having the lowest value among the three sites (Fig. 1). Louisiana had the lowest metabolic quotient (respiration / biomass), while North Carolina had the highest metabolic quotient among the three sites. All trends among sites were consistent between fall 2000 and spring 2001.

Compaction, OM removal, and weed control

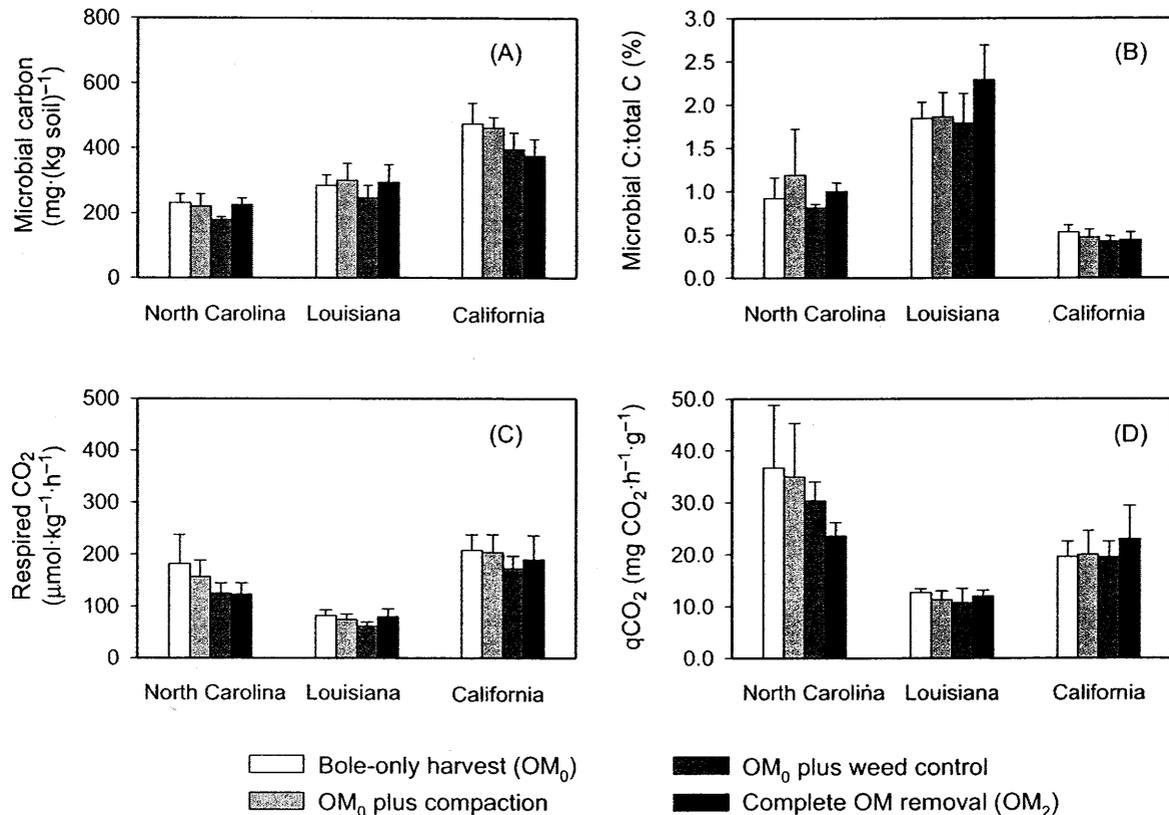
Reduction of soil porosity, surface OM, or weeds had a relatively mild effect on microbial biomass and respiration (Fig. 1, Table 1), with a few exceptions. No significant main effects of compaction were found at the Louisiana or California sites. Microbial biomass was only 1% greater at the Louisiana site and 2% lower at the California site on compacted compared to uncompacted plots when averaged for both sample periods. Similarly, respiration showed a nominal response to compaction at the sites in Louisiana (5% lower) and California (2% lower). The North Carolina site also showed minimal change in microbial biomass due to compaction in the fall, but 12% lower biomass on compacted plots compared to that on uncompacted plots ($P = 0.063$) in the spring. Microbial biomass, averaged for both sample periods, was 5% lower on compacted than on uncompacted plots at the North Carolina site.

Complete removal of surface OM (OM_2) resulted in significantly lower microbial biomass compared to that observed with bole-only harvesting in both the fall (21% lower) and spring (27% lower) at the California site (Fig. 1, Table 1). No differences in microbial biomass were found between treatments at the subtropical sites. Interestingly, respiration did not follow the same trend as microbial biomass. OM removal did not significantly affect respiration at either the California or Louisiana site, yet resulted in 32% lower respiration at the North Carolina site for the fall 2000 sample. As a consequence, the metabolic quotient was significantly lower at the North Carolina site ($P = 0.024$) and higher at the California site ($P = 0.038$) on the OM_2 plots. This response was not consistent across sampling dates, however.

