RECREATION IMPACTS ON HIGH ELEVATION SOILS: A COMPARISON OF DISTURBED, UNDISTURBED AND RESTORED SITES

by

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ABSTRACT

Mountainous regions comprise more than 30% of the world's terrestrial biomes and are valued for livestock forage, mineral and timber assets and recreation opportunities. Disturbance has resulted in major ecological changes in high elevation ecosystems, including vegetation loss, soil compaction, and reduced soil organic matter (SOM). Restoring high elevation disturbed sites has proven challenging for many years, possibly because of our limited knowledge of disturbance effects on belowground biota, and the ecosystem functions they facilitate. This research compares soil physiochemical and biological properties on disturbed, undisturbed and restored subalpine soils in two national forests in Montana and Washington. Soil physiochemical properties measured include soil moisture, bulk density, SOM, soil nitrogen (N; both total and plant available), phosphorous (P) and potassium (K). Biological processes measured include mycorrhizal infectivity potential (MIP), decomposition, enzyme activity, substrate induced respiration (SIR) and N mineralization. Soil moisture and SOM were significantly lower, while bulk density was higher, on disturbed sites. Total nitrogen (N) was lower on disturbed sites, while NO_3^- and NH_4^+ differed only between geographic locations. MIP was low overall and did not differ between disturbance. Decomposition rates did not differ between disturbance after 3, 12 or 24 months. Enzyme activity differed with disturbance and location, with significantly lower activity on disturbed sites for 1 substrate, while nearly significant lower activities for 4 out of 8 substrates measured. SIR differed with disturbance and location, with lower responses on disturbed sites for 6 of 26 substrates. Soil physiochemical and biological characteristics are affected by disturbance and location, however results vary between the parameters measured. This suggests ecosystem components, including soil physiochemical and biological properties are decoupled, responding individualistically to disturbance and restoration.

INTRODUCTION

Background

Mountainous regions comprise more than 30% of the world's terrestrial biomes (Prichard et al. 2000), and are highly valued for livestock forage, mineral and timber assets and recreation opportunities (Chambers 1997). Mieczkowski (1995) suggests alpine and subalpine areas constitute the second most important and valuable tourism resource next to coastal systems. These systems serve as vital watersheds, unique plant and animal habitat and may be important for long-term global carbon and nutrient storage (Chambers 1997, Prichard et al. 2000). Mountain regions may also act as indicators for environmental change, however they are some of the most endangered systems in the world (Broll and Keplin 2005). Despite their widespread global distribution, economic, and ecologic importance, high elevation ecosystems remain relatively understudied.

With expanding human populations, high elevation resources are being increasingly exploited. While disturbances are ubiquitous in most ecosystems (Bengston 2002), increased recreation throughout alpine and subalpine regions has led to a large expansion of campsites, roads and trails worldwide. Brown et al. (1978) suggest recreation may be among the fastest growing causes of disturbance to alpine regions. These disturbances represent a broad range of scales and intensities (Chambers 1997), with severity being influenced by soil characteristics and the physical environment (Bradshaw 1997), resulting in slow recovery following disturbance (Allen et al. 1987).

Recreation use results in major ecological changes, including reduced soil organic matter (SOM), vegetation loss and increased soil compaction, leaving soils susceptible to wind and water erosion (Cole 1986, Zabinski and Gannon 1997). Loss of vegetation and decreased SOM affect carbon inputs and soil compaction reduces soil pore space, aggregate stability, soil moisture, infiltration and soil water recharge (Cole 1986, Marion and Cole 1996). Removing vegetation and litter damages the soil surface and can accelerate degradation resulting in continued vegetative loss and decreased resistance to continued use (Cole 1986, Whisenant 1999; Fig. 1.1). At small scales damaged soil surface conditions, often the most obvious impact of recreation, can also affect future plant establishment due to seed desiccation, reduced "safe" sites for seed germination (Cole 1986) and reduced SOM (Zabinski et al. 2000). The apparent physical impacts of recreation can be spatially variable depending on the dominant vegetation types (Cole 1995) and the overall intensity of use.

Disturbance alters the biotic structure of ecosystems, changing the density or biomass of organisms, and the availability and distribution of resources (Walker and Willig 1999). Disturbances that impact soil physical properties can affect soil biota trophic structure and community composition, resulting in changes in soil nutrient dynamics and thereby affecting plant establishment and growth (Setälä et al. 2000). Soil processes, including decomposition and nutrient mineralization, are largely regulated by soil organisms (Tamm 1991) making it essential to understand the factors affecting their activity and survival.

