

Compaction Alters Physical but Not Biological Indices of Soil Health

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ABSTRACT

Current management and harvesting practices can compact forest soils and degrade soil health. However, effects of soil compaction on microbial processes and composition are poorly understood. We measured microbial community responses to compaction in a sandy loam and a clay loam soil under laboratory and field conditions. Treatments of no, moderate (approximately 20% increase in bulk density), and severe (approximately 40% increase) compaction were manually applied to intact soil cores. A 67-d laboratory experiment, punctuated by four sampling dates, was used to evaluate microbial indices (biomass, respiration, total and culturable bacteria and fungi, N mineralization, surface CO₂ efflux, C use (Biolog), and phospholipid fatty acids [PLFA]) and their relationship to soil physical properties (bulk density, pore-size distribution, water-holding capacity [WHC], gas diffusion). Macropores (>30 μm diam.) were reduced 50 to 90% in compacted samples. In contrast, habitable-sized pores for microorganisms (0.2–30 μm diam.) increased at least 40% in both soils with compaction. Despite these changes, microbial measures were either unaffected by compaction or showed inconsistent increases (e.g., fungal hyphae, C use, total PLFA) across sampling periods and soil types. Surface CO₂ efflux was reduced 34 to 51% in severe compaction samples. Minimal changes in microbial respiration indicate that reduced efflux was due to restricted gas diffusion. Microbial indifference to compaction also was verified at two mixed-conifer plantations in northern California. Soil strength values, ranging from 75 to 3800 kPa (no to severe compaction), were unrelated to either microbial respiration or biomass. The results show broad tolerance of microbial communities from contrasting soil textures to compaction, and indicate a poor link between physical and biological indices of soil health.

FOREST MANAGERS have long acknowledged the potential negative impact of compaction due to ground-based harvesting equipment on forest health and function. As a consequence, guidelines are established for nearly all USDA Forest Service regions that set threshold levels of soil compaction beyond which mitigation is needed (Powers et al., 1998). Decompaction using subsurface tilling is a preferred site-preparation treatment by many public and private land managers following harvesting in the west. Compaction disrupts soil physical integrity by modifying porosity and impeding gas, water, nutrient, and root movement in the profile (Greacen and Sands, 1980), often leading to a decline or cessation of plant growth. Examples of reduced early tree growth due to soil compaction are well documented in literature (Cochran and Brock, 1985; Donnelly and Shane, 1986; Froehlich et al., 1986; Helms and Hipkin,

1986; Conlin and van den Driessche, 1996; Gomez et al., 2002b; Heninger et al., 2002).

On public lands, ameliorative treatment is generally required when soil bulk density exceeds pretreatment levels by 15% on at least 15% of a harvested area (Powers et al., 1998). Although some regions substitute total porosity, macroporosity, or soil strength as threshold parameters in place of bulk density, the intent is unchanged: to monitor and mitigate detrimentally compacted soils. Guidelines for soil compaction are empirical, based on field experience and practicality, and take a conservative approach to soil management by lumping virtually all soils as one regardless of their origin, texture, or organic matter content.

Recent evidence from the North American Long-Term Soil Productivity Study (LTSP), which examines the effects of compaction, organic matter removal, and vegetation control on forest sustainability, challenges this practice. Gomez et al. (2002a, 2002b) found highly variable responses to compaction along a soil textural gradient in ponderosa pine and mixed-conifer plantations in the Sierra Nevada Mountains of California. Compaction was detrimental to plant-water availability and conifer growth in a clay soil, even though plant N uptake and N mineralization were generally improved. Conversely, plant growth and water availability were improved due to compaction in a coarse-textured soil, while N dynamics were unaffected. A complex relationship between compaction and soil microorganisms is apparent from the variety of responses found in field studies. For example, several investigations have found decreases in microbial activity or biomass due to compaction (Dick et al., 1988; van der Linden et al., 1989; Kaiser et al., 1991; Torbert and Wood, 1992; Li et al., 2003), while others report either no relationship (Smeltzer et al., 1986; Jordan et al., 1999; Ponder and Tadros, 2002) or a positive response by microorganisms (Breland and Hansen, 1996).

Numerous physical and biological factors contribute to the ambiguous response of microorganisms to compaction. Changes in the physical habitat, particularly altered pore-size distribution, may benefit the microbial community by increasing the volume of habitable pores while providing protection from larger predators (Postma and van Veen, 1990; Hassink et al., 1993). Alternatively, compaction-induced declines in air-filled porosity can restrict O₂ diffusion (Santruckova et al., 1993), increase CO₂ accumulation (Conlin and van den Driessche, 2000), and favor anaerobic conditions (Linn and Doran, 1984) to the detriment of the general community. Diversity of forest soil types, regional climates, and functional groups of soil organisms adds to the complexity, making

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Abbreviations: AWCD, average well-color development; LTSP, North American Long-Term Soil Productivity; PCA, principal component analysis; PLFA, phospholipid fatty acid; WHC, water holding capacity.

predictions of microbial responses to compaction difficult. Further, the effects of soil compaction are often confounded during harvesting by concurrent mixing and displacement of the surface horizon, inadvertently altering or reducing soil nutrient pools (Dick et al., 1988).

Federal guidelines for public lands in the USA mandate remediation of compacted soils following timber harvesting and related activities. Whether compaction is universally detrimental to soil health, however, often is assumed yet untested in many soils. We challenged this assumption by measuring microbial community responses to compaction in a sandy loam and a clay loam soil under laboratory and field conditions. Our objective was to determine whether moderate or severe compaction decreases microbial community size, activity, or diversity in differing soil textures. The underlying theme was to characterize the link between soil physical and biological properties using several indices of soil health based on the concepts presented by Doran and Safley (1997).

MATERIALS AND METHODS

Laboratory Experiment

Soil Collection and Experimental Design

Intact soil cores (5 cm length by 10 cm diam.) were collected from two forested sites in northern California. The sites are part of the LTSP research network (Powers et al., 1998), and are located on the western slope of the Sierra Nevada Mountains, each about 45 km northeast of Oroville, CA. Site selection was based on providing contrasting soil textures (a clay loam and a sandy loam) from a similar precipitation (1600–1800 mm) and elevation (800–1200 m) zone. The clay loam soil (fine, mixed, superactive, mesic, Typic Palexerult) was derived from metamorphosed basalt, and the sandy loam (coarse-loamy, mixed, superactive, mesic, Typic Dystroxerept) originated from granodiorite. Organic C content of the two soils is 45 and 28 g kg⁻¹, respectively (Gomez et al., 2002b). Vegetation at both sites is dominated by approximately 100-yr-old mixed-conifer overstories of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and sugar pine (*Pinus lambertiana*). The clay loam site (Challenge) was harvested in 1990 and the sandy loam site (Rogers) was harvested in 1997. Factorial combinations of compaction (no, moderate, severe) and organic matter (bole removal, whole-tree removal, whole tree + forest floor removal) treatments were installed, and sites were planted within 1 yr of harvesting. Gomez et al. (2002b) present additional site and soil characteristics.