Active weed control lessened microbial biomass and respiration at the subtropical sites (Fig. 1, Table 1). At the North Carolina site, microbial biomass was 21% lower in the fall and 32% lower in spring with weed control. Similarly, microbial biomass was 14% lower in the fall and 19% lower in spring with weed control at the Louisiana site. Respiration was approximately 30% lower for both measurement periods at the North Carolina site when competing vegetation was controlled. At the Louisiana site, respiration averaged 14% lower when competing vegetation was controlled.

Unlike the subtropical sites, microbial community response to weed control was inconsistent at the California site. Microbial biomass was 15% lower for weed control in the

Fig. 1. Effect of compaction, surface organic matter (OM) removal, and weed control on microbial biomass (A); microbial biomass / total C (B); respiration (C); and metabolic quotient (D). Values are means + SE for fall 2000 samples.



fall, while nearly identical values were found between treatments in the spring. Respiration was 10% and 2% lower in the fall and spring, respectively, when competing vegetation was controlled.

Significant compaction × weed control interactions were noted at the Louisiana and California study sites (Table 1). At the Louisiana site, respiration declined in compacted soil when weeds were controlled ($0.047 \pm 0.006 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for weed control vs. $0.060 \pm 0.006 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for no weed control), yet was stimulated in uncompacted soil when weeds were controlled ($0.063 \pm 0.005 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for weed control vs. $0.053 \pm 0.007 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for no weed control). In contrast, respiration increased slightly in compacted soil at the California site because of weed control ($0.088 \pm 0.022 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for weed control vs. $0.079 \pm 0.018 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for no weed control) and was lower in uncompacted soil because of weed control ($0.071 \pm 0.019 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for weed control vs. $0.084 \pm 0.020 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ for no weed control). The reasons for the opposite trends between the two sites are unclear. However, the relative differences in respiration between the treatment combinations were not large and were found only for the spring sampling date.

Harvesting effects

We measured microbial characteristics in adjoining reference stands at the North Carolina and California LTSP sites to provide a base-line comparison of harvesting effects. Although inferential statistical comparisons could not be made

because the reference stands were not included as replicated, randomized plots in the original experimental design, large differences between stand means were found. This was particularly apparent at California, where the average microbial biomass for the LTSP treatments was 40% less than that of the reference stand (Table 2). Similarly, basal respiration was 54% lower in the harvested stand ($0.134 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) than in the reference stand ($0.293 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) when averaged for fall and spring samples. The harvesting effect was not attributable to differences in soil carbon between the two stands. Average soil carbon content for the LTSP stand was $102 \text{ g}\cdot\text{kg}^{-1}$ compared to $94 \text{ g}\cdot\text{kg}^{-1}$ for the reference stand. Differences in community characteristics between adjoining stands were also found at the North Carolina site. Microbial biomass was 30% lower (Table 2) and respiration was 10% lower in the LTSP stand than in the reference stand.

Community function and structure

Bacterial communities from the subtropical sites metabolized the majority of carbon compounds on Biolog GN plates in both fall and spring samples (Table 3). In contrast, bacteria from the California site exhibited lower carbon utilization, metabolizing an average of 41 (out of 95) compounds in the fall and 56 in the spring. No main treatment effects or interactions due to compaction, OM removal, and weed control were found, with the exception of significantly lower carbon utilization following complete OM removal at the California site in the fall ($P = 0.001$) and spring ($P = 0.086$).

Table 1. Summary statistics for the main effects and interactions of compaction (C), organic matter removal (OM), and weed control (WC) on microbial community.

