AN ABSTRACT OF THE THESIS OF

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Title: Impacts of Post-Fire Salvage Logging on Soil Chemistry, Physical Properties and Bacterial Community Composition in a Mixed-Conifer Forest in Central Oregon.

Abstract approved:

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Land managers, scientists, and the interested public are confronted with uncertainty about the impacts of salvage logging on soil productivity. In recent years, stand-replacing wildfires in the western United States have increased in frequency, prompting the need to evaluate the effect of post-fire treatments on forest ecosystem recovery. This study examined whether compaction and subsoiling after post-fire salvage logging impacted the structure, metabolism, and function of soil bacterial communities, which were assessed using terminal restriction fragment length polymorphism (T-RFLP) and Biolog Ecoplates. Supporting data for these salvage logging effects included soil biological activities, soil chemistry, and physical soil properties in a mixed conifer forest in central Oregon. Post-fire salvage logging treatments had little effect on soil bacterial community richness, suggesting that soil bacteria in these post-fire landscapes are both tolerant of the occurrence of fires and resilient to disturbance. However, even though a statistically significant difference in

bacterial species richness was not detected among treatments, a greater cumulative mean number of species was found across six sampling seasons in the compacted soil treatment compared to the fire-only and subsoiled treatments. This trend may be due to less predation on the soil bacteria by microbivores in the soil pores reduced in size by compaction. Additionally, there was a significant decline in the mean number of species after the spring 2007 sampling. A NMS ordination of the mean number of species suggested that the bacterial community composition changed after spring 2007. Furthermore, the lack of difference in mean number of species among treatments suggests that time since fire had a stronger effect on the structure of the soil bacterial community than did logging disturbance. Plant-available phosphorus and nitrogen concentrations were lower in the mechanically disturbed treatments than in the fire-only treatment. Soil respiration and soil phosphatase rates both were higher in the fire-only treatment. Mechanical disturbance may have long-lasting effects in an already nutrient limited system. No other differences among treatments for soil chemical properties were detected. Soil bulk density was lowest in the subsoiled treatment. Microbial community responses to burning and compaction caused by harvesting can be negative, neutral, or positive. While many factors, in addition to soil chemical and physical properties, affect the microbial community richness and functional diversity, our results support other recent studies showing that soil bacteria are resilient in disturbed environments.

IMPACTS OF POST-FIRE SALVAGE LOGGING ON SOIL CHEMISTRY, PHYSICAL PROPERTIES AND BACTERIAL COMMUNITY COMPOSITION IN A MIXED-CONIFER FOREST IN CENTRAL OREGON

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1.1 LITERATURE REVIEW

The structure and composition of forest ecosystems in the Pacific Northwest have evolved in response to fire. There is concern among land managers that the past century of fire exclusion may be having adverse effects on the forests today, including increased stand density, changes in stand species composition, and increased fuel loads (Neary et al. 1999, MacKenzie et al. 2004). The timing of fires relative to stand age or tree size may be critical in determining the successional trajectories of forest stand structure (Holden et al. 2007). Currently, there is little understanding about ecological restoration of land affected by major wildfire or the environmental effects of post-fire logging (McIver and Starr 2000, 2001, Olsen and Shindler 2007).

Generally, managers decide to salvage fire-killed trees to recoup their economic value before decay (Aho and Cahill 1984, Lowell and Cahill 1996). To land managers, salvage logging is viewed as one component in an array of rehabilitation and restoration techniques (McIver and Starr 2000, 2001). Practices range from lopping and scattering of logging slash, to the removal of dead trees to slow the buildup of insect pest populations and reduce fuel loads (McIver and Starr 2000, 2001).

Opponents of post-fire logging argue that the harvest operations themselves cause damage to burned sites and that those operations remove structure that is

important for ecological functions (Beschta et al. 1995). Recent studies have found that salvage logging may increase the risk of fire because of the increase in unmerchantable material to the forest floor (Donato et al. 2006, McIver and Ottmar 2007). It also has been shown that fuel conditions in conifer plantations planted after salvage logging can increase fire severity, despite the removal of large woody fuels (Thompson et al. 2007).

1.1.1 Post-fire logging effects on soil chemical and physical properties

There is little information on how post-fire salvage logging affects soil chemistry; however, the impacts of timber harvesting and wildfire on soils have been studied in depth (Chanasyk et al. 2003). Most studies have examined the effect of harvesting on soil physical properties, showing a major result of harvesting to be related to forest soil compaction (Chanasyk et al. 2003). Compaction effects have been shown to depend on the soil texture (Williamson and Neilsen 2000, Gomez et al. 2002, Powers 2002, Powers et al. 2005). For example, soil compaction may negatively or positively affect ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) tree growth, depending on soil texture (Davis 1992, Page-Dumroese 1993, Gomez et al. 2002). Compaction of sandy loam soils has been shown to cause an increase in the amount of fine pores and improved soil water retention and growth of young ponderosa pines compared to those grown on non-compacted coarse-textured soil (Gomez et al. 2002). In contrast, compaction in clayey soils, which retain more water and nutrients, has been associated with negative growth responses (Gomez et al. 2002).

To alleviate compaction, the practice of subsoiling is used to fracture the lower soil strata. Disruption of the belowground component may have immediate and long-lasting effects to the whole ecosystem, for example, loss of nutrients like carbon, nitrogen and phosphorus (Froehlich et al. 1985, Perry et al. 1989, Beschta et al. 2004). Subsoiling has been found to increase rooting volume, decrease bulk density, and increase aeration porosity (Carlson et al. 2006).

Forest harvesting equipment, including that used in post-fire salvage logging, frequently results in soil compaction, reducing soil pore size and decreasing oxygen availability and movement of water and nutrients to tree roots (Rab 1996). An increase in volumetric soil water content, soil bulk density, soil strength, and available water holding capacity was found to not be detrimental for early growth of planted Douglas-fir (*Pseudotsuga menziesii* Mirb., Franco) after ground based logging in coastal Washington (Ares et al. 2005). Loblolly pine (*Pinus taeda* L.) on disturbed sites located on fertile "wet pine flats" in South Carolina performed as well or better than trees on minimally disturbed sites with average levels of harvest residues (Eisenbies et al. 2005). Mariani et al. (2006) found that 3-7 years after compaction, there was an increase in total carbon (C) and nitrogen (N) in the uppermost mineral soil, but stem-only harvesting or whole-tree harvesting plus forest floor removal had no effect.

1.1.2 Fire effects on soil chemistry and physical properties

Fire has complex effects on many soil nutrient pools, ranging from a shift in plant and microbial biomass populations to alterations of soil physical and chemical properties (Knicker 2007). Dramatic changes to the forest floor were found to cause increases in total C, total N, ammonium (NH_4), and potential mineralizable N, while decreasing nitrate (NO_3) and litter quality (MacKenzie et al. 2004). Another change to the soil is a reddening due to iron oxides transforming to iron hydrous oxides, such as magnetite and hematite, and the nearly complete removal of organic matter (Certini 2005, Wondafrash et al. 2005). Under the reddened layer, a blackened layer ranging from 1–15 cm deep can be found as a result of charring (Certini 2005).

Fire intensity refers to the rate at which a fire produces thermal energy in a favorable fuel-climate environment where it occurs (Knicker 2007). Fire severity, on the other hand, is the qualitative measure that refers to the overall effect of fire on an ecosystem. It relates to the effect of fire on soil and site resources that control ecosystem sustainability (Neary et al. 1999). The greatest damage to belowground ecosystems results from the fire's duration on the soil surface, or smoldering combustion and subsequent heat transfer belowground (DeBano et al. 1998, Neary et al. 1999).

During forest fires, maximum ground temperatures are typically in the range of 200-300 °C. However, under heavy fuels like slash, instantaneous temperatures can exceed 1,500 °C, but the measured soil-surface temperatures at such sites peak at only 500-700 °C (Neary et al. 1999). The degree of heating at any soil depth depends on

factors such as intensity and duration of heat transfer, heat conductivity of the mineral soil phase, soil porosity, and soil moisture. Heat is transported faster and penetrates deeper in moist soils than in dry soils. Due to their high content of air-filled coarse pores, sandy soils are better insulated against heat transfer than are loams (Knicker 2007). Soil pH increases during soil heating as a result of the organic acids denaturizing (Certini 2005).

Nitrogen is considered to be a limiting nutrient in the forests of the inland Northwest. Fire has direct and indirect effects on the N pool in an ecosystem. The direct effect is N volatilization to the atmosphere when temperatures climb to 200-400 °C during the fire (Neary et al. 1999). After an intense wildfire, 57% of N was lost from the O horizon and mineral soil in southern Oregon (Bormann et al. 2008). The indirect effect is the biological and non-biological processes after and during low-intensity burning that transform organic N into ammonium and nitrate N (Neary et al. 1999). Ammonium is produced during biomass burning, while nitrate requires nitrification. The destruction of vegetation causes an increase in nitrifier abundance; however, without any plants to utilize nitrate, it is lost from the ecosystem either by denitrification or leaching (Knicker 2007). Prescribed burning in a ponderosa pine forest near Flagstaff, Arizona caused an increase in ammonium-N in old growth, pole, and sapling substands and was associated with differences in the initial forest floor weight and the amount of forest floor burned (Covington and Sackett 1992). These researchers also found that there are immediate increases in ammonium after burning,

whereas nitrate increases occur later due to the nitrification of the high ammonium produced immediately after burning.

Carbon is one of the most abundant nutrients on Earth. It has many forms and functions. Fire's most obvious effect on C is the transformation of cellulose from wood to charcoal. In a grassland community, C has been shown to return to its pre-fire levels within one year after fire (Úbeda et al. 2005). In a mixed conifer forest, Bormann et al. (2008) found that 60% of C was lost from the O horizon and mineral soil after the 2002 Biscuit Fire in southern Oregon. The main phosphorus (P) pool primarily is found in soil and not litter. It is a critical plant nutrient, by far the least mobile, and therefore, least available to plants in most soil conditions (Hinsinger 2001). However, the litter contains more organic forms of P that are more readily available to plants than does the soil (Neary et al. 1999, Knicker 2007). If there is complete litter combustion, the impact on the P cycle can be more severe than that indicated by the size of the individual nutrient pools (Neary et al. 1999, Knicker 2007). Inorganic chemical reactions tightly constrain the availability of P to plants (Binkley and Vitousek 1989). Organic forms of P, which generally are not measured in standard soil assays, may be quite important to plant nutrition (McGrath et al. 2001).

A consequence of moderate to severe wildfires is soil water repellency. Several factors affect the strength and persistence of post-fire soil water repellency, including burn severity, soil texture, soil moisture, and time since burning (DeBano et al. 1998, Robichaud 2000, MacDonald and Huffman 2004). It also has been observed that

logging equipment may disrupt water-repellent layers that develop from severe fires (McIver & Starr 2001).

1.1.3 Effects of disturbance on soil bacteria

It has long been known that microorganisms are essential for the functioning and sustainability of all natural ecosystems. Soil bacteria are a vital component of the biotic community in natural forests and they are largely responsible for ecosystem functioning due to their participation in most nutrient transformations (Hackl et al. 2004). Microbes also can indirectly influence plant productivity through actions that enhance the availability of nutrients for plant uptake, or reduce plant productivity through competition for nutrients with plant roots, or by promoting nutrient loss via leaching of mobile nutrient forms (van der Heijden et al. 2007). It has been shown that the diversity and composition of soil bacterial communities at large spatial scales can largely be predicted with a single variable, soil pH (Fierer and Jackson 2006). When considering the ability of ecosystems to respond to changing environmental conditions, it is important to analyze diversity of the system (Prosser 2002).

Microbial community response to varying levels of soil compaction after salvage logging is uncertain. There is evidence that compaction does not modify the mineral soil microbial community size or activity (Chow et al. 2002, Shestak and Busse 2005, Mariani et al. 2006). Conversely, another study by Schnurr-Pütz et al. (2006), indicated that compaction altered the structure and function of the soil microbial community and favored anaerobic prokaryotes.