Samples were collected from the edge of the LTSP plantations in untreated areas with no visible signs of vehicle traffic, soil mixing, or O horizon disturbance. We avoided collecting samples from within the adjacent mature stands to limit the number of excised roots in the soil cores. Mineral soil was collected by gently removing the O horizon, inserting a 10 cm diam. polyvinylchloride (PVC) collar to a depth of 5 cm, and carefully digging around the collar. A 3-cm headspace was left at the top of each core, and the cores were covered with aluminum foil before transport to the laboratory.

Average moisture content and WHC were determined using nine randomly selected cores of each soil type. The remaining cores were wetted to 60% WHC and allowed to equilibrate for a minimum of 2 wk at room temperature (approximately 23°C) before compaction. During the equilibra-

tion period, surface CO₂ efflux was measured every 48 h with an infrared gas analyzer (LI-6200, LI-COR, Lincoln, NE) to monitor the flush of CO₂ from decaying roots. Bulk densities were estimated from core weights and volumes, corrected by the average moisture content of the destructively sampled cores. Samples with CO₂ efflux values or bulk densities greater than one standard deviation from the mean were discarded.

Forty-eight cores per soil type were randomly assigned to the treatments before compaction. Three levels of compaction (no, moderate, severe) were applied to the intact cores. Soils were compacted manually using a weighted and capped PVC pipe, slightly smaller in diameter (9.5 cm) than the soil cores. Preliminary testing had shown that this method produced uniform soil strength with depth. Soil volume was reduced 15% for moderate compaction and 30% for severe compaction. These levels were chosen to cover the range of bulk density increases apt to occur under operational field conditions. Sixteen replications of each treatment were arranged in a completely randomized experimental design. Soil water content was maintained at 60% WHC during the experiment by frequent weighing and additions as necessary.

Soil Physical and Microbial Measurements

Four replications of each treatment were destructively sampled on four harvest dates (4, 11, 32, or 67 d after compaction) to determine short-term changes in soil physical and biological characteristics. Measurements taken on each date included bulk density, microbial biomass, respiration, total bacteria, bacterial biomass, fungal hyphal length, fungal biomass, culturable bacteria and fungi, CO₂ efflux, N mineralization, and C use (Biolog). Phospholipid fatty acids were measured only on Day 67 samples. Surface CO₂ efflux was measured semi-weekly throughout the experiment as well as on harvest dates.

The bulk density of each core was determined by measuring total soil weight (wet) and volume, and correcting for the moisture content determined on subsamples. Soil from each core was then sieved (8 mm), mixed, and subsampled for microbial analyses within 30 min. of disruption. Subsamples for PLFA analysis were frozen at -20°C for subsequent analysis, and subsamples for N mineralization were stored at 4°C before analysis of inorganic N.

Pore-size distribution was determined on intact soil cores by the Division of Agriculture and Natural Resources laboratory, Univ. of California, Davis. Three replicates of each compaction treatment and soil were compared using standard pressure-plate procedures for soil moisture retention curves (Klute, 1986). Volumetric water content was determined at 0, 10, 30, 100, 500, and 1500 kPa. Corresponding maximum pore diameters are >30, 30, 12, 3, 0.6, and 0.2 μm (Papendick and Campbell, 1981).

Respiration was measured by infrared gas analysis on 25 g samples (equivalent dry weight) during the initial 4 h following core sampling. Microbial biomass was measured within 2 h of sampling by substrate-induced respiration (Anderson and Domsch, 1978), using 25 g of soil and 5 g kg⁻¹ of glucose.

Total bacteria and fungal hyphal lengths were quantified by epifluorescent microscopy (Bottomley, 1994). Briefly, 3 g of soil (dry weight equivalent) was mixed with 27 mL of 0.15 M NaCl for 10 min on an orbital shaker. For bacteria, samples were diluted with saline, filtered successively through 8.0- and 3.0-μm filters, preserved with 95% formalin, and stored up to 14 d at 4°C before counting. Samples were equilibrated at room temperature before staining with acridine orange and filtering onto 0.2-μm blackened filters. Total number and size class (<0.5, 0.5–1.5, and >1.5 μm diam.) of bacteria were each counted on 10 fields per filter. Bacterial biomass was

calculated by the method of Bottomley (1994). For fungi, samples (200-fold final dilution) were mixed with 0.2% calcofluor and allowed to stain for 30 min. before filtering on 0.4- μm blackened filters. Hyphal length and width were measured on a minimum of 30 fields per filter to estimate biomass and total length (Bottomley, 1994).

Culturable bacteria were enumerated by dilution plating (duplicate samples) on tryptic soy agar after a 14-d incubation at 28°C. Fungi were enumerated on malt extract agar following a 3-d incubation.

Monthly net N mineralization was measured as the change in NH_4^+ and NO_3^- concentrations between Day 4, 32, and 67 samples using the distillation method of Bremner (1965). Briefly, 5 g of soil were suspended in 50 mL of 2 M KCl, mixed for 1 h, and distilled following the addition of 0.2 g carbonate-free magnesium oxide. Distillates were titrated with 0.001 M HCL to determine NH_4^+ concentration. Nitrate concentration was determined by adding 0.2 g of Devarda's alloy to the sample, further distilling, and titrating with 0.001 M HCL.

Changes in the functional diversity of the microbial community due to compaction were measured on Biolog GN plates (Biolog, Hayward, CA). Soil inoculum was prepared by mixing 3 g of soil (dry weight equivalent) in 27 mL of 0.15 M 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. Biolog plates were incubated in the dark at 28°C for 72 h, and bacterial growth (optical density at 590 nm) was measured three times per day. Average well color development (AWCD) of the 95 wells was corrected by subtracting the optical density of the control well (no C source).

Phospholipid fatty acid community structure was determined using a procedure modified from Frostegard et al. (1993). Soil (3 g) was extracted with a one-phase solution of chloroform, methanol, and citrate buffer (0.15 M, pH4, 1:2:0.8 v/v/v). The solution was then filtered through glass wool, and two additional chloroform rinses were used to extract lipids from the soil. Lipids were fractionated on a silica column (J and W, Folsom, CA) into neutral-, glyco-, and phospholipids. The phospholipids were then converted to methyl esters using a solution of sulfuric acid (4%) in methanol (1:1, v/v), and an internal standard (12 μg of methyl nonadecanoate) was added. Sample analysis was conducted on a Varian 3800 gas chromatograph equipped with an autosampler and coupled to a Star data analysis workstation (Varian Inc., Palo Alto, CA). An HP-5 (60 m \times 0.25 mm 250 μm) capillary column was used with He as the carrier gas and a temperature program as described by Frostegard et al. (1993). Methyl esters were identified by mass spectrometer analysis using an HP 5973 mass-selective detector (Agilent, Palo Alto, CA) coupled to an HP 6890 engine. Individual PLFA content (ng g^{-1} soil) was determined relative to the peak size of the internal standard.