Source	Microbial biomass (carbon)		Microbial carbon / total carbon		Respiration		Metabolic quotient	
	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring
North Carolina								
C	ns	*	*	ns	ns	ns	ns	ns
OM	ns	ns	ns	ns	**	ns	**	ns
C × OM	ns	ns	ns	ns	ns	ns	ns	ns
WC	**	*	ns	ns	*	**	ns	ns
C × WC	ns	ns	ns	ns	ns	ns	ns	ns
OM × WC	ns	ns	ns	ns	ns	ns	ns	ns
C × OM × WC	ns	ns	ns	ns	ns	ns	ns	ns
Louisiana								
C	ns	ns	ns	ns	ns	ns	ns	ns
OM	ns	ns	**	ns	ns	ns	ns	ns
C × OM	ns	ns	ns	ns	ns	ns	ns	*
WC	**	**	ns	ns	*	ns	ns	**
C × WC	ns	ns	ns	ns	ns	**	ns	**
OM × WC	ns	ns	ns	ns	ns	ns	ns	ns
C × OM × WC	ns	ns	ns	ns	ns	**	ns	ns
California								
C	ns	ns	ns	ns	ns	ns	ns	ns
OM	**	*	*	ns	ns	ns	**	ns
C × OM	ns	ns	ns	ns	ns	ns	ns	ns
WC	**	ns	**	ns	**	ns	ns	ns
C × WC	ns	ns	ns	ns	ns	**	ns	**
OM × WC	ns	ns	ns	ns	ns	ns	ns	ns
C × OM × WC	ns	ns	ns	ns	ns	ns	ns	ns

Note: Accompanying treatment means for the main effects are shown in Fig. 1. *, significant at $\alpha = 0.10$; **, significant at $\alpha = 0.05$; ns, not significant at $\alpha = 0.10$.

Table 2. Comparison of microbial biomass between the reference stand and selected Long-Term Soil Productivity (LTSP) treatments at North Carolina and California study sites.

	North Carolina		California	
	Microbial biomass (mg·kg ⁻¹)	% of reference stand	Microbial biomass (mg·kg ⁻¹)	% of reference stand
Reference stand	309 (34)	100	678 (98)	100
Bole-only harvest (OM ₀)	251 (40)	81.2	474 (75)	68.9
OM ₀ plus compaction	207 (21)	66.9	413 (32)	60.9
OM ₀ plus weed control	175 (11)	56.6	418 (63)	61.7
Complete OM removal (OM ₂)	230 (25)	74.4	316 (38)	46.6
LTSP plantation average	216 (27)	69.8	405 (28)	59.8

Note: Microbial biomass values are averages (SE in parentheses) of fall 2000 and spring 2001 samples. OM, organic matter.

Average rate of well color development further articulates the difference in metabolic competence between sites (Fig. 2). Samples from California had a substantially longer lag period and slower metabolic rate than samples from North Carolina or Louisiana (data not shown for Louisiana). Similar metabolic patterns were found for bacterial metabolism of amines and polymers, while slight improvements in growth (40–46 h lag period and slightly higher maximum optical densities) were found for bacteria from the California site growing on carboxylic acids and amino acids. It is unlikely that these site differences in carbon utilization resulted from variation in inoculum density, since total bacterial PLFA content, indicative of bacterial biomass, was greater

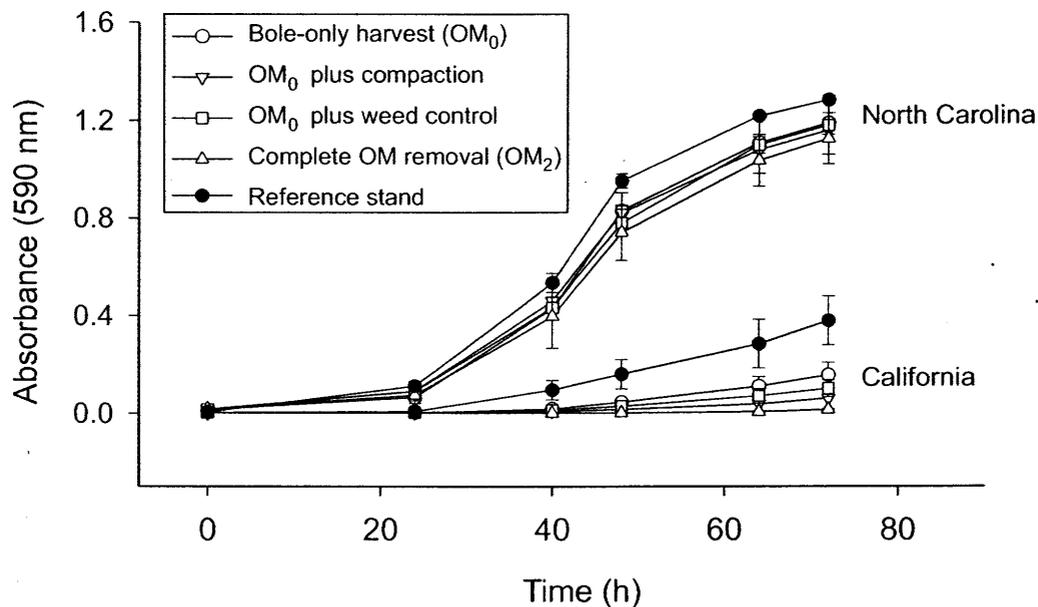
for California (28.0 ng·g⁻¹) than for either the North Carolina (18.0 ng·g⁻¹) or Louisiana (18.3 ng·g⁻¹) site.