Both wildfires and salvage logging are important disturbances to forest ecosystems because they can enhance or impair ecological processes. They can aid in ecosystem restoration by creating structural complexity and landscape heterogeneity lost through past human management. For example, fire creates dead wood and promotes the development of tree cavities for birds to nest in. However, it is unclear how these disturbances affect soil microbial communities. It has been shown that, in a spruce-dominated boreal forest, fire has a distinct and more pronounced effect on soil microbial communities than does harvesting (Smith et al. 2008). Fire typically has a more detrimental effect on fungi than on bacteria (Vásquez et al. 1993, Bååth et al. 1995, D'Ascoli et al. 2005, Guerrero et al. 2005). Overly severe prescribed fires significantly reduce mycorrhiza compared to less severe fire or non-burned treatments (Smith et al. 2004, 2005). However, Choromanska and DeLuca (2001) found that prescribed fire reduced wildfire severity, lessened the losses of labile C and N, and improved the resistance of soil microbial communities to subsequent wildfire, thereby allowing more rapid post-fire recovery. There also were no significant differences in bacterial diversity between burned–salvaged and unburned sites 4–5 years after fire and salvage-logging (Khetmalas et al. 2002). Moreover, forest fires have been shown to decrease the abundance and cause a shift in community composition of both N-fixing and ammonia-oxidizing bacteria (Yeager et al. 2005). Mabuhay et al. (2004) found low microbial community diversity and low biomass C in burned areas 25 years after fire. It has been reported that microbial community responses to burning and harvesting can be mixed, ranging from low resilience, as seen in low-severity

prescribed burning (Fritze et al.1993, DeLuca and Zouhar 2000), to high resilience or complete tolerance following intensive forest management (Edmonds et al. 2000, Busse et al. 2001, Siira-Pietikäinen et al. 2001).

An indirect measurement of soil microbial activity is soil respiration. Thinning treatments have been found to have no impact on soil respiration approximately one year after fire (Ma et al. 2004). Another study showed that selective thinning in a mixed-conifer forest elevated soil respiration response, soil moisture, and soil temperature two and seven years after disturbance (Concilio et al. 2005). Temperature is an important factor when looking at soil respiration rates. Soil temperature increases respiration rates, but sites with extremely high temperatures result in lower respiration rates, more notably in fungi than in bacteria (Pietikäinen et al. 2005). Soil organisms play critical roles in maintaining soil fertility, health, and productivity (Coleman et al. 1992). Soil microbes ultimately depend on aboveground biomass for substrate, and management activities that alter substrate may have substantial implications below ground (Chatterjee et al. 2008). Since soil microbes are responsible for decomposition and nutrient cycling, changes in their composition and function are likely to affect site productivity. Understanding how management affects soils is critical when considering soil microbes and their interaction with aboveground processes.

1.1.4 T-RFLP and Biolog analysis

DNA-based techniques, including terminal restriction fragment length polymorphism (T-RFLP), have allowed researchers to describe natural microbial communities. T-RFLP may provide less resolution of the diversity and composition of

bacterial communities than sequencing or cloning, but it has high sensitivity and the ability to rapidly acquire precise data (Engebretson and Moyer 2003). T-RFLP analysis is based on the restriction endonuclease digestion of fluorescently end-labeled PCR products. Either one or both primers used can be labeled. The output is an electropherogram showing the microbial community profile as a series of peaks varying in height and size. The output allows the researcher to investigate the microbial community in terms of its quantitative or qualitative composition.

Researchers are interested in the function of microbial communities in their environments. Community level physiological profiles (CLPP), such as Biolog ecoplates, have been used to assess the community structure and potential activity of culturable, aerobic and fast growing bacteria. The potential activity of the bacterial community is shown through the utilization patterns of sole carbon source. Studies have shown that soil properties, not treatment differences, cause the separation seen in CLPP (Staddon et al. 1997, Cookson et al. 2008). Other studies have found that disturbed soils have altered metabolic fingerprints compared to undisturbed soils (del V. Gomez et al. 2004, Goberna et al. 2005).

1.1.5 Objectives

The objectives of this research were to determine if compaction and subsoiling from post-fire salvage logging impacts the structure, metabolism, and function of soil bacterial communities and soil chemistry in a mixed conifer forest located in central Oregon. Many studies summarize the impacts of prescribed fire and clear-cutting/thinning separately on microbial structure and function and soil chemistry. Most are compared to unburned or uncut controls; however, in our research, it was not possible to have adjacent unburned control stands after wildfire. This is the first study, to our knowledge, that examines the impact of wildfire and post-fire salvage logging on bacterial communities using terminal restriction fragment length polymorphism (T-RFLP) and Biolog in combination with soil physical and chemical analyses.

IMPACTS OF POST-FIRE SALVAGE LOGGING ON SOIL CHEMISTRY, PHYSICAL PROPERTIES, AND BACTERIAL COMMUNITY COMPOSITION IN A MIXED-CONIFER FOREST IN CENTRAL OREGON.

2.1 INTRODUCTION

Uncertainty and controversy exist among land managers, scientists, and the interested public on the impact of wildfire and salvage logging on soil productivity. In recent years, stand-replacing wildfires in the western United States have increased in frequency, prompting the need to evaluate the effect of post-fire treatments on forest ecosystem recovery (McIver and Starr 2000, 2001, Beschta et al. 2004, Lindenmayer et al. 2004, Sessions et al. 2004). Post-fire salvage logging, currently underway in forests to recover the economic value of burned timber killed by wildfire, may reduce burn severity of soils in the event of reburning by removing large, dead wood (Poff 1989) or may increase the risk of fire (Donato et al. 2006) or fire severity (Thompson et al. 2007). The effects of salvage logging operations (e.g. compaction, subsoiling) on soil productivity and forest recovery remain poorly understood and are a knowledge gap significant to fire recovery projects. Assessment of the ecological costs and benefits of post-fire salvage operations is critical to the intelligent use of management activities and resources.

Soil organisms play critical roles in maintaining soil fertility, health, and productivity (Coleman et al. 1992). These organisms ultimately depend on aboveground biomass for substrate; management activities that alter substrate may

have substantial implications belowground. Clearly, no study on how forest management practices affect soils is complete without considering soil microbes and their interaction with aboveground processes.

Soil bacteria can indirectly influence plant productivity through actions that enhance the availability of nutrients for plant uptake, or reduce plant productivity through competition for nutrients with plant roots, or by promoting nutrient loss via leaching of mobile nutrient forms (van der Heijden et al. 2007). Nutrient availability is strongly linked to pH and cation exchange capacity (CEC). It has been shown that the diversity and composition of soil bacterial communities at large spatial scales largely can be predicted with a single variable, soil pH (Fierer and Jackson 2006). When considering the ability of ecosystems to respond to changing environmental conditions, it is important to analyze the diversity of the system (Prosser 2002).

Phosphorus (P) is a critical plant nutrient, by far the least mobile, and therefore, least available to plants in most soil conditions (Hinsinger 2001). The main P pool primarily is found in the soil and not the litter. However, the litter contains more organic forms of P that are more readily available to plants than soil (Neary et al. 1999, Knicker 2007). If there is complete litter combustion, the impact on the P cycle can be more severe than that indicated by the size of the individual nutrient pools (Neary et al. 1999, Knicker 2007). Inorganic chemical reactions tightly constrain the availability of P to plants (Binkley and Vitousek 1989). Organic forms of P, which generally are not measured in standard soil assays, may be quite important to plant nutrition (McGrath et al. 2001).

Nitrogen is considered a limiting nutrient in the forests of the inland Northwest. Fire has direct and indirect effects on the N pool in an ecosystem. The direct effect is N volatilization to the atmosphere when temperatures climb to 200-400 °C during the fire (Neary et al. 1999). Fifty-seven percent of N was estimated to be lost from the mineral soil and O horizon after the Biscuit Fire in southern Oregon (Bormann et al. 2008). The indirect effect is the biological and non-biological processes after and during low-intensity burning that transforms organic N into ammonium and nitrate N (Neary et al. 1999).

Disturbances such as fire and harvesting can impact the abundance, activity, and composition of soil microbial communities, thereby contributing to changes in nutrient cycling, rates of organic matter decomposition, and ecosystem C accrual (Pietikäinen and Fritze 1995, Neary et al. 1999, Smith et al. 2008). Soil microbes are critical to improved conifer tree and seedling growth, and to symbioses resulting in atmospheric N fixation by certain understory plants. Microbial community response to varying levels of soil compaction after salvage logging is uncertain. There is evidence that compaction does not modify the mineral soil microbial community size or activity (Chow et al. 2002, Mariani et al. 2006, Shestak and Busse 2005). Conversely, a study by Schnurr-Pütz et al. (2006) indicated that compaction altered the structure and function of the soil microbial community and favored anaerobic prokaryotes.

The objectives of this research were to determine if compaction and subsoiling after post-fire salvage logging impacted the structure, metabolism, and function of soil bacterial communities and soil chemistry in a mixed conifer forest located in central

Oregon. Many studies have summarized the impacts of management activities, such as prescribed fire and clearcutting/thinning separately on microbial structure and function and soil chemistry. Most are compared to unburned controls; however, in our research, it was not possible to have adjacent unburned control stands after wildfire. This is the first study to our knowledge to examine the impact of wildfire and post-fire salvage logging on bacterial communities using molecular methods and community level physiological profiles in combination with soil physical and chemical analyses.

2.2 METHODS

2.2.1 Study area

This study was conducted within the Booth and Bear Butte (B&B) Fire Complex, located on the east side of the Cascade Mountains of Oregon in the Deschutes National Forest. The B&B Fire burned 36,733 ha in the summer of 2003. Timber sales approved prior to the B&B fire and subsequently harvested one year after the fire, provided a unique and timely opportunity to study the impacts of salvage logging without the uncertainty surrounding the approval of proposed salvage-logged stands. Salvage logging and subsoiling occurred in summer 2004. Subsoiling was completed on all stands within a 3-day period. Subsoiling, or deep tillage, is employed to decrease soil bulk density, thereby improving aeration and infiltration (Otrosina et al. 1996). These stands, which ranged in size from about 5 to 13 hectares (Table 2.1), were thinned from below with feller bunchers.

Stands within the study are characterized by a dominant overstory of ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) and Douglas-fir

(*Pseudotsuga menziesii* Mirb., Franco) with white fir (*Abies concolor* Gord. & Glend., Lindl. ex Hildebr.) or grand fir (*Abies grandis* Dougl. ex D. Don, Lindl.) occurring as co-dominants, especially in the moister plant association groups and community types (Simpson 2007). Prior to logging, stands were comprised mainly of second growth trees (Table 2.1). Nearly all stands contained a few large, 100 to 200-year-old trees (Table 2.1). On many sites, including the stands in our study, dense shrubs typify early successional stages after fires and logging. An understory of snowbrush ceanothus *(Ceanothus velutinus* Dougl.), dwarf rose *(Rosa gymnocarpa* Nutt.), common snowberry *(Symphoricarpos albus* [L.] Blake), dwarf Oregon-grape (*Mahonia nervosa* [Pursh] Nutt.), trailing blackberry (*Rubus ursinus* Cham. and Schlecht) and red huckleberry (*Vaccinium parvifolium* Sm.) is found on our stands. Soils are Aquic Vitrixerands and Alfic Vitrixerands with sandy loam texture. Elevations of all stands are about 1000 m (Table 2.1). Average temperatures range from -1 ºC in the winter months to 20 ºC in the summer months. Average annual precipitation ranges from 50 to 150 cm. About 70% of the precipitation falls during November through April. During the driest months (July, August, and September), the average monthly precipitation is less than 2.5 cm.

2.2.2 Study design

The study was a randomized complete block design with seven post-fire salvage logged stands (blocks) and three treatments: burning with no further disturbance (undisturbed), compaction from heavy ground-based equipment (compacted), and compaction followed by subsoiling (subsoiled) (Fig. 2.1).

Each 4-6 m grid point was marked with a stake and all stake locations were recorded with the Global Positioning System (GPS). A 10 m buffer zone within the perimeter of each stand was not sampled to avoid potential edge effects. Compacted and subsoiled treatments were identified based on visual indications of equipment use. Within each stand, 3 grid points (plots) were randomly selected from each treatment type for sampling soil chemical, physical, and biological properties. In total, there were 7 replicate stands with 3 treatments each and 3 plots of each treatment, for a total of 63 plots; each plot was sampled over 7 seasons: summer 2005, fall 2005, spring 2006, summer 2006, fall 2006, spring 2007, and summer 2007, for variables indicated in Table 2.2.