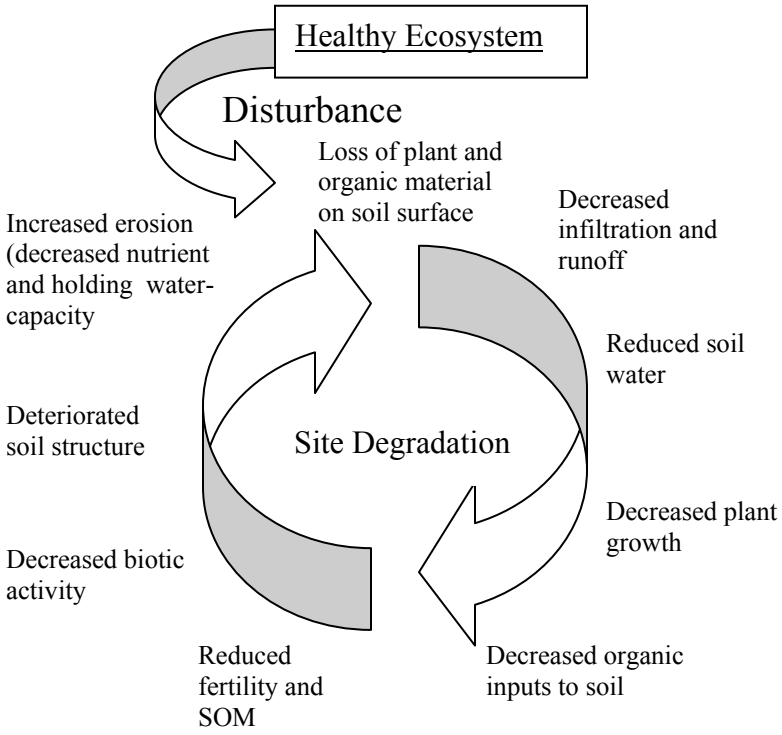


Figure 1.1 A soil degradation cycle adapted from Whisenant (1999) illustrating the importance of soil surface conditions and the pathways possible with from continued disturbance

Recreation sites exhibiting a loss or decrease in organic topsoil often have exposed mineral soil layers at the surface with lower nutrient retention and cycling capacities and more variable plant propagule pools (Chambers 1997), compared to undisturbed sites. In addition to impacts on plant propagules, mycorrhizal fungi have been shown to be sensitive to anthropogenic disturbance (Allen and Friese 1992) and decreased microbial activity has been measured on recreation disturbed sites (Zabinski and Gannon 1997). Soil disturbance and altered vegetation can influence decomposer communities and the trophic structure and composition of soil communities, inducing

changes in soil nutrient dynamics and functional diversity (Setälä et al. 2000). Altered soil communities may have implications on soil resistance to stress and/or continued disturbance (Degens et al. 2000). While some physical impacts of recreation disturbance have been documented (Cole 1986, Marion and Cole 1996) the effects of these impacts on belowground ecosystem function, and nutrient cycling have received relatively little attention and remain poorly understood in high elevation areas, despite their obvious ecological significance (Zabinski and Gannon 1997).

Ecosystems are inherently complex and composed of many interacting biological and physical components. Traditionally ecologists and land managers have focused on vegetation and animal health as indicators of ecosystem integrity, leaving soils often overlooked. Soil is an important resource and an integral component in all living systems. While the majority of terrestrial species reside belowground, we only partially understand their roles in ecosystem structure and function (Wardle 2002), especially in high elevation systems. This lack of understanding of disturbance effects on belowground communities in high elevation systems may be due to the difficulty of measuring soil microbial diversity and function, the heterogeneous nature of soil systems and/or the high diversity of soil biota present in soils. Species diversity among soil microorganisms is greater than any other group of organisms at any terrestrial site with potentially 4000-10,000 eubacterial species in just 1 gram of soil (Allen et al. 2002). Difficulties aside, developing an understanding of disturbance effects on belowground communities is important to effective land management, policy making decisions (Andreasen et al. 2001) and eventual restoration of disturbed sites.