The number of individual PLFAs varied between sites: 25 for Louisiana, 27 for North Carolina, and 32 for California. Visual differences in PLFA community structure patterns were evident between treatments using PCA. Soil compaction and weed control produced distinct patterns at all sites in comparison to patterns produced by bole-only harvesting (Fig. 3). These effects were significant ($\alpha = 0.10$) for PCA 2 at the North Carolina site ($P = 0.002$); for PCA 1 at the Louisiana site ($P = 0.0449$); and for PCA 1 ($P = 0.0647$) and PCA 2 ($P = 0.0611$) at the California site. Complete OM removal did not substantially shift the PLFA profile com-

Table 3. Effect of compaction, organic matter (OM) removal, and weed control on carbon utilization by culturable bacteria at Long-Term Soil Productivity (LTSP) sites.

LTSP treatment	No. of positive wells out of 95 total Biolog GN wells at 72 h					
	North Carolina		Louisiana		California	
	Fall	Spring	Fall	Spring	Fall	Spring
Bole-only harvest (OM ₀)	83 (2)	67 (1)	83 (3)	62 (3)	44 (5)	58 (1)
OM ₀ plus compaction	79 (3)	72 (6)	70 (7)	70 (5)	45 (11)	58 (7)
OM ₀ plus weed control	80 (2)	75 (2)	70 (8)	60 (2)	42 (6)	55 (4)
Complete OM removal (OM ₂)	79 (4)	75 (3)	69 (8)	61 (13)	24 (6)	46 (9)
Reference stand	85 (1)	81 (2)	na	na	49 (8)	62 (4)

Note: Values are means \pm 1 SE; na, not available.

Fig. 2. Average well color development on Biolog GN plates for selected treatments at the North Carolina and California Long-Term Soil Productivity study sites. Values are means \pm SE for fall 2000 samples. OM, organic matter.

pared to that produced by bole-only harvesting. This result was particularly surprising at the California site given the differences in microbial biomass and carbon utilization between the OM treatments. Similarly, the reference stand at the California site had a comparable PLFA pattern to that of bole-only harvesting, even though large differences in microbial biomass and respiration were observed between treatments.

Individual PLFA biomarkers were also significantly affected by the LTSP treatments. Both 10Me 16:0 and cy 19:0 increased, while 15:0 decreased because of compaction and weed control treatments at all sites (Table 4). Two additional biomarkers, a15:0 and cy 17:0, were modified by compaction and weed control at the California site. Fungal PLFA (18:2 ω 6) was approximately 2–3 times as great in the reference stand as at the LTSP plantation at the California site, suggesting that the lower microbial biomass found in the LTSP stand was due to a reduction of fungal biomass.

Regional differences in PLFA community structure are illustrated in Fig. 4. Clear separation of community structure, regardless of treatment, is shown between subtropical and Mediterranean sites along axis 1. Individual PLFAs with

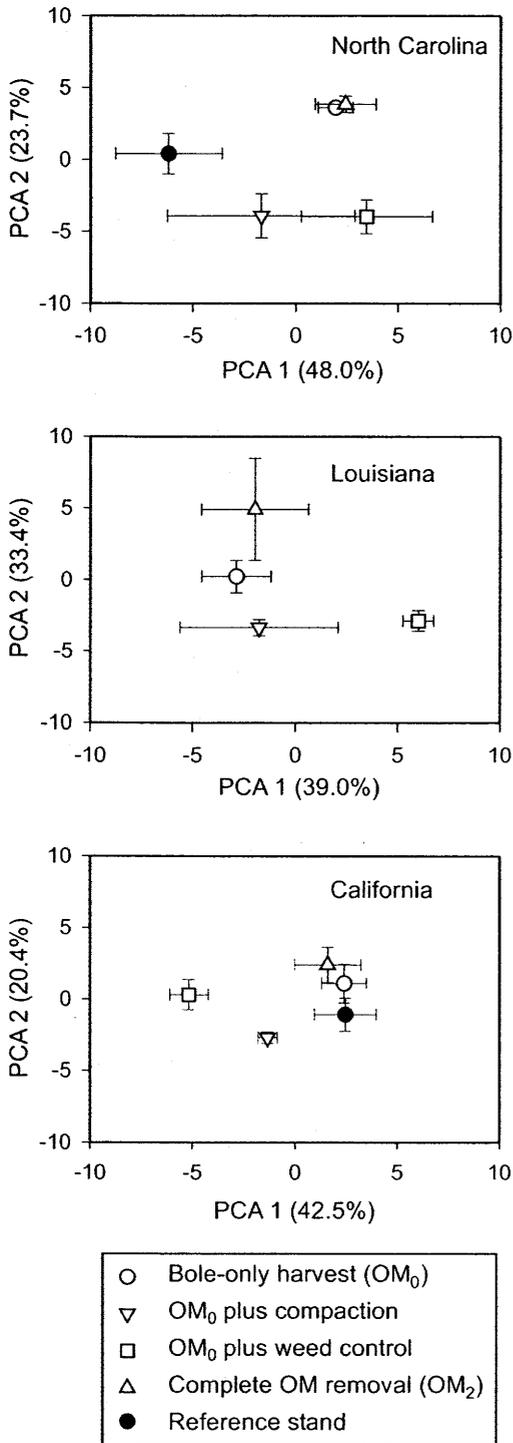
high correlation coefficients for axis 1 included 15:0, 10Me 18:0 (actinomycete), a15:0, cy 19:0, and 18:1 ω 9c (fungi).