2.2.3 Soil chemical analysis

Soils for chemical analysis were collected to 10 cm in depth using a garden trowel at each plot during each summer sampling period (Table 2.2). Soil samples were combined by treatment per stand and then sieved (2.0 mm) and air-dried before being analyzed. Total C and N were analyzed by the dry combustion technique (Bremner 1996, Nelson and Sommer 1996) using a Flash EA112 NC soil analyzer (Thermo Electron Corporation, Milan, Italy). Percent organic matter was measured by the loss on ignition method (Dean 1974). Analysis of cation exchange capacity (CEC) was carried out using the sum of exchangeable cations technique (Robertson et al. 1999a) for the summer 2005 and 2006 samplings, and the ammonium acetate method for the summer 2007 soils. Soil pH was measured via the 1:2 (soil-water) dilution method using deionized water (Robertson et al. 1999a). Available phosphorus was

analyzed using both the sodium bicarbonate (P-Olsen) method and the dilute acid-fluoride method (P-Bray) (Olsen and Sommers 1982). P-Olsen samples were analyzed at the Oregon State University Central Analytical Lab (OSU CAL) with the following modifications: 1) the ammonium paramolybdate solution contained sufficient HCl to neutralize the 2mL aliquot $NaHCO_3$ extractant, 2) a colorimeter tube, rather than a volumetric flask, was used for the color development step, and 3) stannous chloride, instead of ascorbic acid, was used as the reducing agent. The P-Olsen was analyzed at the OSU CAL with the following modifications: 2.9 g weight used with a 60 second shaking time. P-Olsen generally is used with a pH greater than 7.5 (Olsen and Sommers 1982). Since the pH of our soils was between 6.7 and 7.0, the P-Bray data is likely to be more accurate. Nitrogen mineralization potential was measured during the summer 2005 and 2006 samplings via a laboratory incubation following the procedure in Robertson et al. (1999b). In summer 2007, N mineralization potential was determined using the following method at the OSU CAL: 50 ml of deionized water was added to 50 g of soil. The solution was well mixed and incubated at 40 °C for 28 days. After incubation, 50 ml of 2M KCl was added to extract NH_4-N for one hour. Incubation N, which is the anaerobic conversion of organic N to NH_4 and is a rough estimate of biologically available N, was measured in summer 2007 using the procedure described by Keeney (1982) at the OSU CAL with the following modifications: the sample size increased from 5 to 20 g and a 125-mL screw-top extracting bottle was used to accommodate the larger sample size and volume of

solutions. Total P was measured at the OSU CAL using a Kjeldahl extraction (Bremner 1996).

2.2.4 Soil physical analysis

Soil physical properties were measured at various times and replications depending on the property (Table 2.2). Gravimetric water content (% moisture) was measured in each plot at each sampling period to allow calculation of water-filled pore space, an attribute critical to mass flow of nutrients as well as limits to biological activity. Bulk density (Db) was assessed in the fall of 2005 and the springs of 2006 and 2007. These values were used to calculate soil porosity and for determining gravimetric to volumetric water content.

2.2.5 Soil biological analysis

Soil respiration was measured at 3 plots per treatment within each stand for the first 6 sampling periods with a portable infrared gas analyzer incorporated into a photosynthesis system. This analyzer was attached to a closed, dynamic soil respiration chamber designed for use with the Li-6200 (LiCor, Lincoln, NE) (Norman et al. 1992) (Table 2.2). For each measurement, the soil respiration chamber was placed on 10 cm diameter by 5 cm height polyvinyl chloride (PVC) collars that were installed permanently 2 cm into the mineral soil. Air entering the chamber was partially scrubbed to below CO_2 concentrations before starting the readings, and allowed to build to just above ambient CO_2 concentrations during a measurement sequence. Carbon dioxide concentration was recorded at every 5 ppm increase. Soil

respiration data were obtained for all sites in 2005, 2006, and 2007, following the methods given in Law et al. (2001) using a LI6200 infrared gas analyzer. Soil respiration rates were expressed as μmol $m^{-2}s^{-1}$ of CO_2, using the same convention and quantification of soil respiration rates used by Elizabeth Sulzman in her other studies (Sulzman et al. 2005).

Phosphatase enzyme activities were assayed from soil samples collected in spring 2007. Two mm sieved soil slurries were prepared with deionized water. One ml of slurry was incubated with 1 ml of 50 mM *p*-nitrophenyl-phosphate at 30 °C. These assays were run without the conventional buffers (Tabatabai 1994) to measure enzyme activity under actual soil matrix conditions (pH, cation concentrations), rather than the level of enzyme present at optimum soil pH with increased ionic strength. After 1 h, 0.5 ml of 0.5 M $CaCl_2$ was added and reactions were terminated by adding 2 ml of 0.5 M NaOH to the assay. Controls consisted of slurry without substrate and substrate without slurry. After centrifugation, supernatant *p*-nitrophenol (*p*-NP) concentrations were measured at 410 nm, and enzyme activities were calculated on a dry weight basis (Caldwell et al 1999).

2.2.5.1 DNA extraction and amplification

Bacterial species richness was measured at each plot within each stand for the first 6 sampling periods (Table 2.2). A MoBio Power Soil© DNA isolation kit was used for DNA extraction from each soil sample (MoBio Laboratories, Carlsbad, CA). Approximately 0.5 g of soil was added to a mini prep tube containing Teflon beads and cells were lysed using physical disruption. Then, the extract was purified by

binding the DNA to a silicon matrix and rinsing with ethanol containing buffer, before eluting with water. Bacterial-associated genes were amplified using 16S rDNA gene primers 8F (5'-[6-FAM] AGAGTTTGATCCTGGCTCA) and 907R (5' – CCGTCAATTCCTTTRAGTTT) (Edwards et al. 1989, Muyzer et al. 1995) in a 50-µl reaction mix containing: 1x PCR buffer, 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.2 µM Primer, 0.064% BSA. Each soil DNA extract was run twice under the following conditions: 95 °C for 3 min., followed by 30 cycles at 95 °C for 30 s, 55 °C for 1 min., 72 °C for 45 s, and ending with an extension step of 72 °C for 7 min. Once amplified, the two products were pooled to capture full diversity. These pooled products were then purified using a MoBio Ultra Clean DNA Clean Up kit (MoBio Laboratories, Carlsbad, CA) in order to eliminate genomic DNA, excess primers, and unused nucleotides.

2.2.5.2 Restriction and T-RFLP profiles

Products were digested using two restriction enzymes, MspI and Alu1 (Promega, Madison, WI). Digests were run according to manufacturer's specifications by incubating the restriction digest for 3 hr at 37 °C. Restricted samples were submitted to Oregon State University Center for Gene Research and Biotechnology for analysis using an ABI Prism 3100 Genetic Analyzer to run capillary gel electrophoresis. Approximately 1 ng of amplified DNA was submitted for analysis for each sample. The analysis produced one community profile for each sample.

Length and fluorescence of the terminal restriction fragments (TRF) were determined using GeneScan version 2.5 and Genotyper version 3.7 software. The total

fluorescence was summed for each sample and then used to relativize peaks as a fraction of this total fluorescence. Any peak contributing less than 1.5% of the total fluorescence in a single profile was excluded and the peaks recalculated, making the sum of each profile equal to 100. Peaks were then aligned by base pairs and any peaks less than 0.5 base pairs apart were combined for final fragment identifications.

2.2.5.3 Biolog ecoplates

Culturable soil bacterial functional diversity was qualitatively assessed with Biolog substrate utilization ecoplates (Biolog Inc., Hayward, CA, USA) in spring 2006. Each 96-well microtiter plate contained 31 different C substrates plus one negative control with no C substrate, replicated three times. Each well also contained a complex of growth factors at low concentrations and a redox dye (tetrazolium violet) that turned purple as the inoculated microbes used the substrate and respired. One g of soil was placed in 99 mL phosphate buffer and refrigerated overnight. The next day, the samples were shaken for 20 min at 160 rpm with a clinical rotator, resulting in a well-mixed soil slurry. For each sample, 100 μm of the slurry was pipetted under a laminar flow hood into an ecoplate. Plates were incubated at room temperature and color development was determined using a PowerWave X 340 spectrophotometer at a wavelength of 596 nm. These values, which represent the microbial community's ability to use a particular substrate effectively, were recorded at 24-hr intervals for 5 consecutive days (Sinsabaugh et al. 1999). The data used in this analysis are from the day 3 readings and have been standardized to the water control. The water column (all zeros) was removed and all resulting negative values were changed to zero.

2.2.6 Statistical analysis

ANOVA was used to analyze soil chemical and physical data. Models for each soil property varied according to the structure of the data, number of replicates, and repeated measures. The software used for the soil chemistry analyses was S-Plus 2000 (MathSoft 1988-1999). The $p < 0.1$ level of significance was used due to the small number of replicates for the three treatments, since this provides an improved opportunity for rejection of the null hypothesis in such cases (Steel et al. 1997).

Multivariate statistical analysis was performed using PC-ORD version 5.0. (McCune and Grace 2002). Differences in sample community profiles were determined using nonmetric multidimensional scaling (NMS) ordination techniques and Sørensen distance measures, where samples are ordinated in species space and the axes represent variance in species composition among samples. Preliminary ordinations were examined and the data set further modified, first by excluding any peak that occurred in fewer than 5 samples and then by an arcsine square root transformation of each column, appropriate for area percentage data. NMS parameters were set so that 500 iterations were run, starting from random configurations. Monte Carlo test results were compared against real data to determine the significance of a given solution. The ordination with the lowest final stress was chosen for further analysis. Using the Euclidean (Pythagorean) distance measurement, the blocked multiresponse permutation (MRBP) and unblocked multiresponse permutation (MRPP) procedures were used to test the strength and statistical significance of group membership. The p-value and A statistic (A), describing within-group variability, was

recorded for each MRBP and MRPP analysis. Soil chemical and physical properties and the biological factor, respiration, were correlated with community compositional ordinations to investigate links between community composition and functional capability for the six seasons.

NMS, where samples were ordinated in C substrate space, was used to analyze the Biolog spectrophotometer data. The data needed no further transformations after looking at initial ordinations. MRBP was used to test significance of strength and statistical significance of group membership. For outlier analysis, MRPP, and PerMANOVA, Euclidean distance was used.

SAS 9.1 (SAS 2003) was used to analyze differences among treatments in phosphatase enzyme rate, infiltration rate, cumulative number of species, and mean number of species. The repeated measures randomized block design was used with 6 seasons, 7 blocks, and 3 treatments.

Species diversity was measured using the Shannon-Wiener index (H) using: $H = - \sum p_i (\ln p_i)$, where p_i is the ratio of the number of MspI T-RFLP peaks found in each sample to the total number of peaks found in all samples for the MspI T-RFLP data. Biolog substrate diversity was calculated the same, except for p_i, which is the ratio of average well color development (AWCD) on each substrate to the sum of all AWCD on all substrates. The value of the Shannon-Wiener diversity index usually falls between 1.5 and 4.5, where 4.5 means the number of individuals are equally distributed and there is high community complexity (Magurran 1988). Evenness was also calculated for the MspI T-RFLP data using $E = H'/ H_{max} = H'/ \ln S$, where H is the Shannon-diversity index and S is the total number of peaks found in all samples. E is a number between 0 and 1, with 1 representing a situation in which all species are equally abundant and assumes that all species in the community are accounted for in the sample (Magurran 1988).

2.3 RESULTS

2.3.1 Soil chemistry

The means for P-Olsen and P-Bray differed among treatments ($p = 0.03$, $p = 0.001$, respectively, Table 2.3). P-Olsen was higher in the undisturbed treatment than in either the subsoiled or compacted treatments, whereas P-Bray was significantly lower in the subsoiled treatment than in the other two treatments (Table 2.3, Fig.2.2). Total P differed among treatments ($p = 0.1$); it was higher in the undisturbed treatment than in the subsoiled treatment (Table 2.3, Fig. 2.3). Incubation N (Fig. 2.4) and N mineralization in 2007 differed among treatments ($p = 0.01$ for both); both were

significantly higher in the undisturbed treatment than in the compacted treatment (Table 2.3). CEC, LOI, C:N, pH, total C, total N, N mineralization 2005/2006, and net nitrification did not differ among treatments ($p > 0.1$) (Table 2.3). Total N ($F_{[2,36]} = 27.83$, $p = 0.0001$), net nitrification ($F_{[1,18]} = 6.04$, $p = 0.02$), and P-Bray ($F_{[2,36]} = 23.97$, $p = 0.0001$) means were higher in summer 2006 than in summers 2005 or 2007. N-mineralized 2005/2006 ($F_{[1,17]} = 11.07$, $p = 0.004$), was higher in summer 2006 than in summer 2005. CEC was higher in summer 2005 compared to summers 2006 or 2007 ($F_{[2,36]} = 13.02$, $p = 0.0001$). Differences among stands were detected for all measured soil chemical properties (Table 2.3).