Field Validation

Soil physical and microbial characteristics were compared at the two LTSP plantation sites in May 2001. Four transect lines were established in the no, moderate, and severe compaction plots at each site. Five sample points were taken per transect line for a total of 120 sample points. Sampling protocol followed a strict progression at each sample point: (1) surface CO_2 efflux was measured within a 12.6 cm^2 sampling area using a LI-6200 infrared gas analyzer, (2) soil strength was measured to a minimum depth of 15 cm within the same sampling area using a CP20 recording cone penetrometer (Rimik, Australia), and (3) a soil sample (0–15 cm depth) was collected within the sampling area for laboratory analysis of

microbial biomass and respiration. All sampling was completed within 20 min. at a given sample point. Soil samples were sieved (2 mm) and analyzed for microbial biomass and respiration as described above within 24 h of collection. Soil organic matter content also was determined on all samples by loss-on-ignition (Hesse, 1971).

Statistical Analyses

All measures from the laboratory experiment, with the exception of semi-weekly CO_2 efflux, were analyzed using a fixed-model ANOVA and Tukey's mean comparison (SAS Institute, 1998). Soil compaction and sampling date were the main effects. Semi-weekly measurements of CO_2 efflux were analyzed by repeated measures analysis using PROC MIXED (SAS Institute, 1998). For this model, compaction was a fixed effect and time was a random effect since differences in time were not expected but serial correlation of the consecutive measurements was expected. Regression analysis was used to determine the relationship between physical (soil strength) and biological (microbial biomass and respiration) characteristics measured in the field. Data from the two soils were not compared statistically in either experiment. Significance for all statistical analyses was at $\alpha = 0.05$ unless otherwise stated.

Functional diversity was compared using the area-under-the-curve data for each Biolog well (Guckert et al., 1996). Structural diversity was compared using the content (ng g^{-1} soil) of all PLFAs. We used principal component analysis (PCA) to explore (i) compaction related changes in microbial population function and structure and (ii) potential relationships among soil type, treatments, and soil biological and physical properties measured in the laboratory experiment (all microbial and physical measures).

RESULTS

Laboratory Experiment

Soil Physical Properties

Compaction of our cores showed major changes in the physical properties of both soils. Bulk density was 24% higher than the control (no compaction) with moderate compaction in the clay loam soil and 20% in the sandy loam soil. Severe compaction cores had a 44% increase in bulk density for both soil types (Fig. 1).

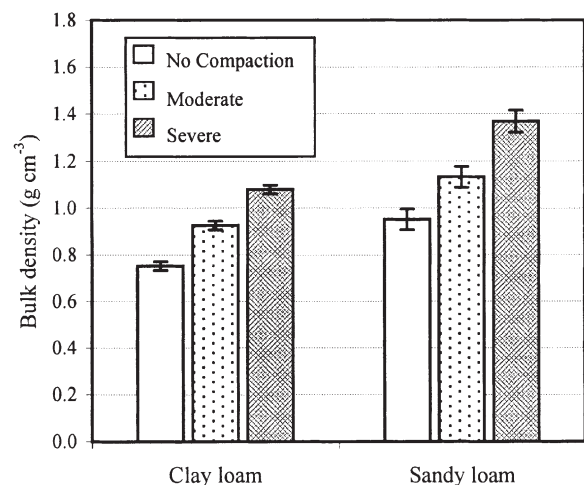


Fig. 1. Bulk density of a clay loam and a sandy loam soil following manual compaction. Values are means (\pm s.e.; $n = 16$) of four replicates from four sampling dates (4, 11, 32, and 67 d after compaction). No statistical differences (Wald-Z test, $\alpha = 0.05$) were found between sampling dates for either soil.

Treatment differences were significant ($P < 0.001$) for both soils. However, no statistical differences in bulk density were found between sampling dates, which is consistent with a lack of physical recovery from compaction during the 2-mo experiment.

Substantial changes in pore volume and pore-size distribution were also related to compaction. Total porosity decreased 26% in the clay loam and 20% in the sandy loam with severe compaction (Fig. 2). Reflected in this overall decline were large decreases in macroporosity ($>30 \mu\text{m}$ pores), offset in part by increases in microporosity ($<30 \mu\text{m}$ pores). Macropores (air-filled pores) in the clay loam soil decreased 68 and 89% for the moderate and severe treatments, respectively. Corresponding declines in the sandy loam soil were 52 and 75% relative to the no compaction treatment. In contrast, microporosity was 75% higher than the control for each compaction treatment in the clay loam and 39% higher for each treatment in the sandy loam. Moderate compaction was associated with changes in the volume of the larger micropores ($3.0\text{--}30 \mu\text{m}$ diam.), while severe compaction was associated with changes in the volume of the smaller pores ($0.2\text{--}3.0 \mu\text{m}$ diam.) in comparison with the control (data not shown). The smallest micropores ($<0.2 \mu\text{m}$ diam.) increased 61% in the clay loam but remained unchanged in the sandy loam. These changes in porosity resulted in increases in volumetric water content. For both soils, increased water content was approximately 20% higher with moderate compaction and 44% with severe compaction. In the clay loam, the combination of decreased macropores and increased water content reduced air-filled porosity below the $0.1\text{--}0.3 \text{ cm}^3 \text{ cm}^{-3}$ volume considered as a critical threshold for root respiration (Grable and Siemer, 1968) (Fig. 2). Main effects of compaction were significant ($\alpha = 0.05$) for changes in total porosity, macroporosity, and habitable pores ($0.2\text{--}30 \mu\text{m}$) in the clay loam, and for macroporosity only in the sandy loam.

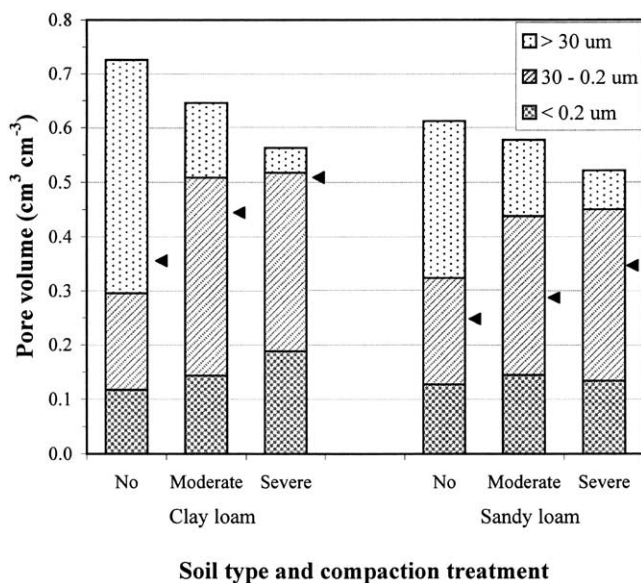


Fig. 2. Pore-size distribution determined from moisture retention curves. Rotated triangles represent volumetric water content during the experiment.