Discussion

Soil compaction

We found little evidence that compaction modified mineral soil microbial community size or activity at either the subtropical or Mediterranean-type climate LTSP sites. This is an intriguing finding given the detrimental effects of compaction on higher life forms (Froehlich 1979; Conlin and van den Driessche 1996) and the importance assigned to monitoring soil compaction on publicly owned forests in the United States (Powers et al. 1998). Findings from other LTSP studies of soil biota support our results. Examples of minor or insignificant changes in microbial indices following compaction include microbial nitrogen at the North Carolina site (Li 2000), microbial carbon and surface CO₂ efflux at an oak–hickory site in Missouri (Jordan et al. 1999; F. Ponder, Jr., personal communication, 2000), percentage of mycorrhizal root tips on conifer seedlings at a mixed-conifer

Fig. 3. Effect of Long-Term Soil Productivity treatments on phospholipid fatty acid community structure. Each points represents the mean + SE from principle components analysis of phospholipid fatty acid mole percent data.



site in northern Idaho (Amaranthus et al. 1996), and litter decay (Kranabetter and Chapman 1999) and bacterial diversity (Axelrood et al. 2002; Chow et al. 2002) at sub-boreal

sites in British Columbia. Compaction, however, was responsible for reduced mycorrhizal diversity at the northern Idaho site (Amaranthus et al. 1996) and reduced nitrogen mineralization at the North Carolina site in the initial 5 years following treatment (Li et al. 2003). Tolerance of microbial communities to compaction at LTSP installations, although not universal, is noteworthy given that the aim of the compaction treatment was to increase bulk density to approximate root-limiting conditions.

Current understanding of the effects of soil compaction on microorganisms is far from complete. Previous studies have identified negative (Smeltzer et al. 1986; Dick et al. 1988; van der Linden et al. 1989; Kaiser et al. 1991; Torbert and Wood 1992; Breland and Hansen 1996), neutral (Kaiser et al. 1991; Santruckova et al. 1993; Breland and Hansen 1996; Jensen et al. 1996; Shestak and Busse 2005), or positive (Startsev et al. 1998) responses, yet few unifying concepts. We believe this reflects the complexity of soil disturbances that occur during mechanized harvesting and, in particular, during the creation of skid trails. Soil displacement, mixing, and removal of organic horizons often result during harvesting, complicating the primary effects of soil compaction. Our study, in comparison, isolated the effects of compaction from any confounding effects of soil displacement or mixing. No skid trails were created, heavy equipment was kept off all plots during harvesting, and logs were fully suspended during removal. Soil mixing was further avoided by temporarily removing surface OM prior to compacting. Therefore, comparison of our results with those from studies of skid trails (e.g., Dick et al. 1988) requires caution.