2.3.2 Soil physical properties

The means for Db at 5 cm and at 10 cm differed among treatments ($p = 0.1$, $p = 0.03$, respectively, Table 2.3). The mean Db at 5 cm was lower in the undisturbed treatment than in the compacted treatment and, on average, Db at 10 cm was lowest in the subsoiled treatment (Table 2.3). Average percent moisture did not differ among treatments ($p = 0.18$) but was lower in the summer season samplings compared to fall and spring ($F_{[2, 97]} = 122.85$, $p = 0.0001$), and was lower in the 2005 sampling compared to 2006 or 2007 ($F_{[2, 97]} = 40.42$, $p = 0.0001$). Some soil physical properties differed among stands (Table 2.3).

2.3.3 Soil biological properties

There were differences among treatments for soil respiration rate ($p = 0.05$); it was higher in the undisturbed soil than in the other two treatments (Table 2.3).

Average respiration rates were lower in 2006 compared to 2005 ($F_{[2, 307]} = 17.93$, $p = 0.0001$), and differed among seasons ($F_{[2, 307]} = 33.20$, $p = 0.0001$). Respiration rates were lower in fall compared to summer ($p = 0.0001$) and spring ($p = 0.0001$). The mean phosphatase activity differed by treatment ($p = 0.07$); it was lowest in the subsoiled treatment and did not differ between the compacted and undisturbed treatments (Table 2.3, Fig. 2.5). There was no difference in phosphatase activity by stand ($p = 0.16$) (Table 2.3).

2.3.3.1 T-RFLP's

The cumulative number of species did not differ among treatments ($p = 0.4$) (Table 2.3, Fig. 2.6). However, there was a consistent trend showing that the compacted soil had a greater cumulative mean number of species than either the undisturbed or subsoiled treatments (Fig. 2.7). All treatments showed a gradual increase in the cumulative mean number of species over time (Fig. 2.6, 2.7). There also was no difference in cumulative number of T-RFLP species by stand ($p = 0.61$) (Table 2.3). The mean number of species did not differ among treatments ($p = 0.23$) but showed difference among sampling periods ($p = 0.001$) (Table 2.3, Fig. 2.8). A NMS ordination of mean number of species showed differences in the bacterial community between the first and second year of sampling (MRBP p value = 0.0001, A = 0.13) (Fig. 2.9).

There were a total of 272 and 153 peaks for the enzymes MspI and AluI, respectively. MspI has a higher frequency of resolving single populations in model communities than AluI. Therefore, all ordination results presented will be on the MspI

data (Engebretson and Moyer 2003). Shannon-Wiener index for the MspI T-RFLP peaks ranged between 3.6 and 4.1 (Table 2.4). Evenness for MspI T-RFLP peaks ranged from 0.63 to 0.73 (Table 2.4). The mean cumulative number of T-RFLP species was lowest in the summer 2005 sampling season ($F_{[5, 90]} = 58.96$, $p = 0.0001$)

A PerMANOVA of all MspI T-RFLP peaks showed that there was a significant grouping of the microbial community by season ($F_{[2,123]} = 4.91$, $p = 0.0002$) and stand ($F_{[18, 105]} = 1.03$, $p = 0.41$). However, there was no difference by treatment ($F_{[2, 105]} = 0.61$, $p = 0.76$) (Table 2.5). LOI, CEC, and percent moisture were the only environmental measures that correlated to the variation in soil samples taken from summer 2005, spring 2006, and spring 2007 (Table 2.5). In addition to these variables, P-Bray correlated with the variation in summer 2006 soil samples. There were no environmental measures that correlated with variation in either of the fall measurement periods. Fall 2006 was the only season for which a difference among stands was not detected (Table 2.5).

2.3.3.2 Biolog

The Shannon-Wiener index for Biolog substrate activity ranged from 2.8 to 3.0 (Table 2.6). NMS ordinations of samples in Biolog C substrate space showed no correlation between C substrate groups and the environmental variables measured (Fig. 2.10). There were no differences in functional diversity (MRBP $p = 0.64$, $A = -0.006$) among treatments. Ordinations of the Biolog data in species space showed that the C substrate groups, amines/amides, amino acids, and carbohydrates, significantly correlated with the variation in species composition in spring 2007 (Fig.

2.11). The amines/amides are more correlated with axis 3 (r = 0.460) (Fig. 2.11), the amino acids with axis 1 (r = 0.634) (Fig. 2.11), which explains more variation than axis 3, and the carbohydrates correlated with axis 2 (r = -0.456) (not shown).

Individual Biolog substrates that significantly correlated with the variation in soil samples were: LA (L-arginine), LAS (L-asparagine), DX (D-xylose), DMA (D-malic acid), and IE (i-erythritol). LA (r = 0.564) and LAS (r = 0.457) were positively correlated with axis 3, whereas DX (r = -0.441) and DMA (r = -0.498) were negatively correlated with axis 3, which explained 62.9% of the variation. IE was negatively correlated with axis 1 (r = -0.492), which explained 22.6% of the variation. There were no community differences with respect to treatment (MRBP p = 0.112, A = 0.02). However, there were differences in the microbial community by stand (MRBP p = 0.003, A = 0.1).

2.4 DISCUSSION

The effects of compaction and subsoiling after post-fire salvage logging on soil bacterial communities and their function were minimal. We found, however, that disturbance caused by salvage logging lowered plant available N and P and microbial metabolism (respiration). Clearcutting has been shown to decrease total N, NO_3-N, NH_4-N, PO_4-P, and total C in the forest floor (Schmidt et al. 1996). However, other studies have found either no significant difference (Maynard and MacIsaac 1998), or an increase in these nutrients in cut treatments (Vitousek and Matson 1985, Frazer et al. 1990).

2.4.1 Soil chemical properties

Phosphorus is an important plant growth-limiting nutrient in soils. The decrease in total and plant available P (P-Bray) in the disturbed treatments in this study may be linked to fractions of the organic matter that were not measured. There were no differences in plant available P between the undisturbed and compacted treatment using the P-Bray method. Some P stored in plant residues becomes associated with the active and passive fractions of soil organic matter, where it can be stored for future release and very slowly converted to soluble forms that plants can use (Brady and Weil 2002). Practices that cause only very small changes in total soil organic matter (as seen in our study) also can have large effects on the relatively small pool of active organic matter, which generally is one of the first fractions to be affected by changes in land management (Brady and Weil 2002). Andisols typically have high natural fertility, except that P availability is severely limited by the

extremely high P retention capacity of the andic materials (Brady and Weil 2002). The amorphous minerals in Andisols have a greater capacity to sorb phosphate in which the greatest sorption occurs before the secondary clays form in volcanically derived soils (Olander and Vitousek 2005).

Results of a recent study in an oak (*Quercus petrea* L.) forest showed that long-term harvest using skidding techniques significantly lowered the amount of total P in the 0-10 cm soil depth (Makineci et al. 2007). Clearcut and partial cut treatments in boreal coniferous forests have been shown to decrease total P relative to uncut treatments (Schmidt et al. 1996, Lindo and Visser 2003).

Incubation N also was highest in the undisturbed treatment. This anaerobic conversion of organic N to ammonium is used as a measure of the amount of plant available N. Compaction has been shown to reduce the turnover rate of N-rich microbial biomass (Holmes and Zak 1994), increase the percentage of water-filled pores and potential denitrification (Torbert and Wood 1992), and reduce N mineralization by restricting the accessibility of organic material (Breland and Hansen 1996). DeLuca and Zouhar (2000), similar to the findings in our study, reported an increase in the levels of NH_4^+-N immediately following harvesting and prescribed fire. Prieto-Fernandez et al. (1993) also found an increase in the amount of ammonium after fire due to the volatilization of organic N. Ammonium is produced during biomass burning, while nitrate requires nitrification. The destruction of the vegetation contributes to an increase in nitrifier abundance. However, without plants to utilize nitrate, it is lost from the ecosystem either by denitrification or leaching (Knicker

2007). Prescribed burning in a ponderosa pine forest near Flagstaff, Arizona contributed to an increase in ammonium-N in old-growth, pole, and sapling substands and was associated with differences in the initial forest floor weight and the amount of forest floor burned (Covington and Sackett 1992). Schmidt et al. (1996) found that harvesting decreased total N and mineralizable N, and Lindo and Visser (2003) found decreases in NH_4-N after clearcut harvesting.

We found no differences in pH, cumulative number of species and species composition among treatments or stands. Fierer and Jackson (2006) found that pH can predict the diversity and composition of the bacterial community. Our findings support this finding, even though we have a small spatial scale.

2.4.2 Soil physical properties

There were no differences in Db between the compacted and undisturbed treatments. Similar results were found by Moghaddas and Stephens (2008) in Californian Sierra Nevada mixed-conifer stands. Machine traffic has been shown to increase soil strength mostly in the 20-50 cm interval rather than the surface (Ampoorter et al. 2007). We measured Db only to 10 cm; it is possible there may have been an increase in Db on the lower soil strata. Frost heaving and freeze-thaw cycles generally increase Db near the soil surface (Krumbach and White 1964, Benoit and Bornstein 1970). The soils in our study area are derived from volcanic ash with sandy loam texture. Andisols have been shown to be less compressible than other denser soils due to their high shear strength (McNabb and Boersma 1993). Coarse-textured soils tend to be less susceptible to compaction than fine-textured soils (Williamson

and Neilsen 2000, Powers 2002, Gomez et al. 2002). Our results contrast with those of Page-Dumroese (1993) and Davis (1992), who found that bulk densities of volcanic ash soils with silty loam and sandy loam textured soils, respectively, increased significantly after compaction.

2.4.3 Soil biological properties

Stand and seasonal differences seemed to have a more pronounced effect than harvesting treatments on the soil biological properties following post-fire salvage logging. Results of the PerMANOVA analyses showed that the bacterial community structure did not differ among treatments. A total of 272 peaks were found with the enzyme MspI. This is higher than the total found by del V Gomez et al. (2004) who looked at the effects of various land-use gradients on the bacterial community in Argentina. These differences could be due to differences in ecosystems and soil types (ours was an andisol and theirs was a mollisol). Different soil types are characterized by certain unique properties, therefore differing soil types could have an impact on the bacterial community found within it. The Shannon-diversity for MspI T-RFLP data indicated that individuals in our samples were equally distributed and showed high community complexity. Evenness implied that all species were equally abundant. We did not see a difference in the cumulative mean number of T-RFLP species among treatments, suggesting that the habitat needs of the bacterial community were adequately met, even following compaction and subsoiling. However, we did see a trend that compacted soil contained slightly more cumulative mean number of species. 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, meaning that even a 50% reduction in available porosity would still leave the majority of surface area uninhabited. It also has been shown that compaction of a silt loam soil completely eliminated accessible pores for microbivores (van der Linden et al. 1989). This inability of predators to access small pores in compacted soil may help to stabilize the microbial community (Breland and Hansen 1996). However, protection from predation may benefit community stability at the cost of reducing plant nutrient availability (Busse et al. 2006). Moldenke et al. (2000) found that compaction caused by skid roads in the Deschutes National Forest, contributed to a shift in the foodweb to one that utilizes primarily bacteria; it also reduced the general size categories of inhabitants and shifted their life history toward short-lived species. Khetmalas et al. (2002) found no significant differences in bacterial diversity between burned–salvaged and unburned stands 4–5 yr after fire and salvage-logging. Recent studies also have found that compaction was not detrimental to microbial community size, activity, function, and structure (Shestak and Busse 2005, Busse et al. 2006). It has been reported that microbial community responses to burning and harvesting range from low resilience, as seen in low-severity prescribed burning (Fritze et al. 1993, DeLuca and Zouhar, 2000), to high resilience or complete tolerance following intensive forest management (Edmonds et al. 2000, Busse et al. 2001, Siira-Pietikäinen et al. 2001). Previous studies have found that compaction can have negative (Dick et al. 1988, van der Linden et al. 1989, Torbert and Wood 1992, Breland and Hansen 1996), neutral (Breland and Hansen 1996, Shestak and Busse 2005), or positive (Startsev et al. 1998)

effects on microorganisms, and that these effects are likely due to the complexity of soil disturbances.