Surface Efflux of Carbon Dioxide

Surface CO_2 efflux was assessed semi-weekly as an integrative measure of microbial respiration and gas diffusivity. No statistical differences in CO_2 efflux were observed before treatment (time zero) (Fig. 3). The effects of compaction were strongest in the clay loam soil: treatment means for the 67-d experiment were 2.14, 1.68, and $1.05 \mu\text{mol m}^{-2} \text{s}^{-1}$ for no, moderate, and severe treatments, respectively. For the sandy loam, respective means were 0.80, 0.60, and $0.53 \mu\text{mol m}^{-2} \text{s}^{-1}$. The main effect of compaction was significant for the clay loam ($P < 0.0001$) and not for the sandy loam ($P = 0.439$).

Repeated measures analysis showed a significant time effect for both soils ($P = 0.035$ and 0.020 clay loam and sandy loam, respectively). Regardless of treatment, there was elevated CO_2 efflux for the sandy loam soil at the start of the experiment, suggesting a flush of CO_2 from excised roots (Fig. 3). Increased respiratory activity lasted only until Day 10, however. There was no indication of a CO_2 flush from decaying roots at the start of the experiment in the clay loam soil but efflux in the no compaction treatment rose to an unusual peak on Day 10 before stabilizing. A treatment \times time interaction was found for the clay loam ($P = 0.012$), as the compacted treatments generally showed less temporal variation in CO_2 efflux compared with the control.

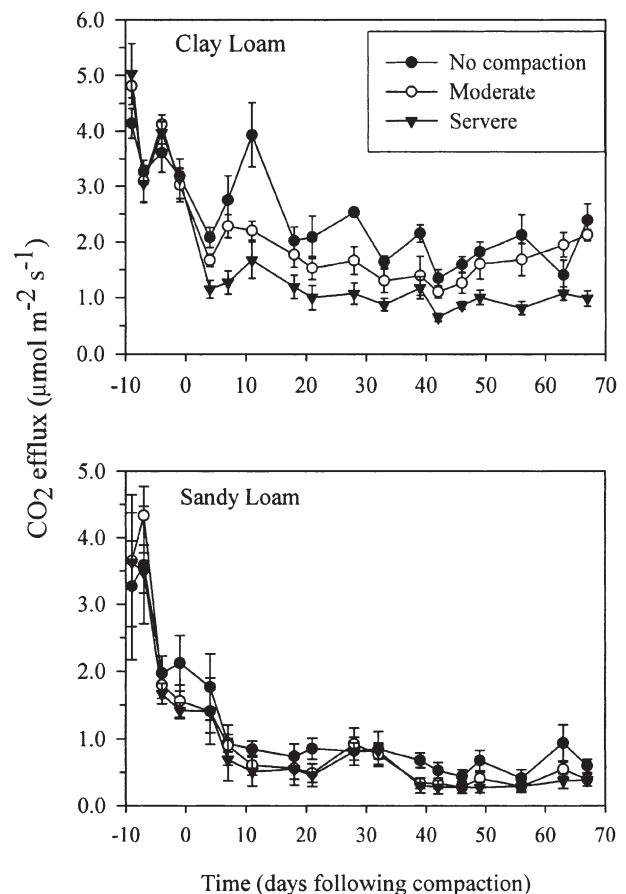


Fig. 3. Effect of moderate and severe compaction on surface CO_2 efflux. Values are means ($n = 4$) with standard error bars.

Table 1. Effects of compaction on microbial community size and activity in sandy loam and clay loam soils.†

Soil type	Days after compaction	Compaction	Community size			Community activity		
			Microbial biomass	Total bacteria	Viable bacteria	Fungal hyphae	Respiration	N mineralization
			mg C kg ⁻¹	— × 10 ⁷ g ⁻¹ —	m g ⁻¹	μmol g ⁻¹ h ⁻¹	mg N kg ⁻¹	
Clay loam	4	no	905ns	6.3ns	1.5ns	9.0ns	0.20ns	nd
		moderate	814	7.3	1.1	9.2	0.23	nd
		severe	935	9.2	1.4	8.8	0.26	nd
	11	no	1253ns	8.4ns	1.3ns	13.9ns	0.25ns	nd
		moderate	1030	6.2	1.5	12.5	0.20	nd
		severe	1229	6.2	1.1	11.1	0.28	nd
	32	no	1162ns	11.9ns	1.4ns	8.8b	0.25ns	-17.8b
		moderate	1068	11.5	1.2	10.4ab	0.24	-0.87ab
		severe	1059	13.3	1.3	12.6a	0.21	9.3a
	67	no	1010ns	12.1ns	1.5ns	11.8ns	0.24ns	14.0ns
		moderate	1259	13.4	1.3	7.4	0.26	8.2
		severe	1178	12.8	1.6	8.5	0.19	4.3
Sandy loam	4	no	544ns	3.7ns	0.5ns	4.5b	0.12ns	nd
		moderate	654	3.9	0.4	4.8ab	0.11	nd
		severe	597	5.2	0.6	5.8a	0.15	nd
	11	no	482ns	4.0ns	0.8ns	6.4ns	0.11ns	nd
		moderate	626	5.0	0.8	6.1	0.13	nd
		severe	682	5.1	1.0	7.3	0.17	nd
	32	no	355ns	3.3ns	0.4ns	7.5ns	0.08ns	15.9ns
		moderate	401	4.0	0.4	7.8	0.08	9.0
		severe	431	3.8	0.4	8.5	0.08	7.7
	67	no	453ns	2.0ns	0.5ns	10.7ns	0.14ns	-9.7ns
		moderate	465	2.2	0.3	11.7	0.09	-6.7
		severe	427	1.8	0.4	13.8	0.09	-13.8

† Means ($n = 4$) within a column and sampling date not followed by the same letter are significantly different at $\alpha = 0.05$. nd = no data; ns = not significant.

Microbial Community Size and Activity

Microbial characteristics varied considerably between soils, but not between compaction treatments. The clay loam generally had twice the community size and activity as the sandy loam soil (Table 1). Few differences in community characteristics were related to compaction, however. Only 3 out of 44 comparisons (6 microbial indices \times 4 sampling dates \times 2 soils; N-min only reported for two sampling dates) showed statistically significant treatment effects (Table 1). Fungal hyphal length was greatest in the severe treatment on Day 4 in the sandy loam and on Day 32 in the clay loam. Nitrogen mineralization also was greater following severe compaction on Day 32 for the clay loam. No negative effects with compaction were found.

There was a significant main effect of time on all microbial measures except viable bacteria and respiration for the clay loam. No general pattern of increase or decline across sample dates was found, however, indicating a random variability with time. Compaction \times time interactions were found for respiration in the sandy loam and N mineralization in the clay loam.