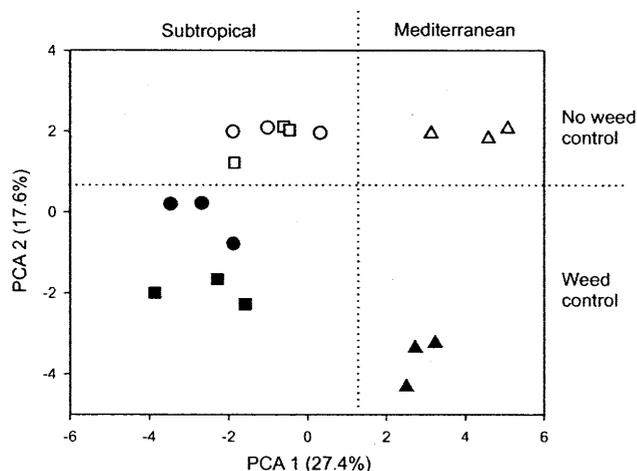
Soil compaction alters pore-size distribution and pore continuity, leading to reduced gas diffusion, nutrient and water movement, and accessible pore volume for soil organisms and roots (Greacen and Sands 1980). It stands to reason that microbial indices should reflect such changes to their habitat. A simple explanation for our contrary finding is that bulk density and total porosity recovered to pretreatment levels via biotic (roots, soil fauna) or abiotic (expansion and contraction) processes. This appears to be the case at the subtropical sites, where partial recovery of soil bulk density was found by the fifth year after treatment (Page-Dumroese et al. 2006). In contrast, soil porosity had not recovered on compacted plots at the California site. Bulk density values were 45% greater on compacted than on uncompact plots 5 years after treatment, with a sharp increase in uninhabitable micropores <0.1 μm in diameter (Paz 2001). Pores between 0.2 and 30 μm, preferred habitat of bacteria and fungi, declined by approximately 47% following compaction (Paz 2001). This suggests that the habitat needs of the microbial community were adequately met even following a large decline in available pore space. In support of this mechanism, Hassink et al. (1993) found that bacteria occupy only approximately 0.4% of the surface area of available pores in sand, loam, and clay soils. Thus, a 50% reduction in available porosity would still leave the majority of surface area uninhabited.

Inability of predators to access small pores in compacted soil may help to stabilize the microbial community (Breland and Hansen 1996). van der Linden et al. (1989) found that compaction of a silt loam soil completely eliminated accessible pores for microbivores. At the California site, nematode-

Table 4. Effect of site disturbance on soil phospholipid fatty acid (PLFA) content.

PLFA marker	PLFA content (mole %)					Reference stand	Min. significant difference
	Bole-only harvest (OM ₀)	OM ₀ plus compaction	OM ₀ plus weed control	Complete OM removal (OM ₂)			
North Carolina							
15:0	2.1ab	0.0c	0.8bc	2.2a		1.6 (0.8)	1.4
10Me 16:0	1.1b	3.7ab	4.6a	3.1ab		2.8 (0.4)	2.8
cy 19:0	2.8b	6.0a	7.4a	2.6b		4.0 (0.1)	2.3
18:2ω6	5.9a	5.9a	3.9a	5.9a		5.8 (0.3)	2.4
Louisiana							
15:0	2.3a	0.4b	0.6b	2.3a			1.2
10Me 16:0	1.3c	3.2b	4.7a	0.9c			0.9
cy 19:0	3.9b	8.1a	8.5a	3.5b			2.9
18:2ω6	2.8a	2.6a	2.8a	3.6a			1.6
California							
15:0	2.0a	0.1b	0.1b	1.9a		1.6 (0.2)	1.0
10Me 16:0	1.6b	3.6a	3.3a	2.0b		1.8 (0.5)	1.1
a15:0	4.9a	3.8b	3.7b	5.2a		4.2 (0.6)	0.9
cy 17:0	0.4b	1.5a	0.9ab	0.6b		0.7 (0.4)	0.8
cy 19:0	2.2b	5.6a	4.2a	2.1b		2.1 (0.3)	1.5
18:2ω6	1.7a	2.2a	1.6a	1.3a		3.8 (0.3)	0.9

Note: Only those bacterial PLFAs that showed significant differences between treatments plus fungal marker 18:2ω6 are shown. Means (followed by SE in parentheses for the reference stand only) within a row not sharing a common letter, excluding the reference stand, differ at $\alpha = 0.05$ by Tukey's studentized range test.

Fig. 4. Variation in phospholipid fatty acid community structure by climate zone (squares, North Carolina; circles, Louisiana; triangles, California).

accessible pores (>30 μm diameter) and protozoa-accessible pores (>5 μm diameter) both declined by approximately 70% following compaction (Paz 2001). Physical isolation of microorganisms is a double-edged sword, however. Protection from predators may benefit community stability at the cost of reducing plant nutrient availability. Compaction has been shown to reduce the turnover rate of nitrogen-rich microbial biomass (Holmes and Zak 1994), increase the percentage of water-filled pores and potential denitrification (Torbert and Wood 1992), and reduce nitrogen mineralization by restricting the accessibility of organic material (Breland and Hansen

1996). Hence, the conclusion from our study that compaction is generally benign to the microbial community is incomplete in the context of soil-plant processes.