Community level physiological profiles (CLPP), such as Biolog ecoplates, were used to assess the community structure and potential activity of culturable, aerobic and fast growing bacteria. The potential activity of the bacterial community is shown through the utilization patterns of sole-carbon-source. Biolog ordinations showed that the consumption of the amine/amide and amino acid guilds better explained the differences among compacted soil compared to the other two treatments. This could indicate that there was a shift in the bacterial communities, although it is hard to distinguish whether the change in the substrate utilization patterns are due to a change in the functional abilities only or also to a change in the community composition. The bacterial community in the compacted soil may have favored compounds with N in their chemical structure. This shift may be due to changes in substrate availability during decomposition. The slight oxygen restrictions may have produced a shift in the microbe populations, favoring those with more efficient anaerobic metabolism. Studies showing that soil properties, not treatment differences, cause the separation seen in CLPP (Staddon et al. 1997, Cookson et al. 2008), suggest that there may be soil chemical differences not measured in our study that are affecting the soil bacterial community. Other studies have found that disturbed soils have altered metabolic fingerprints compared to undisturbed soils (del V. Gomez et al. 2004, Goberna et al. 2005). Garland et al. (1997) found that the addition of a specific C source to a bioreactor contributed to significant changes in the overall substrate

utilization profile, but that no significant increase occurred in the corresponding well on the microtiter plate. Such findings suggest cautious interpretation of the functional relevance of substrate utilization profiles. In our study, the Shannon-Wiener index showed that the AWCD for the Biolog substrates was equally distributed among samples.

Phosphatase enzyme activity was lowest in the subsoiled treatment but did not differ between the compacted and undisturbed treatments or by stand. Dick et al. (1988) found that compaction lowered all enzyme activities assayed (including phosphatase) by 41-75%. Other studies also have found a decrease of phosphatase in compacted soil (Jordan et al. 2003, Tan et al. 2008). Phosphatases not only are crucial in organic P transformation, but also are significantly affected by soil pH, which controls P availability independent of organic matter content or disturbance levels. We did not find differences in pH among treatments. Both phosphatase and chitinase activity are suppressed by their products; high phosphate levels repress phosphatase activity (Rolstone et al. 1975, Nannipieri et al. 1978). In contrast, we found the most phosphate and phosphatase activity in the same treatment, undisturbed, which was burned, but not otherwise disturbed.

An indirect measurement of soil microbial activity is soil respiration. The higher respiration rate in the undisturbed treatment was likely due to the higher amounts of plant available P and N in the undisturbed treatment compared to the other treatments, suggesting more microbial activity. Thinning treatments have been found to have no impact (Ma et al. 2004), cause an increase (Concilio et al. 2005), or cause a

decrease (Lindo and Visser 2003) in soil respiration. These differences could be due to the forest types: a mixed-conifer old-growth forest, a mixed-conifer forest, and a boreal forest, respectively. The differences in understory vegetation in these forests could cause differences in soil respiration fluxes, due to the indirect influence of vegetation on soil moisture and temperature. Law et al (2001) showed that soil surface CO_2 effluxes were lowest for bare soil, and highest near shrubs, some of which were nitrogen fixers that have higher photosynthesis rates. A visual inspection of the treatments on each site indicated less vegetation growing in the compacted and subsoiled treatments. A few of the sites had large amounts of snowbrush ceanothus, a known nitrogen fixer, which seemed to have a higher percent cover in undisturbed treatments. This may be a reason why the soil respiration rates were higher in the undisturbed treatment.

2.5 CONCLUSION

Postfire salvage logging had little effect on soil bacterial community richness, suggesting that soil bacteria in these post-fire landscapes are tolerant of the occurrence of fires and are resilient to disturbance. However, the trend of more mean cumulative number of species in the compacted soil treatment may indicate slightly favorable conditions and less predation on the bacterial community. Mean number of species did not differ by treatment but there was a significant decrease in mean number of species after the spring 2006 sampling. This finding suggests that time since fire has a greater impact on bacterial community composition than does logging disturbance. Numerous studies have shown that fire has a greater effect on soil fungi than on soil bacteria (Dick et al. 1988, Vázquez et al. 1993, D'Ascoli et al. 2005), perhaps because of the relatively larger size of fungi compared to bacteria. Decreased soil respiration rates in the compacted and subsoiled treatments may indicate less microbial activity and may be associated with the decrease in nitrogen fixing plants growing within them. Decreased plant available P and N in the soil after post-fire salvage logging disturbances could have long-lasting effects in a system that is already nutrient limited.

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TABLES

Table 2.1: Stand locations and characteristics.

Stand	Unit #	Salvage (ha)	Elevation (m)	% Slope	Aspect	Lat/Long
TD	37	10.1	1030	4	SSE	N 44°31'46 W 121°42'29
UN	54	6.9	955	6	N to NE	N 44°29'25 W 121°42'15
MS	83	6.7	1000	6	E	N 44°29'46 W 121°43'48
Big	85	11.7	970	21	N to NE	N 44°29'26 W 121°42'38
SP	118	7.3	970	3	E	N 44°00'00 W 121°42'45
AKA	140	7.1	955	4	SE	N 44°32'05 W 121°40'56
FT	143	5.3	1030	12	SE	N 44°31'35 W 121°42'39

Table 2.1 continued

Stand	Unit #	PSME* BA*,[a] (cm)	PSME Trees/ha[b]	PSME Trees/ha[c]	PIPO* BA[a] (cm)	PIPO Trees/ha[b]	PIPO Trees/ha[c]	Other Species BA[a] (cm)	Other Species Trees/ha[b]	Other Species Trees/ha[c]
TD	37	91	12	4	104	20	20	742	79	0
UN	54	0	0	0	147	49	0	162	10	4
MS	83	68	10	1	5	3	0	256	86	0
Big	85	82	11	1	12	1	0	299	144	2
SP	118	109	13	1	20	6	0	142	34	2
AKA	140	295	64	3.5	115	7	3	342	114	3
FT	143	59	2	2	47	13	1	282	86	2

* Note: Tree data are prior to logging; BA = basal area; PSME = *Pseudotsuga menziesii* (Douglas-fir); PIPO = *Pinus ponderosa* (Ponderosa pine)

[a]Trees with dbh 7.6 – 81.2+ cm

[b]Trees with dbh 7.6 – 53.1 cm

[c]Trees with dbh 53.4+ cm

Table 2.2: Response variables measured for each stand.

Salvage							
Soil Properties	2005		2006			2007	
	Summer	Fall	Spring	Summer	Fall	Spring	Summer
Chemical							
CEC	3[a]			3[a]			3[a]
% OM LOI	3[a]	3[a]	3[a]	3[a]	3[a]	3[a]	
C:N	3[a]			3[a]			3[a]
pH	3[a]			3[a]			3[a]
Total C	3[a]			3[a]			3[a]
Total N	3[a]			3[a]			3[a]
N mineralization	3[a]			3[a]			3[a]
NH_4/NO_3	3[a]			3[a]			3[a]
Net nitrified	3[a]			3[a]			3[a]
Incubation N	3[a]			3[a]			3[a]
Total P							3[a]
P-Olsen	3[a]			3[a]			3[a]
P-Bray	3[a]			3[a]			3[a]
Physical							
Texture	once/stand[b]						
Moisture	3[a]	3[a]	3[a]	3[a]	3[a]	3[a]	
Bulk density		1[c]	1[c]			1[c]	
Biological							
Respiration	9[d]	9[d]	9[d]	9[d]	9[d]	9[d]	
Bacterial richness	9[d]	9[d]	9[d]	9[d]	9[d]	9[d]	
Functional diversity						3[a]	
Phosphatase activity						3[a]	

[a] combined samples within treatments per stand
[b] texture was measured only once per treatment per stand
[c] selected stake per treatment per stand
[d] per stand

Table 2.3: Soil chemical, physical, and biological properties by treatment and stand.

Soil Chemical Properties

Treatment	CEC* ($cmol_c\ kg^{-1}$)	LOI*	C:N	pH**	Total C	Total N	N min. 2005/2006 (ppm)	N min. 2007 (ppm)
Compacted	18.61[a] (0.85)	9.10[a] (0.27)	20.62[a] (1.13)	6.76[a] (0.05)	3.15[a] (0.23)	0.16[a] (0.01)	0.71[a] (0.07)	28.11[a] (2.92)
Subsoiled	19.06[a] (0.83)	9.66[a] (0.34)	19.82[a] (1.17)	6.69[a] (0.05)	3.02[a] (0.24)	0.16[a] (0.01)	0.74[a] (0.08)	32.73[a,b] (4.65)
Undisturbed	19.63[a] (0.93)	9.48[a] (0.32)	20.53[a] (1.21)	6.86[a] (0.07)	3.15[a] (0.20)	0.16[a] (0.01)	0.74[a] (0.10)	38.03[b] (4.82)
$F_{[df,df]}$	$1.01_{[2,12]}$	$0.96_{[2,11]}$	$1.04_{[2,12]}$	$2.21_{[2,12]}$	$0.13_{[2,12]}$	$0.07_{[2,12]}$	$0.10_{[2,12]}$	$6.53_{[2,12]}$
p	0.39	0.41	0.38	0.15	0.88	0.93	0.91	**0.01**
Stand								
AKA	21.77[a] (1.01)	10.53[a] (0.44)	22.05[a] (1.33)	6.67[a] (0.09)	4.12[a] (0.20)	0.19[a] (0.02)	0.90[a] (0.14)	37.77[a] (4.12)
Big	17.94[b,c] (1.60)	6.86[b] (0.17)	20.65[a,b] (1.71)	7.08[b] (0.09)	2.56[b] (0.37)	0.13[b] (0.02)	0.43[b] (0.02)	18.93[b] (3.34)
FT	20.47[a,b] (1.95)	12.25[c] (0.35)	20.38[a,b] (1.64)	6.74[a] (0.09)	3.61[a] (0.41)	0.18[a] (0.02)	1.01[a] (0.15)	50.27[c] (5.83)
MS	19.52[b] (0.98)	8.99[d] (0.39)	18.40[b] (2.20)	6.71[a] (0.06)	3.07[a,b] (0.33)	0.17[a] (0.01)	0.84[a] (0.11)	30.33[d] (1.24)
SP	18.42[b] (0.77)	8.54[d] (0.25)	19.32[a,b] (1.91)	6.68[a] (0.07)	2.75[b] (0.25)	0.15[b] (0.01)	0.84[a] (0.04)	39.13[a,c] (5.23)
TD	16.62[c] (0.82)	9.80[a] (0.30)	20.51[a,b] (1.77)	6.94[c] (0.04)	2.83[b] (0.20)	0.15[a,b] (0.02)	0.66[c] (0.06)	24.93[e] (2.05)
UN	18.95[b] (1.27)	8.97[d] (0.34)	20.92[a,b] (2.00)	6.56[a] (0.06)	2.80[b] (0.24)	0.14[b] (0.02)	0.42[b] (0.10)	29.33[d,e] (3.89)
$F_{[df,df]}$	$4.70_{[6,12]}$	$13.86_{[6,11]}$	$4.70_{[6,12]}$	$3.87_{[6,12]}$	$3.40_{[6,12]}$	$4.02_{[6,12]}$	$8.67_{[6,12]}$	$12.16_{[6,12]}$
p	**0.01**	**0.0001**	**0.01**	**0.02**	**0.03**	**0.02**	**0.001**	**0.0002**

Note: Data are averaged across years unless indicated otherwise. Within a column, means with a common lowercase letter are not significantly different at $p < 0.1$. Means are listed with standard errors in parentheses. Bolded p values indicate a significant difference at $p < 0.1$.