Carbon Use (Biolog)

Carbon use by bacteria varied between soils and among compaction treatments. Average well-color development was two to three times greater for the clay loam compared with the sandy loam soil (Fig. 4). Bacterial responses to compaction were unique for each soil. In the clay loam, severe compaction was associated with greater AWCD compared with no compaction ($P = 0.052$). Differences between treatments were greatest on Day 67, although the compaction \times time interaction was not significant ($P = 0.843$). In contrast, a transient response with compaction was found for the sandy loam

soil. Significantly greater C use was noted in the severe compaction treatment than either moderate or no compaction ($P < 0.0001$) on Day 11 only, yielding a significant compaction \times time interaction ($P < 0.0001$). Differences among compaction treatments were consistent regardless of substrate type (carbohydrates, carboxylic acids, amino acids, polymers). Substrate richness (number of 95 compounds metabolized) also responded positively with compaction in the clay loam soil. Moderate and severe compaction treatments averaged 12% greater substrate richness compared with the control soil ($P = 0.013$), primarily as a result of metabolism of carbohydrates (N-acetyl-D-galactosamine, i-erythritol, D-galactose, α -D-glucose, D-mannitol, and L-rhamnose). No differences in substrate richness were found among treatments for the sandy loam soil.

Principal component analysis of C use data did not indicate that compaction treatment differences were a significant source of data variability, with two exceptions. Severe compaction samples had larger component loadings than either moderate or no compaction samples on Day 67 (clay loam) and on Day 11 (sandy loam). In both cases, however, treatment differences were subtle and the main principal components (PCs) only explained $<65\%$ of the variation in the data. Differences in substrate use between treatments appeared to be random.

Phospholipid Fatty Acid Profiles

Forty PLFAs were identified in each soil on Day 67 of the experiment. Total PLFA content was more than two-fold greater in the clay loam than the sandy loam soil (Table 2), presumably indicative of greater microbial biomass. No differences in individual bacterial (including actinomycetes) or fungal PLFA were found in the clay loam soil. In contrast, 10 out of 15 bacterial

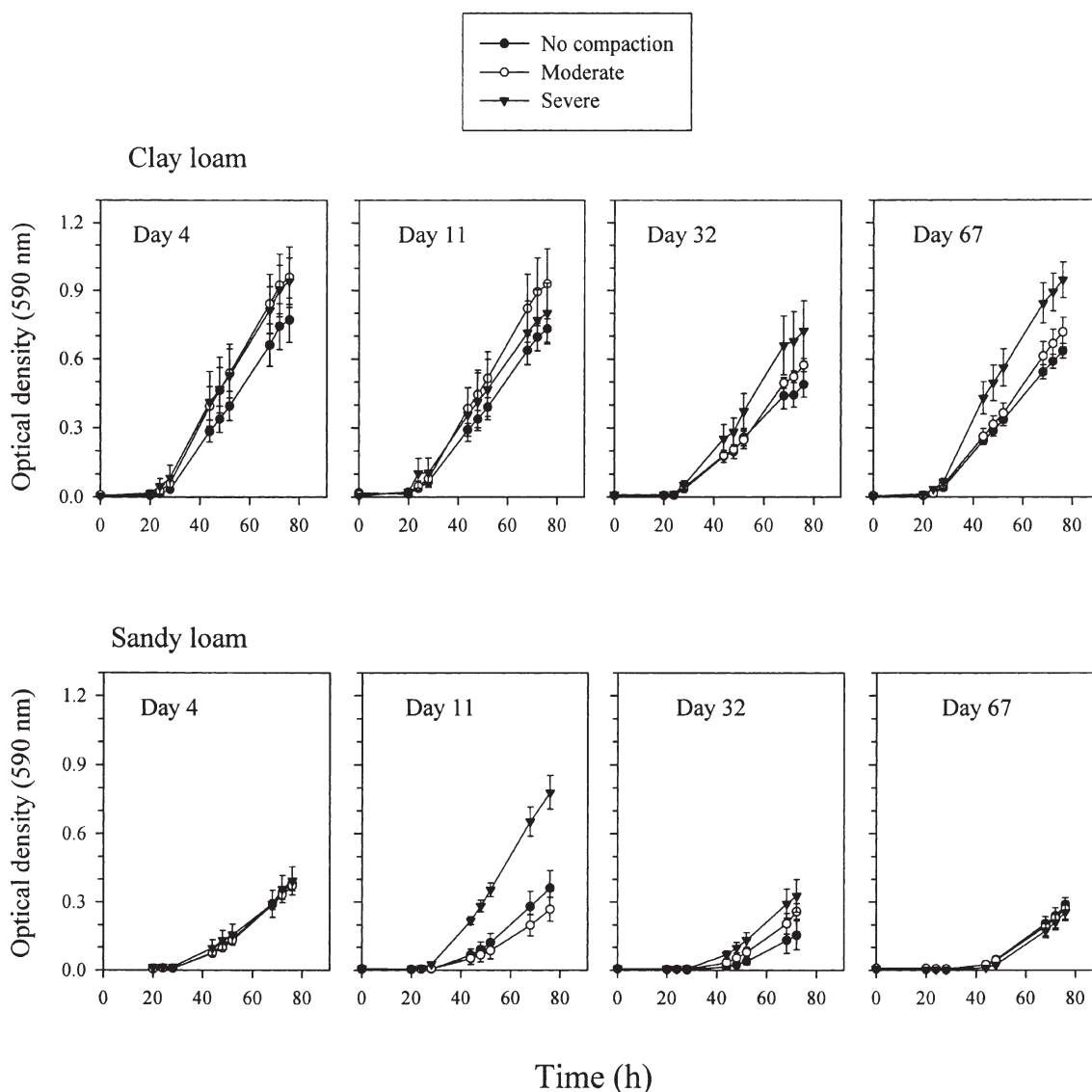


Fig. 4. Compaction effects on carbon utilization profiles (Biolog) for both soils. Temporal change in average well color development (95 single carbon compounds) is presented (\pm s.e.; $n = 4$).

PLFAs increased with severe compaction in the sandy loam soil. Moderate compaction was associated with a decline in fungal and actinomycete PLFA, although the treatment effect was not significant ($\alpha = 0.05$) due to considerable within-treatment variation.

Principal component analysis interpretation was similar to the ANOVA results for both soils. No pattern of variability was related to compaction in the clay loam soil. However, for the sandy loam soil, the first principal component (PC1) explained 40% of the variability in the dataset and was related to differences between treatments. Individual PLFAs that had the highest loadings on PC1 (contributing to the variability explained by PC1) were the same as those listed in Table 2 with P values ≤ 0.05 .