Further, this generalization does not account for the changes in PLFA community structure found at all sites following compaction. Visual separation of compacted and uncompacted treatments in PCA was associated with changes in several individual PLFAs. Interestingly, a common response among sites was found for three PLFAs: 10Me 16:0 and cy 19:0 increased more than twofold, while 15:0 decreased sharply because of compaction. Although caution is suggested when interpreting changes in individual PLFA biomarkers (Haack et al. 1994), we believe this response resulted from reduced root growth and rhizosphere activity in compacted soil. Specifically, 15:0 is a positive indicator of root activity (Olsson et al. 1996), while 10Me 16:0 has been shown to double when roots are absent (Zak et al. 1996; Ringelberg et al. 1997). Biomarker cy 19:0 is an indicator of starvation conditions (Guckert et al. 1986) and may indicate a decline in readily available carbon associated with loss of root proliferation. Additional explanations for compaction-induced changes in community structure, such as limitations from reduced air-filled porosity, water logging, and nutrient diffusion, also have merit. Further study is needed to identify the mechanism(s) responsible for the PLFA shift and to clarify its ecological significance.

Surface OM removal and harvesting

We hypothesized that removal of insulating surface OM would be more detrimental to soil biota in the summer-dry climate of California than under the relatively consistent, year-round moisture conditions found at the subtropical sites.

Although this generally held true, the response to surface OM removal was not dramatic at any site.

After 10 years, complete OM removal had no effect on the selected microbial indices at the North Carolina site, with the exception of lower respiration for the fall sampling date. A similar lack of response to OM removal was reported for microbial nitrogen and nitrogen mineralization (Li 2000) at this site and for viable bacterial and fungal populations at LTSP-affiliated sites in Louisiana and Texas (Carter et al. 2002). We also found no detrimental effect of complete OM removal at the other subtropical site. The only clear response was found at the California site, where microbial biomass and carbon utilization were significantly lower in the fall and spring when OM was removed. Not all indices followed suit, however. Neither respiration nor PLFA community structure was affected by OM removal. This comes as a surprise, particularly in the case of PLFA community structure, which has been shown to be sensitive to site disturbance (Zogg et al. 1997; Waldrop et al. 2000; Siira-Pietikäinen et al. 2001). Instead, carbon utilization, a simple measure of functional diversity of culturable bacteria, was more sensitive in detecting site differences and treatment effects. Heterotrophic bacteria from the California site were less capable of metabolizing the suite of 95 carbon compounds than were communities from the subtropical sites, particularly in the fall when soil moisture content was low and surface OM was absent.

Complete removal of surface OM during site preparation is an extreme treatment. Our findings fail to corroborate earlier reports that maintaining litter and slash is beneficial to microbial communities in the mineral soil (Lundgren 1982; Ross et al. 1995), however. Instead, they suggest that other site factors associated with exposing mineral soil, such as erosion losses and protection of site nutrient pools, are of greater concern. The relatively small influence that surface OM had on soil temperature and moisture helps to explain our finding. At the North Carolina site, for example, Li et al. (2003) found that OM removal resulted in only a 1–2 °C increase in mean annual soil temperature and no change in mean annual soil moisture content in the surface 10 cm. Similarly, Paz (2001) found a 2–4 °C increase in soil temperature (10 cm depth) and no significant change in soil moisture content due to OM removal during midsummer at the California site.

In contrast to removing surface OM, overstory harvesting strongly affected the soil microbial communities. At the California site, microbial biomass, respiration, and fungal PLFA were 1.5–2 times as great in the uncut reference stand compared to the LTSP plantation. Bacterial community structure and carbon utilization were similar between the reference stand and LTSP plantation, suggesting that harvesting had a greater impact on fungi than on bacteria. This agrees with several studies that have found that clear-cutting reduces fungal populations (Bååth 1980; Bååth et al. 1995, Forge and Simard 2000) and either increases or has no effect on bacterial size and function (Niemala and Sundman 1977; Sundman et al. 1978; Lundgren 1982). We surmise that the decline in fungi resulted from changes in OM substrate quality associated with physical disruption of the O horizon and from reduced root and litter turnover compared to that in the

mature forest stand. Soil moisture availability and temperature were likely secondary factors, since they were not strongly affected by harvesting at the California site (Paz 2001).

The microbial community at the North Carolina site was also affected by overstory harvesting, although to a lesser degree than the California site. Average microbial biomass was 30% lower and respiration was 10% lower at the LTSP plantation than at the reference stand. This underscores the site-specific nature of harvesting and its effects on soil biota. In support, previous studies have reported a complete range of responses (negative, neutral, positive) by soil microorganisms to harvesting (Niemala and Sundman 1977; Lundgren 1982; Entry et al. 1986; Frazer et al. 1990; Tolander and Zak 1994; Bauhus and Barthel 1995; Chang et al. 1995; Ross et al. 1995; Edmonds et al. 2000; Forge and Simard 2000; Siira-Pietikäinen et al. 2001).