*CEC (cation exchange capacity), LOI (loss on ignition), Db (bulk density)

**pH is for a 1:2 (sample:water) dilution.

Table 2.3 continued

	Soil Chemical Properties					Soil Physical Properties		
Treatment	**Net nitr. (ppm)**	**Inc. N (ppm)**	**Total P (ppm)**	**P-Olsen (ppm)**	**P-Bray (ppm)**	**Db* - 5 cm depth**	**Db* - 10 cm depth**	**Moist. (%)**
Compacted	0.92[a] (0.08)	29.51[a] (3.23)	1189.53[a] (66.72)	13.38[a] (1.32)	9.57[a] (0.85)	0.98[a] (0.04)	1.02[a] (0.02)	17.62[a] (1.71)
Subsoiled	0.94[a] (0.10)	35.19[a,b] (4.95)	1152.09[a] (79.99)	11.80[a] (0.86)	7.29[b] (0.39)	0.95[a] (0.04)	0.87[b] (0.05)	18.44[a] (1.73)
Undisturbed	0.95[a] (0.10)	40.47[b] (4.83)	1296.25[b] (74.35)	16.81[b] (1.44)	9.81[a] (0.82)	0.90[b] (0.04)	1.01[a] (0.03)	20.60[a] (2.45)
$F_{[df,df]}$	$0.08_{[2,12]}$	$6.65_{[2,12]}$	$2.86_{[2,12]}$	$4.65_{[2,12]}$	$13.5_{[2,12]}$	$2.76_{[2,12]}$	$4.97_{[2,10]}$	$2.01_{[2,12]}$
p	0.92	**0.01**	**0.1**	**0.03**	**0.001**	**0.1**	**0.03**	0.18
Stand								
AKA	1.13[a] (0.10)	42.90[a] (4.60)	1340.11[a] (20.59)	20.22[a] (2.89)	12.0[a] (1.11)	0.93[a] (0.08)	0.91[a] (0.07)	19.31[a,b] (3.08)
Big	0.60[b] (0.04)	20.97[b] (3.16)	1073.24[b] (147.47)	12.23[b] (1.71)	8.0[b] (0.62)	1.0[a] (0.02)	1.0[a,b] (0.05)	15.88[b] (2.16)
FT	1.24[a] (0.15)	52.07[a] (6.04)	1423.69[c] (39.67)	13.74[b,c] (2.57)	7.78[b] (1.06)	0.77[b] (0.06)	0.85[a] (0.10)	22.39[a] (3.06)
MS	1.11[a] (0.14)	32.87[c] (0.90)	1228.86[b] (56.94)	15.98[c] (1.39)	8.78[b] (1.05)	1.04[a] (0.04)	1.06[b] (0.04)	15.20[b] (2.24)
SP	1.06[a] (0.06)	40.70[a] (5.35)	1073.0[b] (60.03)	13.97[b,c] (1.39)	8.67[b] (0.65)	1.02[a] (0.05)	0.96[a] (0.04)	20.98[a,b] (4.74)
TD	0.86[c] (0.07)	26.67[d] (1.79)	985.41[b] (76.0)	10.82[b] (0.76)	7.33[b] (1.05)	1.0[a] (0.03)	1.02[a,b] (0.06)	20.95[a,b] (2.99)
UN	0.54[b] (0.09)	29.23[b,c,d] (5.76)	1364.05[a,c] (63.84)	11.02[b] (1.34)	9.67[a,b] (1.72)	0.83[a,b] (0.06)	0.98[a] (0.03)	17.48[a,b] (2.24)
$F_{[df,df]}$	$8.44_{[6,12]}$	$10.92_{[6,12]}$	$6.37_{[6,12]}$	$3.30_{[6,12]}$	$7.35_{[6,12]}$	$7.70_{[6,12]}$	$1.45_{[5,10]}$	$2.76_{[6,12]}$
p	**0.001**	**0.0003**	**0.003**	**0.04**	**0.002**	**0.002**	0.29	**0.06**

Table 2.3 continued

	Soil Biological Properties			
Treatment	**Respiration (μmol $m^{-2}s^{-1}$)**	**Phosphatase (μmol $g^{-1}h^{-1}$)**	**Cumulative Number of TRFLP Species**	**Mean Number of TRFLP Species**
Compacted	2.45^{a} (0.12)	28.08^{a} (3.35)	52.12^{a} (3.98)	10.02^{a} (0.464)
Subsoiled	2.36^{a} (0.12)	22.74^{b} (1.72)	43.83^{a} (3.98)	8.95^{b} (0.464)
Undisturbed	2.93^{b} (0.14)	32.63^{a} (3.78)	47.31^{a} (3.98)	$9.31^{a,b}$ (0.464)
$F_{[df,df]}$	$3.24_{[2,42]}$	$2.77_{[2.54]}$	$1.11_{[2,12]}$	$1.38_{[2,12]}$
p	**0.05**	**0.07**	0.36	0.28
Stand				
AKA	2.25^{a} (0.20)	26.44^{a} (3.37)	50.39^{a} (6.30)	10.06^{a} (2.32)
Big	2.05^{a} (0.11)	20.06^{b} (1.40)	39.22^{a} (6.30)	8.94^{a} (2.32)
FT	2.92^{b} (0.19)	38.62^{c} (6.94)	50.83^{a} (6.30)	9.22^{a} (2.32)
MS	2.99^{b} (0.23)	$26.96^{a,c}$ (4.95)	45.56^{a} (6.30)	9.89^{a} (2.32)
SP	2.24^{a} (0.17)	$31.86^{a,c}$ (4.62)	53.50^{a} (6.30)	8.89^{a} (2.32)
TD	2.49^{a} (0.15)	$23.59^{a,b}$ (3.26)	52.56^{a} (6.30)	8.89^{a} (2.32)
UN	3.11^{b} (0.24)	$27.19^{a,b,c}$ (5.99)	42.33^{a} (6.30)	10.11^{a} (2.32)
$F_{[df,df]}$	$2.62_{[6,42]}$	$1.63_{[6,42]}$	$0.77_{[6,12]}$	$0.78_{[6,12]}$
p	**0.03**	0.16	0.61	0.78

Table 2.4: Shannon-Wiener Diversity index and Evenness for MspI T-RFLP peaks by treatment, stand, and sampling period.

	***Shannon-Wiener (H)**	****Evenness (E)**
Compacted	4.1	0.73
Subsoiled	4.0	0.70
Undisturbed	4.0	0.72
AKA	4.0	0.71
Big	3.7	0.66
FT	4.0	0.71
MS	3.9	0.70
SP	4.0	0.71
TD	4.0	0.71
UN	3.9	0.69
Summer 2005	4.0	0.71
Fall 2005	4.1	0.73
Spring 2006	4.0	0.71
Summer 2006	3.6	0.63
Fall 2006	3.6	0.64
Spring 2007	3.6	0.65
Combined Summer samples	3.9	0.70
Combined Fall samples	4.1	0.72
Combined Spring samples	4.0	0.71

* A number close to 4.5 means that the number of individuals are equally distributed and there is high community complexity

** A number close to 1 means that all species are equally abundant

Table 2.5: Statistical outcomes for NMS ordinations for each season, and MRBP and PerMANOVA tests for differences by stand and treatment (TRT).

Season	NMS	MRBP - TRT	MRBP - Stand	PerMANOVA	Vectors
Summer 2005	stress = 10.80 instability = 0.000001 2-d	A = -0.004 p = 0.60	A = 0.109 p = 0.002	stand = 0.003 treatment = 0.46	LOI, CEC
Fall 2005	stress = 9.77 instability = 0.000001 2-d	A = -0.0047 p = 0.56	A = 0.1575 p = 0.003	stand = 0.002 treatment = 0.53	None
Spring 2006	stress = 10.75 instability = 0.000001 3-d	A = 0.0227 p = 0.09	A = 0.1244 p = 0.001	stand = 0.001 treatment = 0.29	LOI
Summer 2006	stress = 9.344 instability = 0.000001 3-d	A = 0.0050 p = 0.36	A = 0.0659 p = 0.02	stand = 0.02 treatment = 0.29	P-Bray, % Moisture CEC
Fall 2006	stress = 10.07 instability = 0.000001 3-d	A = 0.0120 p = 0.22	A = 0.0081 p = 0.38	stand = 0.49 treatment = 0.43	None
Spring 2007	stress = 8.304 instability = 0.000001 3-d	A = -0.0104 p = 0.70	A = 0.883 p = 0.01	stand = 0.01 treatment = 0.57	%Moisture

Table 2.6: Table of Shannon-Wiener diversity index for spring 2007
Biolog substrate average well color development by treatment and stand.

	***Shannon-Wiener (H)**
Compacted	2.95
Subsoiled	2.89
Undisturbed	2.91
AKA	2.97
Big	2.76
FT	2.86
MS	2.97
SP	2.90
TD	2.98
UN	2.82

* Note: A number close to 4.5 means that the numbers of individuals are equally distributed and have high community complexity

FIGURES

Figure 2.1: Stand layout with treatments.

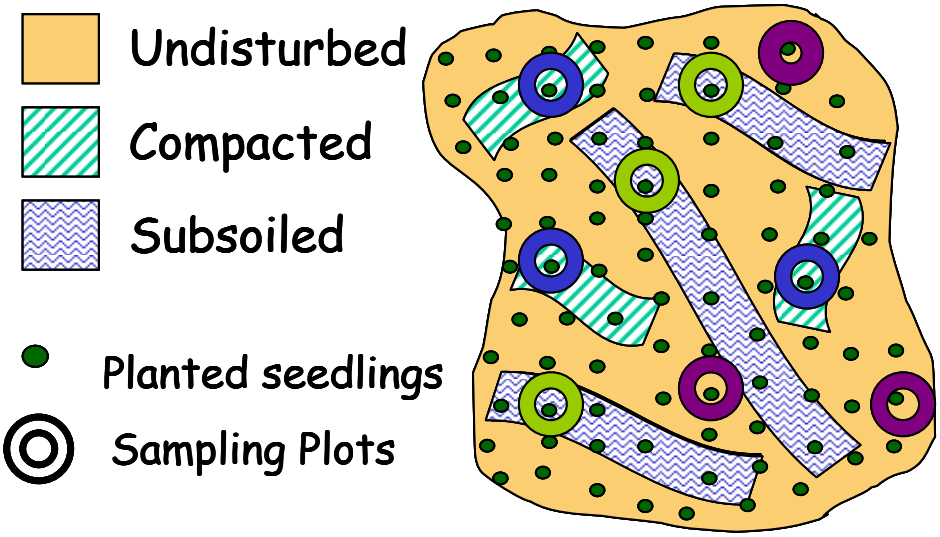

Figure 2.2: Means and standard error (SE) for plant available phosphorus by treatment.

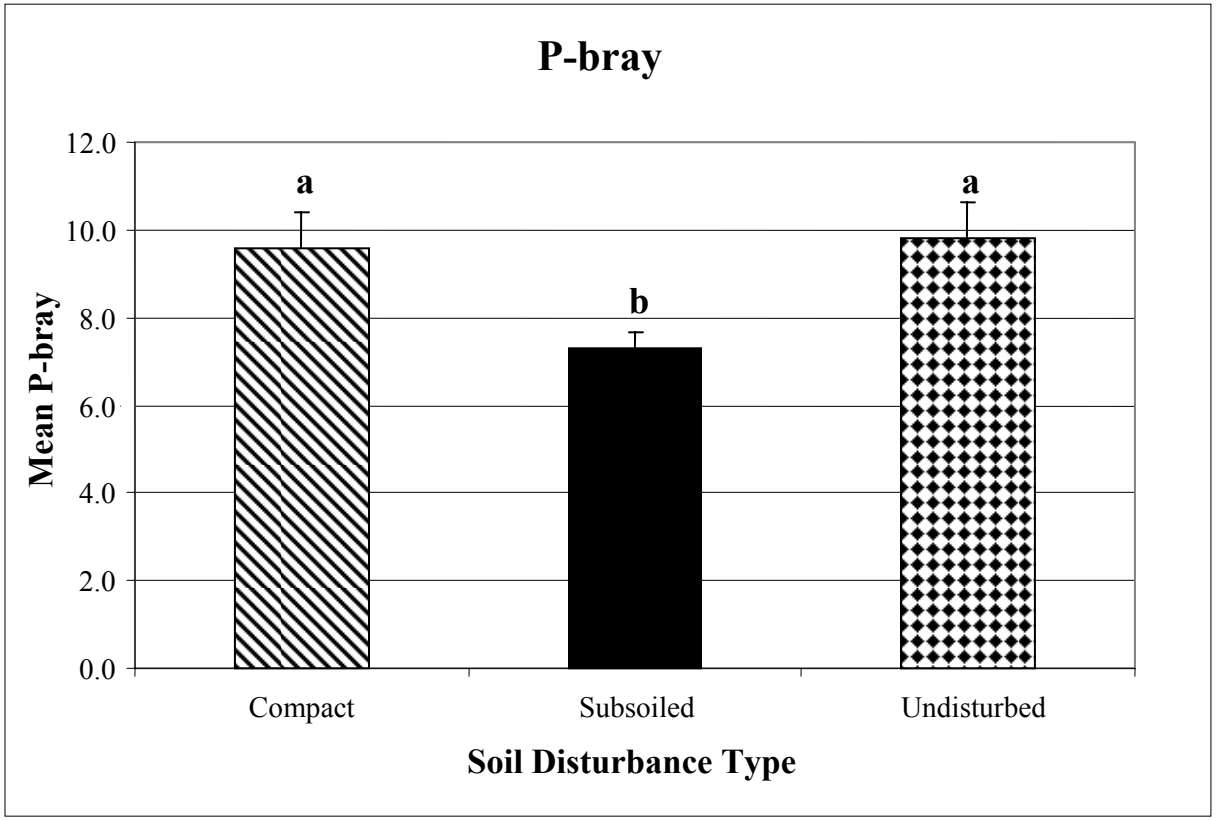

Figure 2.3: Means and SE for total phosphorus by treatment.