Restoration is widely defined as the return of an ecosystem to its original, or close to original, condition prior to disturbance (Bradshaw 1997, Fig. 1.2), or to that of a nearby reference system (Zedler et al. 2001). Disturbance can impact ecosystem structure and function, each made up of different elements that can be used to define and illustrate the damage a particular system can suffer (Bradshaw 1987) following a disturbance. Structure is the number of species and their relative abundance while function refers to the different processes (i.e., nutrient cycling) in a community (Bradshaw 1987, Moore 2001). Alternatives to restoration include reclamation (Fig. 1.2), or "bringing back to a proper state", not necessarily the original (Bradshaw 1997), or recovery through natural processes, which often requires too much time. The original system is usually high in both structure and function (Fig. 1.2). Disturbance often results in a shift to the lower left corner of the conceptual model, with both structure and function decreasing. Vegetation is almost completely gone on many recreation sites, affecting community structure while also influencing soil properties including SOM inputs and microbial communities, directly affecting ecosystem function. Complete restoration is often not possible due to economic and ecologic constraints. Depending on the severity of the disturbance and the amendments employed it may only be possible to reach certain structural and functional characteristics present prior to disturbance (Fig. 1.2). Knowledge of the populations and community processes within a given ecosystem is essential for its restoration (Chambers 1997). Unique climatic, geologic and edaphic features of subalpine systems, the severity and frequency of the disturbance, and site durability (Cole 1995) all compound the effects of disturbance and increase the difficulty of restoration (Brown and Johnston 1979, Chambers 1997).

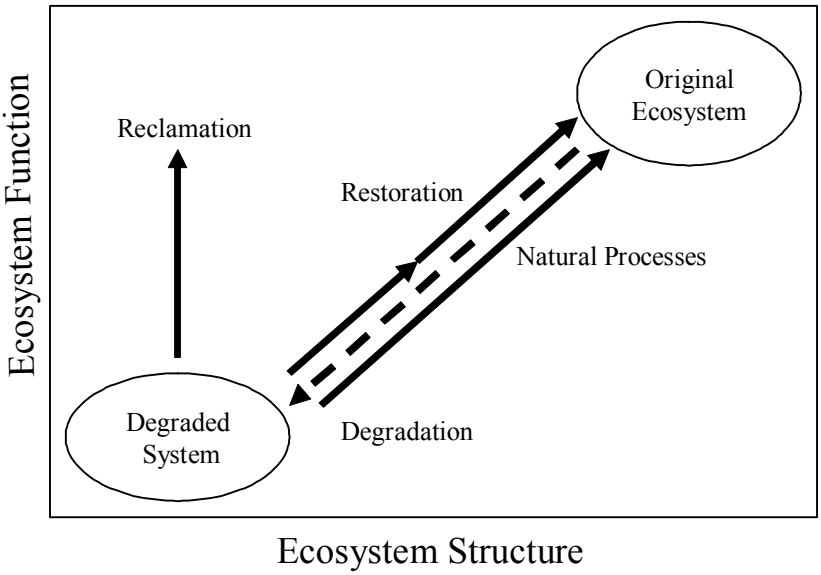


Figure 1.2. Different trajectories a degraded system may take following restoration (modified from Bradshaw 1997). Restoration implies bringing the ecosystem back to its original state in terms of structure and function (Bradshaw 1997), however there are a number of alternatives including reclamation, or the replacement of the original with a different system.

From a restoration perspective it may be more relevant to know which key functional roles have been affected by disturbance, and how to potentially redirect these back toward an undisturbed state (Fig. 1.1), then focusing on restoring individual species composition.

Research Objectives

Due to the complexity and heterogeneity of soil systems, physically, chemically and biologically, as well as the inherent interactions between the three (i.e., compaction and loss of soil pore space negatively affecting soil water and in turn soil microbial

habitat), I measured a number of soil properties to extrapolate disturbance effects on high elevation soils above and belowground. The following properties were assessed on undisturbed, disturbed and restored sites: 1) soil chemical and physical properties including bulk density, nitrogen (N), phosphorus (P), potassium (K) concentrations and soil organic matter (SOM; Chapter 2); 2) mycorrhizal infectivity potential (MIP), a measure of the density of infective arbuscular mycorrhizal fungal propagules in the soil; 3) decomposition rates; 4) soil enzyme activity, effective indicators of the capacity of the microbiota to mineralize carbon and mineral nutrients and thus a measure of the functionality of the soil microbial community (Kourtev et al. 2002); 5) substrate induced respiration (SIR), a physiological method to assess the catabolic diversity of soil microbial communities utilizing respiration responses of soil microbes to a number of simple organic compounds (Degens and Harris 1997); and 6) N mineralization rates (Chapter 3).