Multivariate Analysis

Ninety-six soil cores (3 treatments \times 2 soil types \times 4 sampling dates \times 4 reps) were analyzed for 12 biologi-

cal and physical properties in this experiment. Principle component analysis was used to explore data variability related to the soil properties and to elucidate potential relationships to soil type, compaction treatment, and property type. Nitrogen mineralization and PLFA were excluded from the analysis since they were not measured on all sampling days resulting in a data matrix with 96 rows (soil cores) and 10 columns (soil properties).

This dataset was well explained by PCA: three PCs accounted for 84% of the variability. Soil type accounted for the largest portion of the variation, as the two soils clearly separated along PC1 (Fig. 5). Soil properties with the heaviest loadings on PC1, indicative of major differences between the two soils, were CO_2 efflux, bulk density, total porosity, respiration, microbial biomass, and total bacteria.

Separate PCAs for each soil type identified three components that explained a total of 73 and 76% of the data variability for the clay loam and sandy loam,

Table 2. Effect of compaction on phospholipid fatty acid (PLFA) content (ng g⁻¹ soil).†

PLFA	Clay loam compaction			Sandy loam compaction		
	No	Moderate	Severe	No	Moderate	Severe
Bacterial						
14:0	2.06	1.66	1.61	0.31b	0.20c	0.65a***
i15:0	5.52	4.44	3.58	0.87b	0.71b	1.64a***
a15:0	2.60	2.10	1.61	0.34b	0.32b	0.65a***
15:0	1.07	1.21	1.50	0.31b	0.24b	0.54a**
i16:0	4.97	3.81	4.29	1.22b	1.07b	2.22a***
16:1 ω 7	1.42	1.74	1.48	0.28b	0.16c	0.41a***
16:1 ω 5	1.96	1.88	1.49	0.20	0.11	0.12
10Me-16:0	0.35	0.17	0.42	0.15	0.21	0.22
i17:0	1.16	0.72	0.59	0.17b	0.13b	0.64a**
a17:0	0.42	0.58	0.70	0.28	0.20	0.08
cyc17:0	0.95	1.49	1.68	0.21a	0.09b	0.22a*
17:0	0.58	1.37	1.76	0.41ab	0.24b	0.95a*
18:1 ω 7	1.28	1.29	1.29	0.09	0.22	0.05
18:0	2.63	2.35	2.69	1.60b	1.15b	2.16a**
cyc19:0	0.58	0.59	0.61	0.04	0.04	0.07
Actinomycetes						
10Me18:0	1.62	0.65	0.49	0.48	0.32	0.50
Fungal						
18:2 ω 6	1.76	1.79	2.58	0.32	0.21	0.32
Total	54.16	48.51	48.97	14.4b	11.1b	21.9a***

* $P \leq 0.05$.** $P \leq 0.01$.*** $P \leq 0.001$.† Means within a row and soil type ($n = 4$) not followed by the same letter are significantly different at $\alpha = 0.05$. Main effects of compaction for an individual PLFA and soil type were not significant in ANOVA unless noted.

respectively. Clear separation of the compaction treatments was found for the clay loam along PC1 (Fig. 6). Porosity (total, habitable, air-filled) and bulk density were the primary contributors to the separation as shown by their distance from the origin along PC1. In contrast, biological properties separated primarily along PC2, and thus were unrelated to the variation among compaction treatments. Treatment separation was also found for the sandy loam, although the differences were not as large as those for the clay loam. Again, the major contributing soil properties for PC1 were primarily physical (bulk density, total porosity, air-filled porosity). Variability in biological properties (microbial biomass, respiration, total bacteria) contributed to treatment separation along PC2 for both soils.

The relationship between soil properties and compac-

tion treatments is determined by their respective location along the PC axes. For example, increased compaction in both soils was positively related to bulk density; inversely related to CO₂ efflux, total porosity, and air-filled porosity; and generally unrelated to microbial biomass, respiration, total bacteria, and fungi.

Finally, several of the soil properties of the clay loam grouped into distinct clusters (Fig. 6), representing highly related variables (e.g., microbial biomass, respiration, total bacteria). Interestingly, CO₂ efflux was clustered with total porosity and air-filled porosity, indicative of the relationship between CO₂ efflux and soil porosity. Respiration, in contrast, showed little correlation to CO₂ efflux. The relationship between CO₂ efflux and soil physical properties was less apparent in the sandy loam soil. This likely reflects the greater tolerance of CO₂ efflux to compaction in the coarser-textured soil (Fig. 3).

Field Validation

Field investigation results from the two LTSP sites corroborated our laboratory findings that a weak relationship exists between soil physical and biological properties in compacted soils. Mean bulk density ranged from 1.00 to 1.30 Mg m⁻³ across compaction plots at Challenge (clay loam) and from 1.2 to 1.45 Mg m⁻³ at Rogers (sandy loam). Soil strength also varied greatly, from 446 to 3865 kPa at Challenge and from 75 to 3391 kPa at Rogers. Correlation of these physical parameters with microbial characteristics was low, however. As an example, Fig. 7 shows the lack of relationship between soil strength and microbial biomass across 120 sample points. Soil strength also was unrelated to either respiration or surface CO₂ efflux at both sites. Instead, soil organic matter content showed a stronger relationship

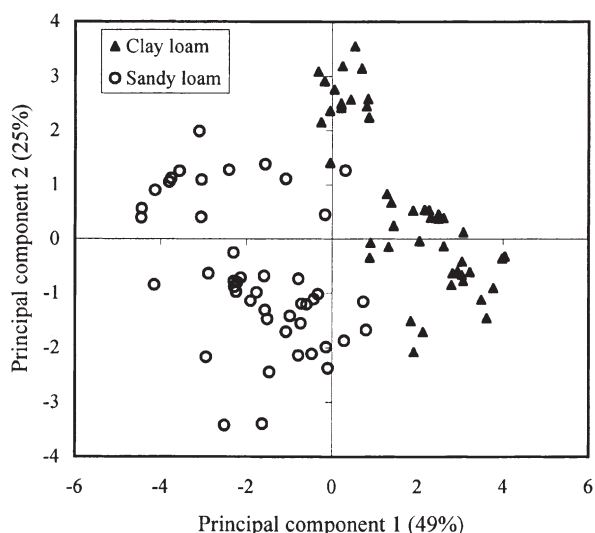


Fig. 5. Principal component analysis results for both soils showing sample relationship to principal components.