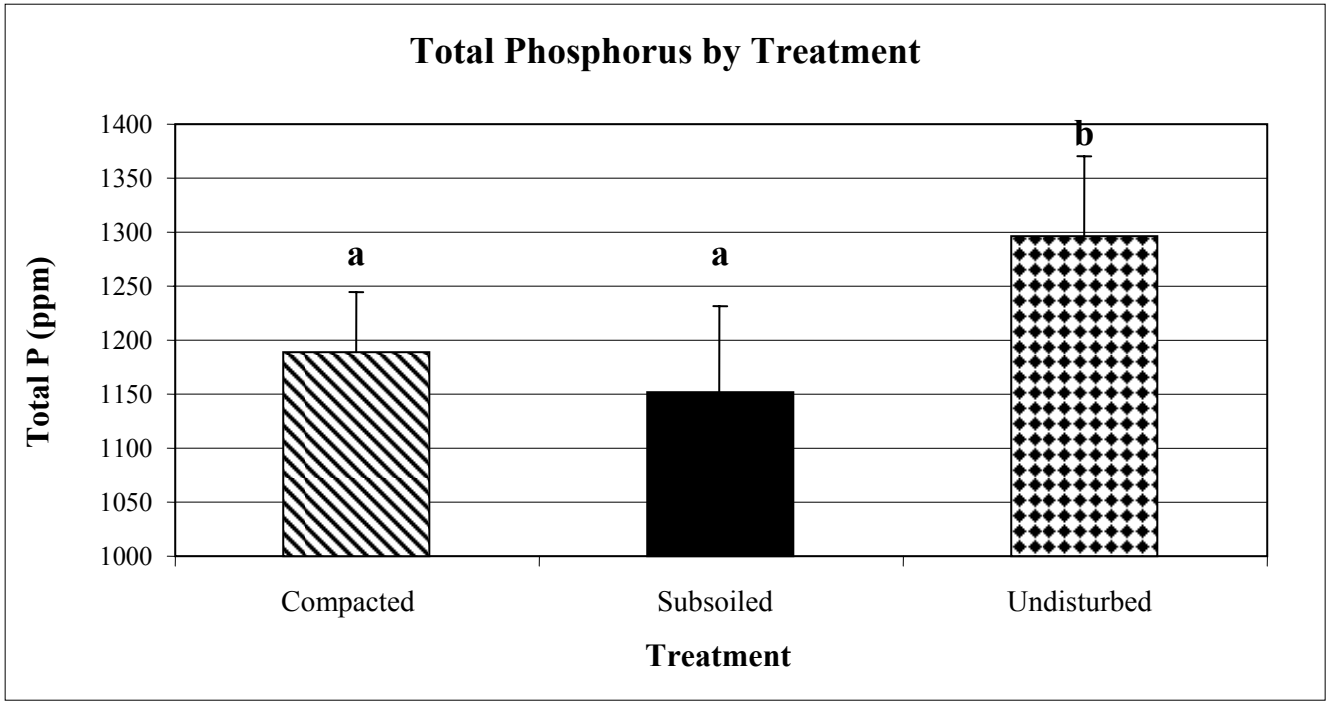

Figure 2.4: Means and SE for plant available nitrogen by treatment.

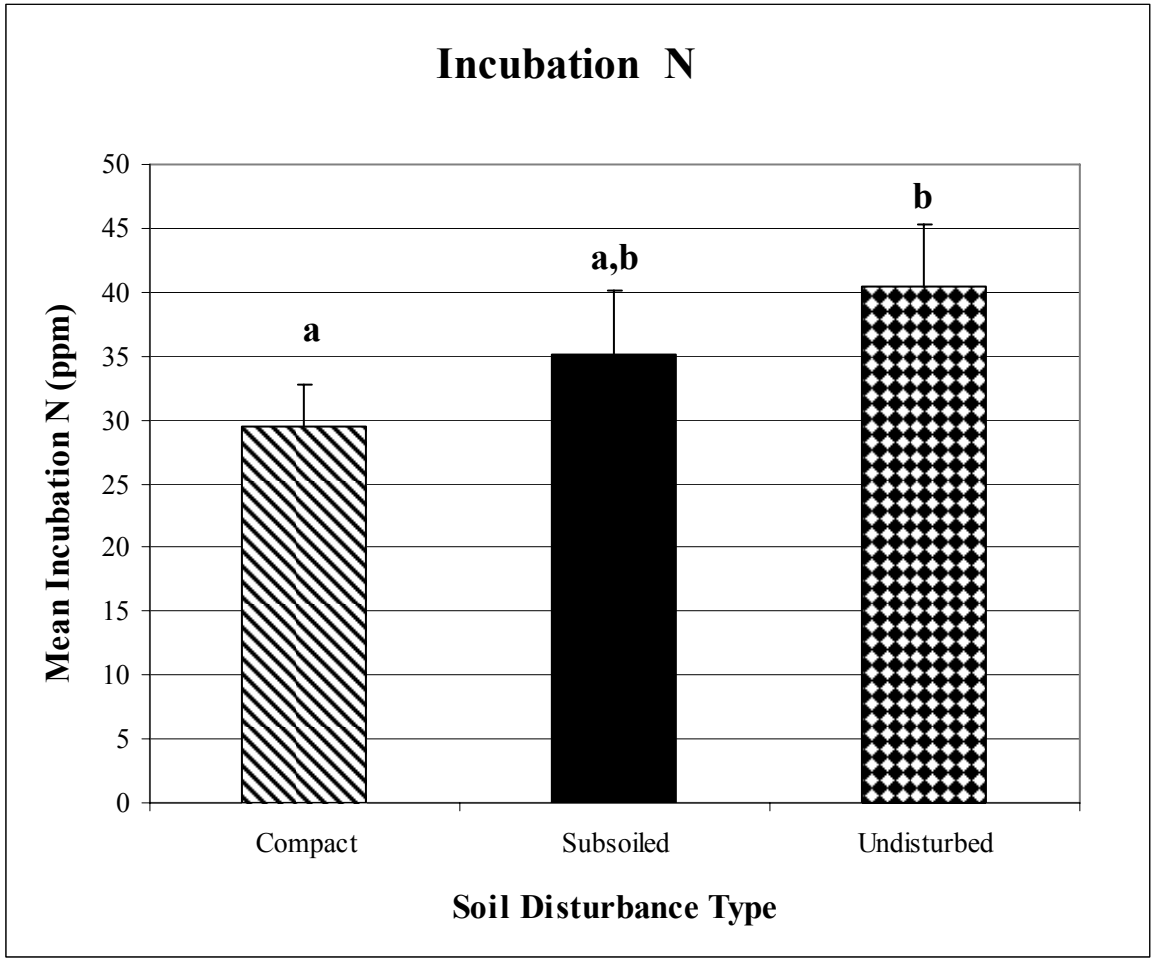

Figure 2.5: Means and SE for phosphatase activity by treatment.

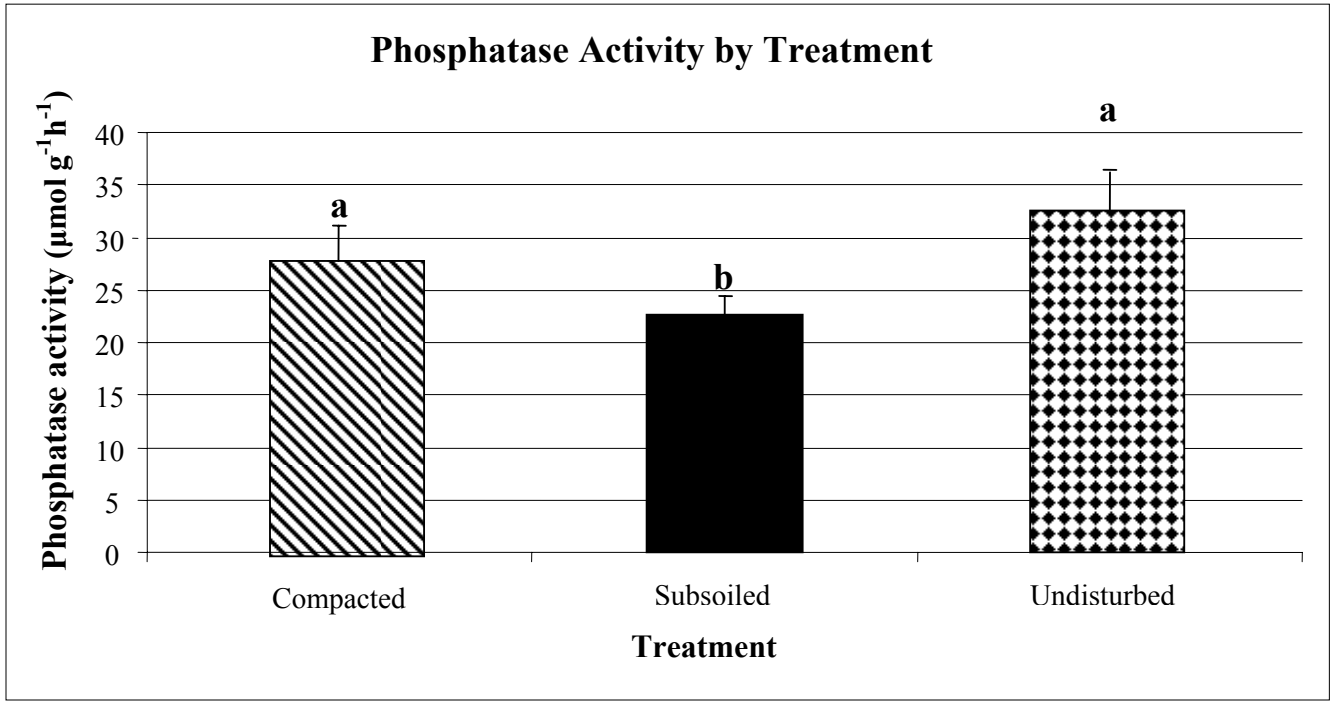

Figure 2.6: Cumulative number of T-RFLP species by season and treatment.

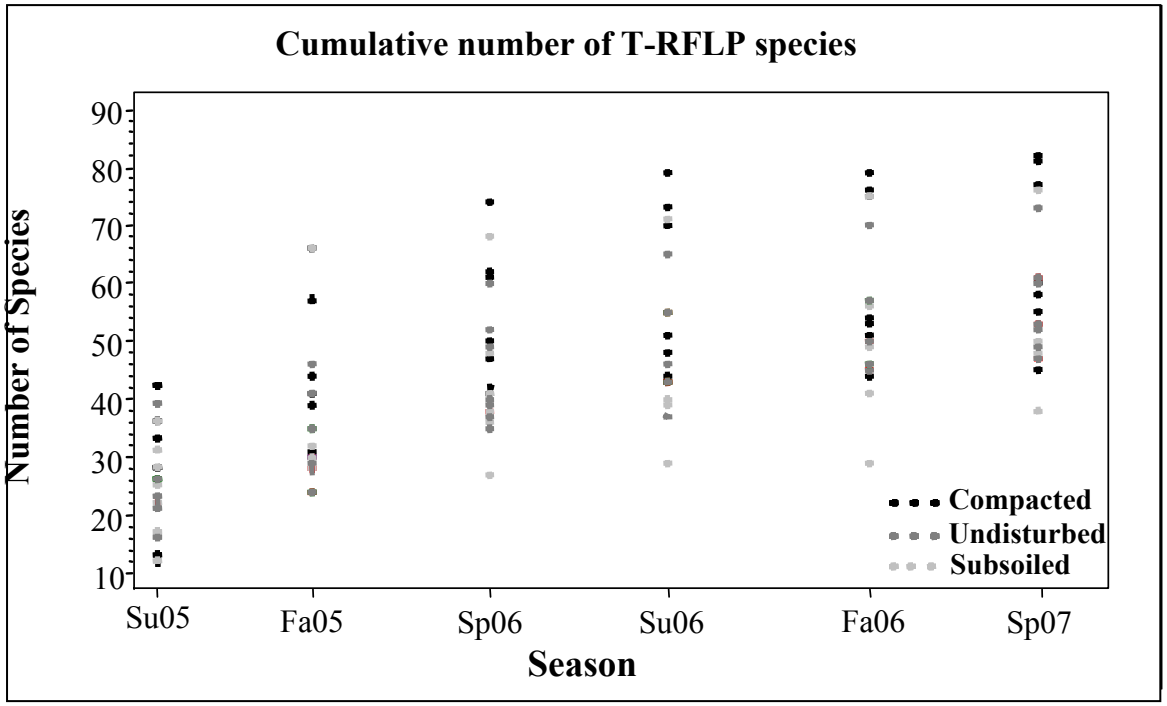

Figure 2.7: Cumulative mean number of T-RFLP species by season and treatment.