This research tests a broad hypothesis that disturbance alters soil physical chemical and biological characteristics, and that restoration moves these characteristics back toward undisturbed conditions (Fig.1.1). The direction of the alteration may vary with the parameter, as disturbed sites may show an increase in soil bulk density and N mineralization, for example, but a decrease in microbial catabolic diversity. By gaining information as to which ecosystem components are affected we can adjust restoration practices to alleviate those most negatively impacted. Because recreation impacts on mountain ecosystems vary geographically (Mieczkowski 1995), this research took place at four locations in the Northern Rocky and the North Cascade Mountains, USA.

Chapter 2 of this thesis addresses disturbance effects on the physical and chemical soil characteristics including bulk density, N, P, K and SOM. Chapter 2 also discusses potential restoration amendments to alleviate the most negatively impacted physical characteristics promoting vegetation establishment. Chapter 3 addresses the effects of disturbance on soil functional components. Specifically, mycorrhizal infectivity potential (MIP), decomposition, soil enzyme activity, substrate induced respiration (SIR) and N mineralization. Enzyme assays, measured by the activity of 8 soil enzymes involved in the cycling of C, N and P and SIR, measured by the respiratory responses of soil microbial communities to 26 simple organic compounds, represent the responses of diverse microbial assemblages to a wide range of substrate types. From an ecosystem perspective these measures provide insight into the effects of recreational disturbance on soil communities and their relationships to general disturbance characteristics (i.e., compaction, loss of vegetation and altered SOM). Chapter 4 discusses the effects of recreation disturbance and restoration on soil physiochemical and biological characteristics and the overall implications for high elevation restoration. I also discuss soils amendments necessary to alleviate the most negatively impacted characteristics, physical chemical and biological, based on my findings.

While soil processes, such as decomposition and nutrient mineralization, are fundamentally important to the functioning of entire ecosystems (Setälä et al. 2000, Tamm 1991), we have only limited knowledge of the response of these processes to disturbance. Anthropogenic disturbances often occur as press disturbances, which are chronic stress agents, as opposed to pulse disturbances, which occur as discrete events, followed by a re-organization phase (Bengtsson 2002). Recreation impacts occur as

spatially discrete press disturbances. Recreation impacts, including campsites and social trails and areas, occur on the scale of meters to ten's of meters, within a larger context of relatively undisturbed landscape providing an opportunity to look at the spatial dynamics of soil system response and recovery from disturbance on a feasible scale.

Due to the inaccessibility and relatively harsh climatic conditions characterizing high alpine sites, restoration is often difficult and only sometimes successful. Also, the intensity and severity of the disturbance will have variable effects on soil components and systems recovery. By examining a gradient of disturbance including disturbed, undisturbed and restored sites, over a wide geographic area, I can provide insight into a central question encountered by land managers when restoring degraded lands of how to assess the severity of the impact of disturbance to guide restoration and how to measure success or failure on a particular site in a particular location (Harris 2003).

HIGH ELEVATION DISTURBANCE EFFECTS ON PHYSICAL AND CHEMICAL SOIL CHARACTERISTICS

Introduction

All environments are affected by anthropogenic disturbance, but few are as delicate as high elevation ecosystems (Bell and Bliss 1973). A number of physiochemical characteristics of alpine and subalpine systems compound disturbance effects, making restoration difficult. In addition to severe environments and short growing seasons, soils are often poorly developed and depths to fractured rock or bedrock are small. Soil course fragment content is variable and fine textured soils dominate (Mayck 2000). What mineral soil may be present in these systems is highly sensitive to both trampling (Cole and Fitchler 1983, Cole 1987) and erosion. Following removal of vegetation, soil characteristics are among the most important indicators of recovery potential (Chamber 1997), are the slowest to recover, and most difficult to restore.

Recreation impacts are both spatially and temporally variable, depending on vegetative communities, environmental factors and amount and duration of use. Impacts are often severe, and while small in scale (meters), can compromise the integrity of natural ecosystems (Marion and Cole 1996). The factors that limit successful restoration of high elevation sites (Zabinski and Cole 2000, Zabinski et al. 2002) include low-productivity, poorly developed soils, extreme climates and a limited understanding of suitable growing conditions on high elevation disturbed soils. While vegetation responses to recreation impacts have been well documented (Cole and Fichtler 1983,

Marion and Cole 1996), the effects on soil physical and chemical characteristics are less understood.