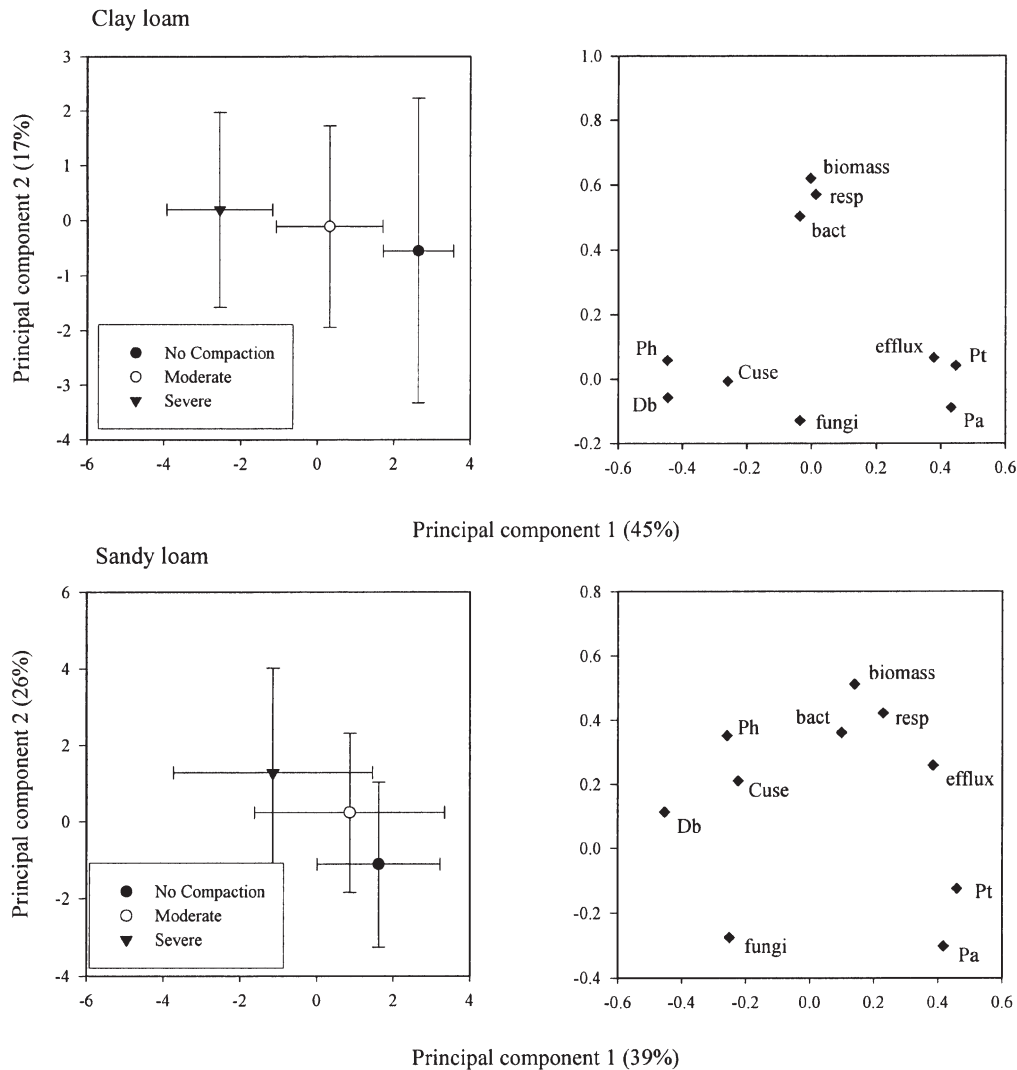


Fig. 6. Principal component analysis results for each soil showing coefficients of each PC and variable loadings on the first two components. All symbols represent standardized variables: Db = bulk density; Pt = total porosity; Ph = habitable porosity; Pa = air-filled porosity; efflux = CO₂ efflux; resp = respiration; biomass = microbial biomass; Cuse = carbon source utilization; bact = total bacteria; fungi = fungal hyphae.

to both microbial biomass and respiration, particularly at Challenge.

DISCUSSION

Soil physical changes due to compaction are well documented in forestry literature (Dickerson, 1976; Froehlich et al., 1985; Lenhard, 1986). Compaction alters pore-size distribution and water-retention capabilities, and reduces hydraulic conductivity and gas diffusion (Huang et al., 1996; McNabb et al., 2001; Richard et al., 2001; Startsev and McNabb, 2001). Our results showing increased bulk density and modified pore-size distribution due to compaction of both soils, therefore, were anticipated. Our goals, however, were to investigate microbial community responses to compaction, and to determine whether a relationship between soil physical and biological properties exists.

The results showed that compaction was not detrimental to microbial community characteristics. Eight indi-

ces of community size, activity, function, and structure were compared, providing a cross-section of traditional and modern techniques for comparison of coarse-level community changes. No statistically significant decline with compaction was found for any of the indices, regardless of soil type or sampling date. In fact, several indices (C use, PLFA, and fungal hyphae) increased with compaction, suggesting rapid and successful adaptation to the altered environment.

Carbon use (Biolog) and PLFA are common measures of the functional and structural diversity of soil bacteria, respectively. Although considered complimentary (Buyer and Drinkwater, 1997; Widmer et al., 2001), the methods differ with respect to their target organisms. Carbon use measures the functional ability of culturable bacteria, while PLFA provides a coarse-level profile of the total bacterial community. Greater C use and PLFA content were found with severe compaction compared with the control and moderate compaction treatments.

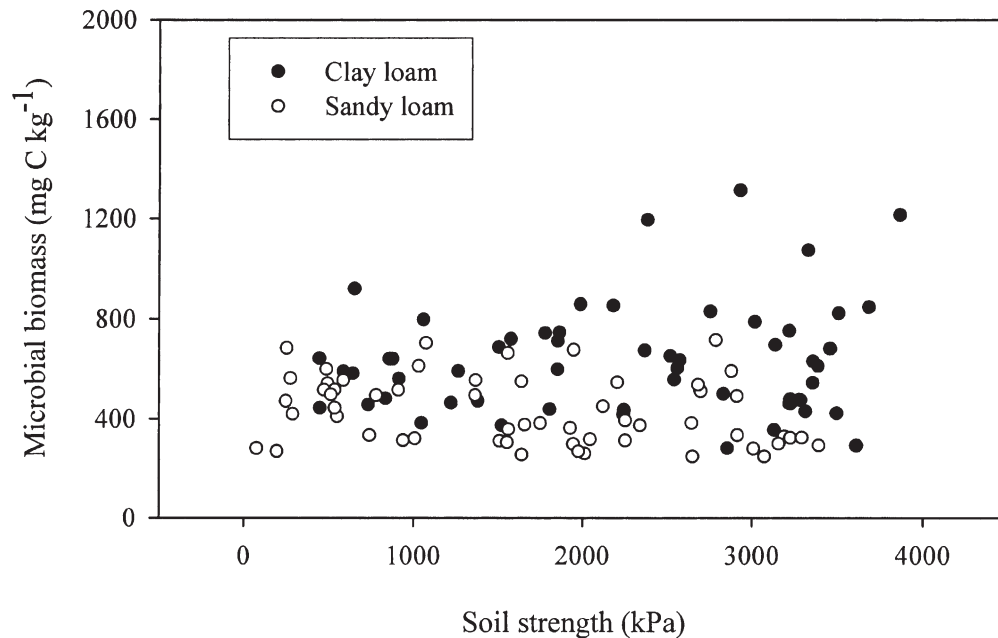


Fig. 7. Soil strength and microbial biomass measurements show no relationship for two Long-term Soil Productivity Study sites in Northern California. Microbial biomass and soil strength were determined on samples collected within 2 cm of each other ($n = 60$ sample points per site) in the surface 15 cm.