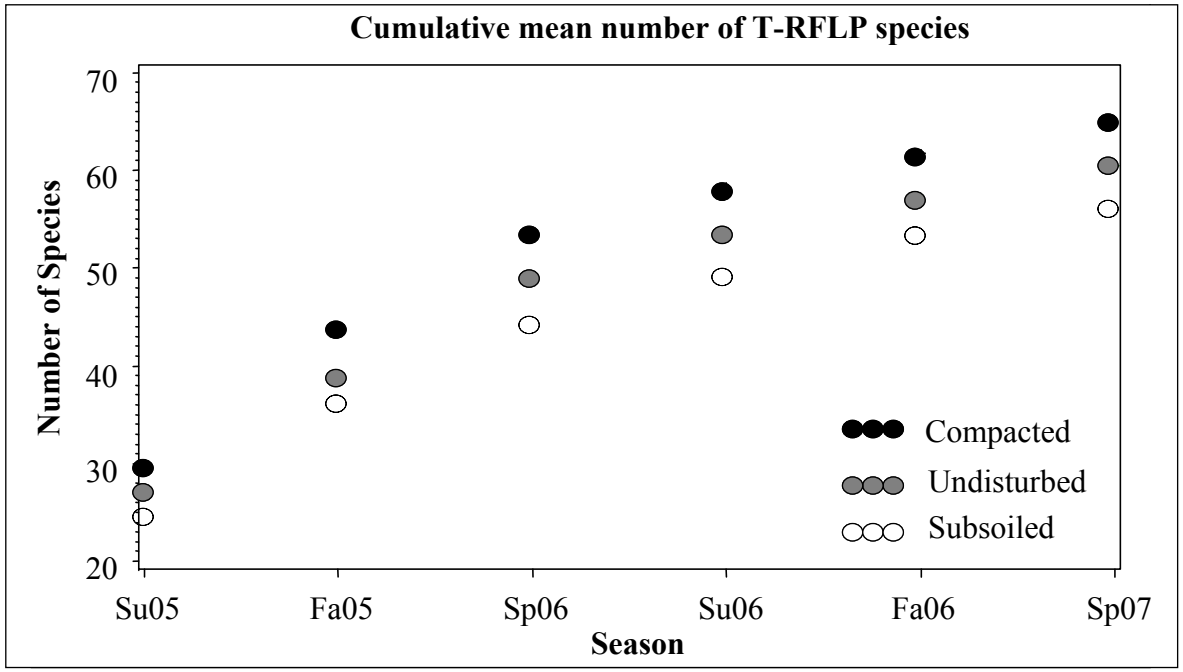

Figure 2.8: Mean number of T-RFLP species for a given season and treatment.

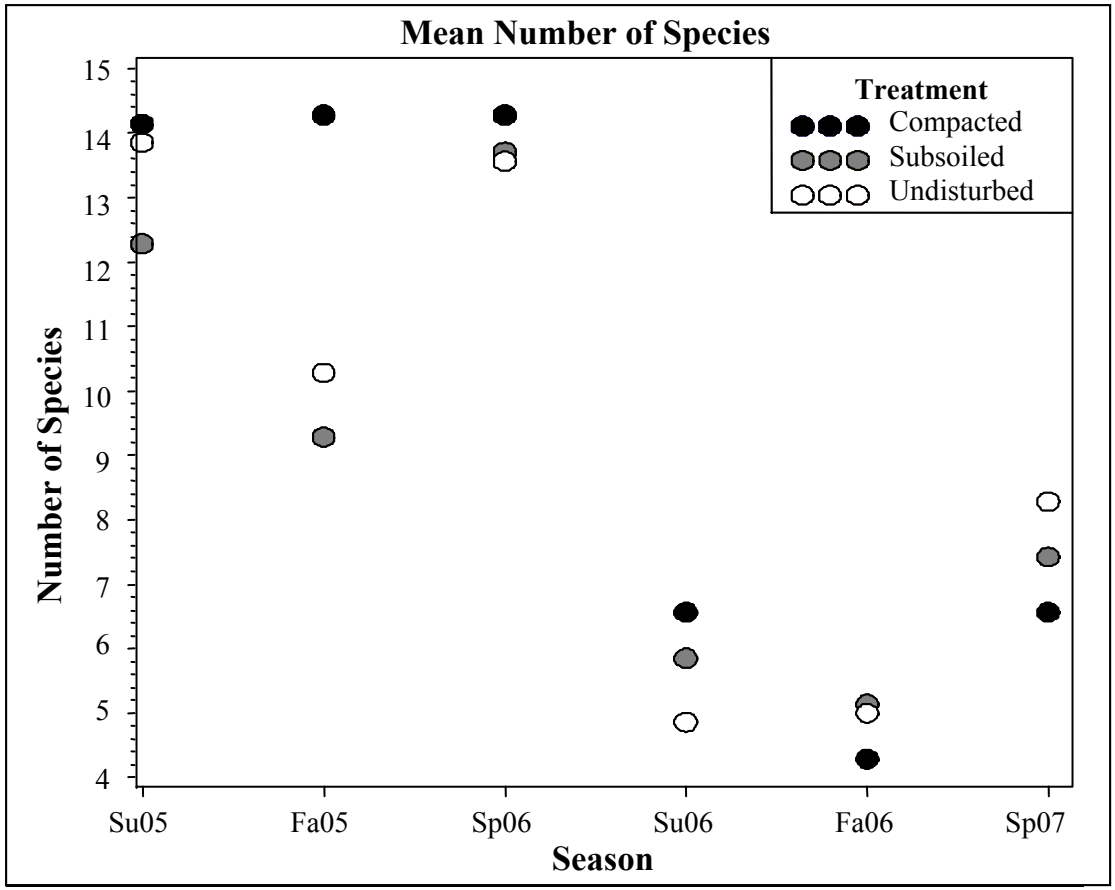

Figure 2.9: NMS ordination of the mean number of species by treatment. The plot shows samples in T-RFLP species space. The amount of variance explained by each axis appears in parentheses. The 3-D ordination had a final stress of 18.7 and final instability of p <0.0004.

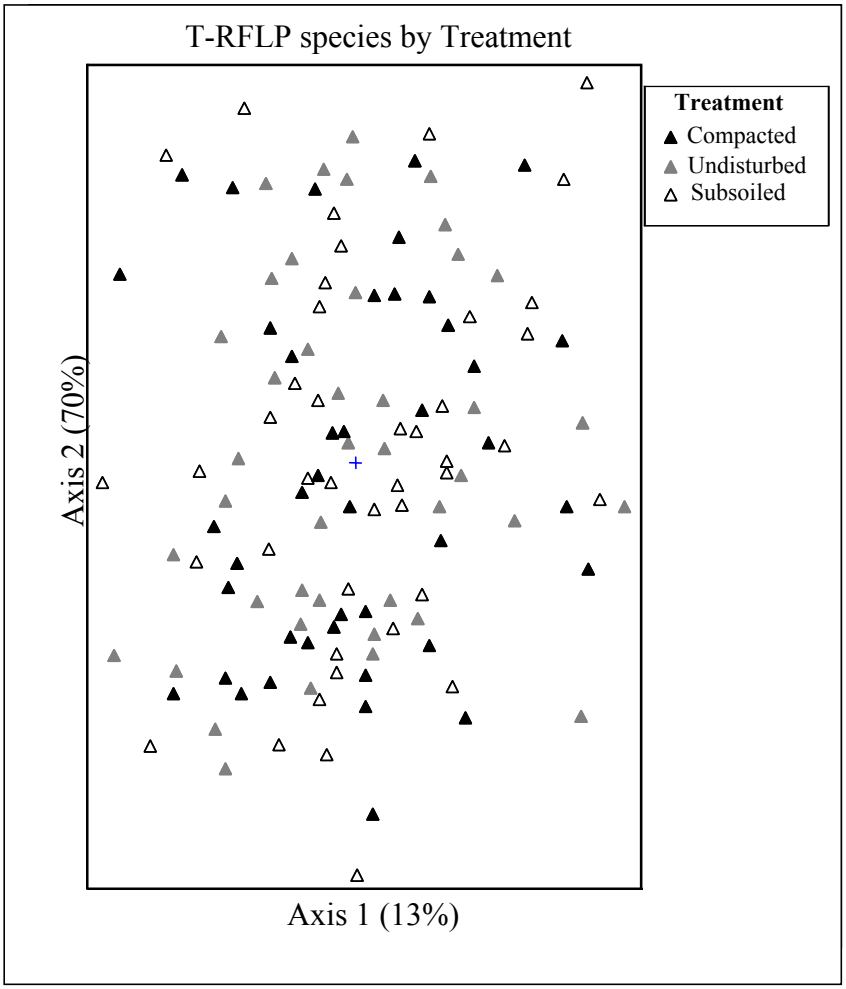

Figure 2.10: Spring 2007 Biolog NMS ordination of samples in carbon substrate space. The amount of variance explained by each axis appears in parentheses. The 3-D ordination had a final stress of 11.6 and final instability of p <0.0004.

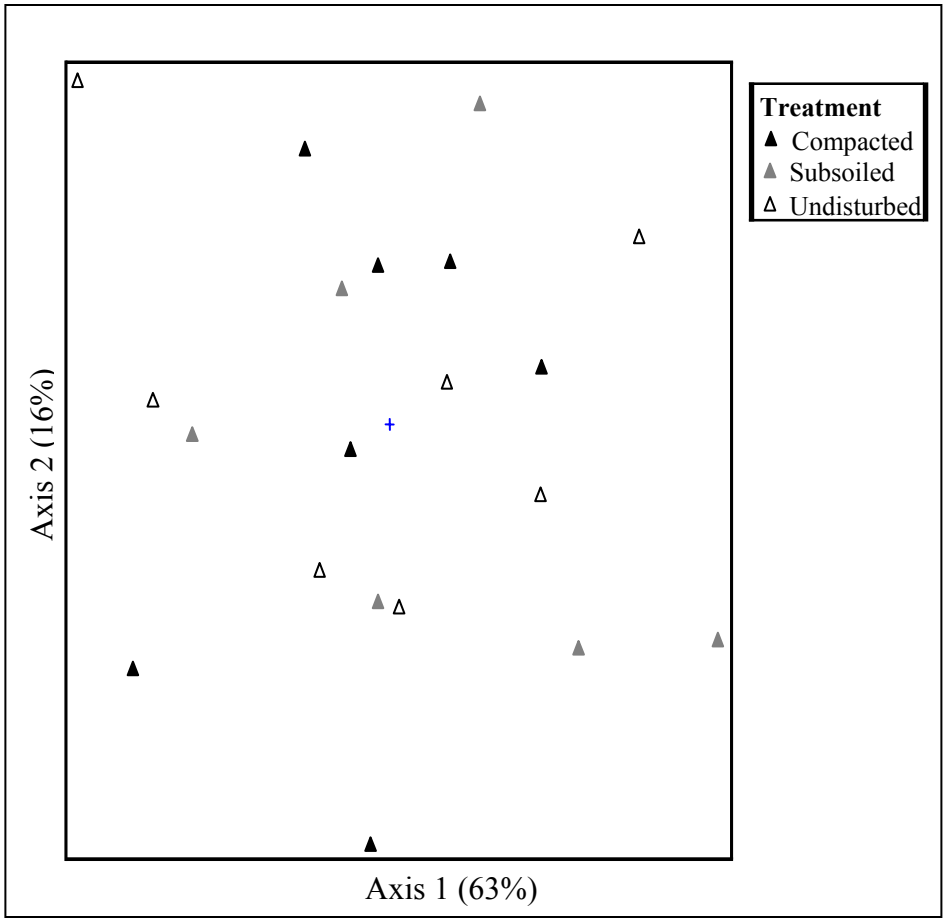

Figure 2.11: NMS ordination of Biolog samples in species space. The amount of variance explained by each axis appears in parentheses. The 3-D ordination had a final stress of 11.6 and final instability of p <0.0004. The vector shows the direction and magnitude of correlation between sample units and amines/amides and amino acids. The numbers appearing after the vector label are the r values for correlation with axis 1 and 3, respectively.