Studies of soils in alpine and subalpine areas are relatively rare (Holtmeier 2003). Alpine soils are typically young, heterogeneous and poorly developed (Korner 2003). Over short distances a variety of soil types, nutritional contrasts and vegetative mosaics may occur. Soil profiles on steep slopes are often shallow and occur with thin till and colluvial veneers overlying bedrock (Macyk 2000). Cold temperatures limit the chemical and biological processes of soil genesis in alpine and subalpine systems. Alpine and subalpine soils are formed primarily by on-site erosion of parent rock, gravity, sedimentation (Korner 2003), climate, biological activity and vegetation.

Soil organic matter (SOM) is widely recognized as a critical component of soil quality and productivity (Arshad and Coen 1992) because of its influence on nutrient cycling, soil structure, water availability, and other important chemical, physical and biological properties (Yakovchenko et al. 1998). SOM increases with altitude, commonly reaching a peak in montane forests and lower alpine zones due, in part, to reduced microbial activity (Korner 2003) and lower decomposition rates. Cold, acid, arid, and sandy soils contain higher proportions of organic matter as plant debris than as humus because of low temperature, pH, and/or lack of water limit comminution of litter by fauna (Oades 1988). Plant roots are often concentrated in the upper 25 cm of the soil profile (Chambers 1997). Soil aggregation and stability are directly related to SOM. As roots, hyphae and organic matter are reduced in soils, so is aggregation (Oades 1988) and soil stability. This becomes increasingly important in high elevation disturbed areas

where vegetation is no longer present and soil stabilization and sedimentation are a concern.

There are three main objectives to this chapter: first, to describe and compare undisturbed soil physical and chemical properties at four high elevation sites in Montana and Washington. Site differences include climate, topography and geology, all of which can determine soil physicochemical characteristics. By evaluating undisturbed soil characteristics I can determine whether soils are similar enough to make comparisons of disturbance and restoration effects across a wide geographic range. Soil properties I compare include texture, bulk density, pH, moisture, OM and nutrients. Soil nutrients include soil nitrogen (N), both total and plant available (NO_3^-, NH_4^+) N, phosphorous (P), and potassium (K), all macronutrients (Gurevitch et al. 2002) essential in functioning of vegetative communities, but often limited in high elevation systems (Urbanska and Chambers 2000). The second objective is to measure disturbance effects on soil physical and chemical characteristics. The last objective is to identify the effects of restoration amendments, including scarification and compost addition, on soil physical and chemical characteristics.

Disturbed soil characteristics are compared to adjacent, undisturbed and restored (when applicable) soils at each geographic location and between all locations. I hypothesize that disturbed soils will have greater bulk density, and lower soil moisture and SOM compared to soils on undisturbed and restored sites. I also hypothesize that soil chemical properties will differ on undisturbed, disturbed and restored sites, however the direction of the change is not always clear, i.e., disturbed sites could have higher nutrient levels because of lower rates of immobilization or lower nutrient levels because of

impaired nutrient cycling processes. Restored soil properties should be intermediate or similar to those of undisturbed soils.

Methods

To address the objectives of this research, I chose sites in four locations in the northwestern USA. There were two locations in Montana, which include three sites at Emerald Lake (EL) in the northern Gallatin Mountains in southwestern MT and 2 sites at Heart Lake (HL) in the northern Bitterroot Mountains in western MT. The two other locations are in Washington and include three sites at Cascade Pass in Northern Cascades National Park (NOCA) and five sites in Mount Rainier National Park (MORA; Figure 2.1). At all sites, disturbed and restored (when available), were paired with adjacent undisturbed sites.

Soil Analysis

Soil samples were collected using a 5.6 cm diameter soil corer. Cores were taken to a 5 cm depth at 10 randomly chosen points on each site. Samples were composited in the field, sealed in 2 gal Zip Loc® bags, kept cool and transferred back to the lab. Once in the lab soils were homogenized and sieved through a 2mm sieve to remove coarse fragments.

Soil texture was determined using particle separation analysis, detailed in Gee and Bauder (1986), using sand, silt and clay fractions to differentiate textural classifications. Soil moisture was measured gravimetrically (Gardner 1986).