Interpreting the ecological effects of harvesting on microorganisms is a challenge. For example, does a 40% reduction in microbial biomass following harvesting, as measured at the California site, suggest an unhealthy or out-of-balance system? Or is the change in population size appropriate to meet the changing needs of a planted forest? In an example of resilience by forest soil microorganisms, Griffiths and Swanson (2001) examined a chronosequence of old-growth Douglas-fir stands in the Pacific Northwest and found that most microbial indices had recovered 15–40 years after harvesting. Jones et al. (2003), in a review of ectomycorrhizal literature, point out that while clear-cut logging can reduce total ectomycorrhizal inoculum, it typically does not influence the percentage of mycorrhizal-infected root tips on regenerating tree seedlings. Further, they suggest that the developing ectomycorrhizal communities, although less diverse than in older forest stands, are better adapted to the changing conditions in young forest stands. This is complemented by the results of Atlas et al. (1991), who compared community size and function of soil microorganisms following severe chemical disturbance and found that although the community size declined, the surviving organisms were generalists capable of maintaining a diversity of functions. Evidence from our study is supportive of these examples. Microbial biomass was reduced following harvesting at the California site without a corresponding shift in either carbon utilization or PLFA community structure. Continued monitoring of the soil community until canopy closure and development of an O horizon is needed to confirm this presumed resilience.

Weed control

Weed control had the largest and most consistent effect among the LTSP treatments on microbial biomass, activity, and community structure. This was particularly true at the two subtropical sites, where microbial biomass and respiration were 15%–30% lower on both sampling dates when weeds were controlled. Also, distinct PLFA patterns were found for weed-control treatments, indicating altered microbial community structure due to the continual absence of understorey vegetation. Interestingly, these declines in community characteristics counter the response of tree growth, which was universally higher when weeds were absent (Powers et al. 2005).

A parallel can be drawn between our results and those of

Vitousek and others (Vitousek and Matson 1985; Vitousek and Andariese 1986; Vitousek et al. 1992), who also examined the effects of intensive management in a North Carolina loblolly pine plantation. Vitousek's 5-year study found that weed control had a stronger influence on site nitrogen dynamics than did several harvesting and site preparation treatments. They identified a herbicide-caused decline in microbial nitrogen and suggested that it was largely responsible for increased net nitrogen mineralization, net nitrification, and off-site nitrogen loss. In effect, weed control reduced the microbial population size and its capacity to sequester nitrogen. Similarly, we found decreased microbial biomass and Li et al. (2003) reported increased nitrogen mineralization and nitrification at the North Carolina LTSP site due to weed control.

Weed control can alter microbial communities by either (1) direct herbicide toxicity or (2) reduced soil carbon input from root turnover, litterfall, and rhizosphere exudates by the elimination of understory vegetation. Although some evidence points to direct herbicide effects on soil organisms in North Carolina (Andariese and Vitousek 1988), Vitousek et al. (1992) disregarded this possibility, since changes in microbial function lasted considerably longer than the herbicide residence time. Also, other studies of herbicide toxicity have shown no detrimental effects on microbial communities in plantation soils of varying texture and OM content (Busse et al. 2001a, 2001b). Thus, we hypothesize that the persistent effect of weed control in rapidly growing, short-rotation pine forests is a function of reduced input of OM into soil.

The effect of weed control was less pronounced at the California site than at either subtropical site. Microbial biomass and respiration declines were small and inconsistent, while no effect on carbon utilization was observed. Similar results were reported after 10 years of shrub control in ponderosa pine plantations in the Mediterranean-type climate of northern California (Busse et al. 2001b). We believe that these site differences are a function of the dominant understory life form and its growth potential. The California site has shrub-dominant, comparatively slow-growing understory vegetation, whereas the subtropical sites are more productive and have a greater dominance of herbaceous species.

Conclusion

We found that microbial communities in mineral soil at both the subtropical and Mediterranean-type climate LTSP sites were largely unaffected by disruption of soil porosity, OM, and understory vegetation. Of the treatment combinations, only weed control at the subtropical sites resulted in a consistent, moderate change in community size, activity, and structure. A lack of response to compaction was particularly noteworthy. Comparison of LTSP treatments with adjacent reference stands indicated that the initial perturbation created during clear-cut harvesting, and its affect on carbon input and microclimate, outweighed any additional impact of compaction, aboveground OM removal, or vegetation control on soil biota.

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