However, the response was not universal. In the sandy loam soil, C use was greater in severe compaction samples on Day 11 only, while PLFA content of several bacterial markers was greater on Day 67. Treatment differences in C use increased with time in the clay loam soil, while no differences in PLFA markers were found. These discrepancies, plus the lack of corroboration with other microbial measures, suggest that the stimulation of bacterial diversity by compacting was both inconsistent and inconclusive.

A caveat to the general observation of microbial tolerance to compaction was a decline in surface CO_2 efflux for the clay loam soil. Semi-weekly measurements averaged 50% less CO_2 efflux for the severely compacted treatment compared with the control. We were particularly interested in whether this response was due to reduced microbial respiration, gas diffusion, or a combination of both. Reduced CO_2 efflux in compacted soil has been observed by many (Torbert and Wood, 1992; Dulohery et al., 1996; Conlin and van den Driessche, 2000), and the primary role of restricted gas diffusion is often cited (Currie, 1984; Xu et al., 1992; Pumpanen et al., 2003). Exchange of gases between soil and atmosphere occurs mainly by molecular diffusion and requires an adequate and continuous system of air-filled pores (Currie, 1984). Evidence from our study supports this idea. A strong relationship between CO_2 efflux, air-filled porosity, and total porosity was identified in multivariate analysis (indicated by the close grouping of these variables in Fig. 6). Additionally, compaction had little effect on soil respiration or microbial biomass at each of the four sampling dates. Both parameters were measured during the initial 4 h following sampling, before any appreciable recovery of the microbial community would be anticipated. Although actual rates of

gas diffusion were not measured, we surmise that the reduction in CO_2 efflux resulted from limited air-filled porosity, irrespective of biological activity.

Compaction favored smaller, habitable-sized pores (0.2–30 μm) at the expense of large pores. Small pore volume increased 72% in the clay loam and 39% in the sandy loam with severe compaction, while macropores were nearly eliminated in both soils. This observation helps explain the indifference shown by microorganisms. Habitat condition (available pore space) was improved by compacting, and apparently offset any detrimental effects of restricted air, water, or nutrient flow. Whether the reduction in large pores also led to fewer bacterial and fungal predators, as suggested by Hassink et al. (1993) and Postma and van Veen (1990), was not tested.

That compaction drastically reconfigured pore structure without a reduction in microbial habitat size also helps explain the results from our field study and from numerous other LTSP study sites across North America. Microbial biomass and respiration were unrelated to physical measures of soil compaction (bulk density and soil strength) at the two LTSP sites. Similarly, nominal changes in microbial biomass, PLFA structural diversity, genetic diversity of bacteria, mycorrhizae, and litter decay due to compaction have been found at other LTSP sites (Jordan et al., 1999; Kranabetter and Chapman, 1999; Li, 2000; Chow et al., 2002; Ponder and Tadros, 2002). Axelrood et al. (2002) noted some differences in bacterial composition between treatments at LTSP sites in British Columbia, although total bacterial diversity was high regardless of compaction treatment. To date, Li et al. (2003) have reported the only decline in microbial community response to compaction within the network of LTSP sites. They found reduced N mineraliza-

tion in a loblolly pine plantation for 5 yr following treatment, and suggested the potential role of poor aeration or limited physical access to organic N.

We deliberately wetted all soil cores to optimum moisture content (50–60% WHC) before compacting. As a consequence, substantial differences in soil aeration were attained following treatment. This was most evident in the clay loam soil. About 40% of the pores were air filled in the control treatment, compared with <10% in the severely compacted soil. Heterotrophic activity (respiration) did not differ between treatments during the 10-wk experiment, however. Nor was an increase in PLFA markers for anaerobic bacteria (17:0cyc and 19:0cyc) found. This finding differs from the results of Linn and Doran (1984), who found heterotrophic activity declined considerably as the air-filled pore space dropped below 40% in an intensively managed agricultural soil. Whether the disparity between studies is related to differences in total soil porosity or air permeability, or is simply a reflection of inherent differences between agricultural and forest soils is unclear. From a practical standpoint, restrictive aeration is a transient condition (at most) in the summer-dry, Mediterranean climate of California. Results may differ, however, for poorly drained soils in regions of high precipitation, where anaerobic conditions are likely extended on compacted sites.

The indifference shown by the two microbial communities to compaction provides an interesting contrast to response of tree growth at the LTSP sites. Gomez et al. (2002b) found that severe compaction reduced tree growth nearly in half at the clay loam site and increased tree growth more than two-fold at the sandy loam site. The growth decline at the clay loam site was considered a function of severe mechanical impedance to root growth as the soil dried during the spring and summer months. Microbial biomass and activity, in contrast, showed little response to a wide range of soil strength values in the field study. The differential response of the two life forms to compaction underscores this concept and highlights the insubstantial link between soil physical disturbance and microbial characteristics at the LTSP sites.

Both the laboratory and field studies were designed specifically to test the physical effects of compaction on microbial communities. Skid trails, in contrast, typically confound physical compaction with soil mixing and displacement during harvesting operations. Soil organic matter and nutrient pools often are reduced in skid trails, to the detriment of microorganisms (Dick et al., 1988). At the LTSP sites, heavy equipment was kept off all plots during harvesting, and tree boles were fully suspended during removal. Soil mixing was further avoided by temporarily removing surface organic matter before compacting. The results of our study, therefore, are applicable to one of several compaction-related problems associated with harvesting.

CONCLUSIONS

The effects of forest soil compaction on microbial community size, activity, and diversity were compared

in a clay loam and a sandy loam soil. Microbial biomass, respiration, cultural and total bacteria, fungal hyphae, N mineralization, C use, and PLFA community structure were not detrimentally affected by compaction, regardless of soil type. Results from the controlled environment study were validated against field data collected at the two sites, where microbial biomass and respiration were unrelated to a wide range of soil compaction. A few examples of microbial stimulation following compacting were evident, specifically fungal hyphae, C use, and total PLFA content; however, they were inconsistent between soils and among sampling dates. The general response of the two soil communities to compaction, therefore, was expressed as tolerance.

Our results agree with most other studies of soil compaction from the network of LTSP sites in North America that show tolerance or resilience by microbial communities. We suggest the fundamental explanation for these observations lies in the reconfiguration of pores following compaction. Compacting both the clay loam and the sandy loam soils resulted in reduced total porosity and a near elimination of large pores. In contrast, habitable pore volume, accessible primarily to bacteria and fungi, increased in both moderately and severely compacted soils. Therefore, with the exception of poorly drained soils or for those regions receiving high annual precipitation where saturation is a concern, soil physical changes associated with compaction appear to be of little consequence to the microbial community.

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