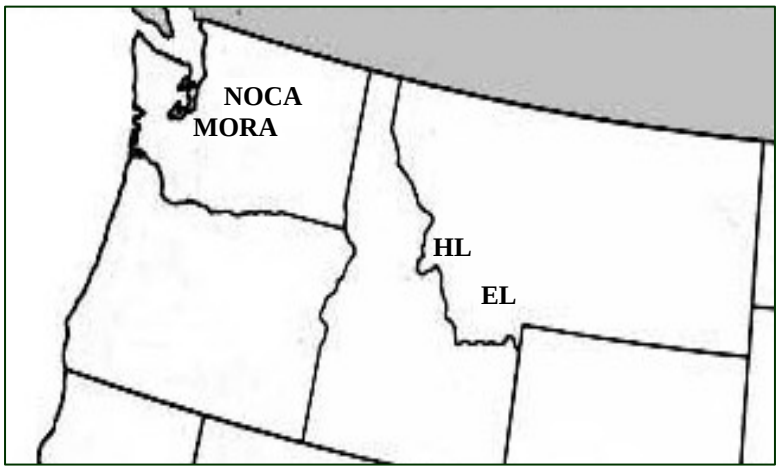


Figure 2.1. Locations of 4 study sites, Emerald Lake (EL) and Heart Lake (HL), MT and Northern Cascades National Park (NOCA) and Mount Rainier National Park (MORA).

Table 2.1. Study site characteristics at each location.

Location	Number of Sites				Elevation (meters)	Soils
	Disturbed	Undisturbed	Restored	Type of Disturbance		
Emerald Lake	3	3	0	campsite	2714	silt loam
Heart Lake	2	2	1	campsite	1770	silt loam
NOCA	1	3	2	campsite	1450-1650	sandy loam
MORA Paradise Sunrise Crystal Lake	 2 0 1	 2 2 1	 0 2 0	 social trail restored road campsite	 1931 1950 1775	 loamy sand loamy sand loamy sand

A 50 g wet sample was weighed, placed in an open aluminum container and dried at a constant 60 ºC for 48 h and reweighed.

Gravimetric water content was calculated as follows:

$\theta g = [(g \text{ moist soil}) - (g \text{ dry soil})]/(g \text{ dry soil})$ Eq. 2.1.

Bulk density was measured using both a known volume coring tool and the irregular hole method, adopted from Howard and Singer (1981). Bulk density can be a measure of soil compaction, when soil textures are similar, as in adjacent disturbed and undisturbed sites. Three randomly located cores were hand excavated from each site using a soil corer (5.6 cm diameter) and the volume of the remaining hole was determined by lining the hole with plastic wrap and filling it with a known measure of sand. At all but one location, HL, where only the irregular hole method was used, bulk density measures were also taken with a known volume soil corer (AMS, American Falls, ID). Any surface organic matter was removed prior to sampling. With both methods, excavated soil was transported in individual soil sampling bags, kept cool, and brought back to the lab where they were weighed wet, dried at 60 °C for 48 hr, and reweighed.

For nutrients analysis approximately 200 g of soil was taken from the homogenized soil samples. Samples were sent, in soil sample bags, within 5 d of field extraction to MDS Harris Services (Lincoln, NE). Potassium was measured using ammonium extraction, soil P content was measured using the Olsen P method, NO_3^- was analyzed using cadmium reduction and HCl extraction, total nitrogen using Kjeldahl digestion and pH using 1:1 soil/water slurry. Organic matter was determined by mass loss on ignition

Data Analysis

Differences between undisturbed soils were tested between locations using ANOVA (Table 2.2). To test for differences and restoration effects, overall patterns in soil organic matter (SOM) and nutrients in relation to location and disturbance were analyzed using 2-

way ANOVA (SPSS General Linear Model Univariate ANOVA, SPSS, Inc., Chicago, IL. Version 13.0). The model included 2-way interactions of disturbance and location, with disturbance as a fixed effect and location a random effect. Post hoc comparisons were not performed for differences between location, since location was a random effect variable in the ANOVA. Least square difference post hoc tests were used to determine which variables differed significantly with disturbance ($p < 0.05$). Differences in soil parameters between disturbed and undisturbed sites were analyzed at each location using paired t-tests, which compare the mean of sample differences between pairs of data to the hypothetical mean (Sokal and Rohlf 1995). The 2-way ANOVA's with location random allow conclusions regarding general patterns between disturbance types over a geographical range, while the paired t-tests allow comparisons between disturbance effects considering differences within each location. Variables were transformed as necessary to pass the assumptions of ANOVA, most notably Levene's test of equality of error variances. Organic matter was cube root transformed and total N fourth root transformed. The Kruskal-Wallis nonparametric test was used to compare NH_4^+, NO_3^-, P and K because these variables could not be transformed to pass the equality of variance assumption of ANOVA. Nonparametric tests were used to examine both location and disturbance differences at a significance of 0.05.

To examine soil parameters between disturbed and undisturbed sites, I used a paired t-test. When including restored sites I used a 2-way ANOVA since these sites were not available at all locations. While ANOVA is a useful tool when making statements regarding disturbance effects over a large geographic scale, I also wanted to examine differences masked in the ANOVA by soil differences (other than texture and

pH) between sites. Paired t-tests allow the removal of soil differences as a factor and are a more powerful statistical test comparing pairs (disturbed vs. undisturbed) at each individual location (e.g., EL campsite 1 and adjacent undisturbed site). When hypotheses were directional, i.e., SOM will be lower in disturbed versus undisturbed soil, a 1-tailed t-test was used. A 2-tailed t-test was used when the hypothesis was non directional, i.e., NH_4^+, NO_3^-, will differ however, whether higher or lower on disturbed versus undisturbed sites is questionable. In some instances differences were not significant with the ANOVA but were with the paired t-test. There were no significant interaction terms with any of the ANOVA's therefore they will not be discussed.

Study Sites

The Emerald Lake Basin is a subalpine system (2,714 m elevation) in the northern Gallatin Mountains in southwestern Montana (45°24'N, 111°32"W.). Mean annual precipitation at Shower Falls, Montana SNOTEL (2469 m elevation, 45°40'N, 110°95"W) is 127.76 cm (40 yr mean), mean annual temperature is 1.3 °C (6 yr mean), and the area is snow free between July and October. The soils are moderately fine Argic Cryoborolls. Tree species include *Abies lasiocarpa*, *Pinus albicaulis*, and *Picea englmannii*. Understory vegetation consists of *Festuca idahoensis*, *Deschampsia caespitosa*, and *Vaccinium scoparium*.

In the summer of 2003 I began a study of 3 campsites on the northeastern side of the lake. The first, located in a subalpine meadow, is 11.5 m wide and 13 m long. The other two sites are predominantly forest, the first is 4 m long and 10.5 m wide and the

second is 8 m wide and 9 m long. All sites are almost completely devoid of vegetation and were used as campsites throughout the study.

The Heart Lake Basin is a subalpine system (1,770 m elevation) in the northern Bitterroot Mountains in western Montana (46°57'N, 114°58"W). Mean annual precipitation is 174.50 cm (25 yr mean, Hoodo Pass, Montana SNOTEL, 1844 m elevation, 46°59'N, 115°02"W), mean annual temperature is 3.75 °C (6 yr mean, Hoodoo Pass, Montana SNOTEL), and the area is snow free between July and October. The soils are fine-grained Andic Cryocrepts. Tree species include *Abies lasiocarpa*, *Pinus contorta*, *P. albicaulis*, *P. monticola*, *Picea engelmannii* and *Tsuga mertensiana*. Understory vegetation includes *Xerophyllum tenax*, *Vaccinium globulare* and *Menziesia ferruginea*.

In the summer of 2003 I began a study at 2 sites, one of which was closed for use in 1995 and used for a study of restoration treatments (Zabinski and Cole 2000). The largest campsite is 6 m wide and 11 m long, the smaller campsite, located directly north, is 7.5 m wide and 9 m long. The largest campsite was divided into 25 1 m^2 plots in which restoration treatment were applied (Zabinski and Cole 2000). Treatments included control plots with no amendments, plots with scarification of soil to 15 cm, scarification plus compost amendment (Ekocompost®), scarification plus soil inoculum, in the form undisturbed soil slurry mixed with stream water and incorporated to 15 cm, and scarify plus compost and soil inoculum. Revegetation on half the amended sites was by broadcast seeding and seedling transplant (Zabinski and Cole 2000). Disturbed samples were taken from control plots and restored samples were taken from scarified plots with

compost and inoculum addition. Both disturbed and restored sites are nearly devoid of vegetation.

Cascade Pass is a subalpine zone (1450-1650 m elevation) in the Northern Cascade Mountains and is located in Northern Cascades National Park Washington (48°27'N, 121°08"W). Mean annual precipitation is 177.85 cm (29 yr mean, Park Creek Ridge, Washington SNOTEL, 1402 m elevation, 48°27'N, 120°55"W) mean annual temperature is 4.04 °C (6 yr mean. Park Creek Ridge, Washington SNOTEL). The soils are volcanic and range from hydric, silty sand loams, to fine, mixed, granitic (greus) sandy loams. Tree species include *Abies amabilis*, *Tsuga mertensiana*, *Pseudotsuga menziesii* and *Thuja plicata*. Understory vegetation includes *Sorbus americana*, *Polygonum bistorta, Polemonium spp., Castilleja spp*., and *Vaccinium scoparium*, which was the dominant species.

In the summer of 2003 I began a study at 2 sites on Cascade Pass, the upper most site is 9 m wide and 10 m long and the lower site is 4m wide by 8 m long. Both sites were restored in the early 1970's. Soil amendments included peat moss and bark chip incorporation and sites were planted with *Lupinus spp*., *Phleum spp*. and *Ericaceous spp*. Vegetation on restored campsites is sparse but present. In the summer of 2004 I began study at a third site in Pelton Basin (1445 m elevation) below the two upper sites. The Pelton Basin site is 15m wide by 30 m long. This site is almost completely devoid of vegetation. The Pelton Basin site was camped on throughout the study.

Mount Rainier (4,392 m elevation) lies west of the Cascade Mountains, 100 miles east of the Pacific Ocean. Mean annual precipitation is 299.24 cm (Paradise, Washington SNOTEL, 1561 m elevation, 46°47'N, 121°45"W) and mean annual temperature is 4.46

°C (6 yr mean, Paradise, Washington SNOTEL). Subalpine vegetation at Mount Rainier consists of *Chamaecyparis nootkaensis*, *Tsuga mertensiana, Abies lasiocarpa, Vaccinium parvifolium, Erythronium montanum, Caltha leptosepala, Lupinus perennis, Castilleja parviflora, Xerophyllum tenax, Erythronium grandiflorum*, and *Ranunculus eschscholtzii*.

In the summer of 2004 I began a study at 5 sites in 3 different locations in Mount Rainier National Park in WA. The first two disturbed sites are on Mount Rainier's south slope near the Paradise Inn (46° 47'N, 121°44"W). The upper most site (30 m wide x 50 m long), is at Glacier Vista (1,931 m elevation) and the second site (8 m wide x 20 m long) is just below, at approximately the same elevation, on the Deadhorse Creek Trail. Both are large social areas in subalpine meadows, disturbed by increased visitor concentrations and off trail travel. While restoration efforts have been made in areas near our sites, neither has been actively restored and both are devoid of vegetation.

Two restored sites are near the Sunrise Visitor Center (1,950 m elevation) in the northeast section (46°54'N, 121°38W) of the park. The first site is 20 m wide x 20 m long and the second site is 15m wide x 30 m long and both are sections of a restored road en route to the main Sunrise Camp area. Restoration work was done in 1995, and included scarification, seedlings, and application of erosion fabric with no chemical soil amendments (i.e. fertilizer or compost) applied.

The fifth site in Mt. Rainier National Park is an active campsite near Crystal Lake (1775 m elevation), also on the northeast side of the park (46°54'N, 121°30'W). The site is 7 m wide by 10 m long and is devoid of any vegetation.

RESULTS

Comparison of Undisturbed Soils Across Location

Soils differ depending on parent material, topographic relief, climate, soil organisms and time (Buscot 2005). All soils had low clay content, textures ranged from silt loam to loamy sand and were slightly acidic, with pH ranging from 4.47 at NOCA to 5.50 at MORA (Table 2.2). The pH of soils from EL and HL were intermediate.

Table 2.2. Undisturbed soil characteristics for all locations. Letters indicate significant differences between values in a column.

Location	Site	pH	Soil Texture	OM %	Total N %	NH_4^+ ppm	NO_3^- ppm	Bray P ppm	K ppm
MT	EL	4.97ab	silt loam	13.63b	0.54b	5.06a	2.67a	17.67a	95.67a
	HL	5.3ab	silt loam	16.65ab	0.38b	12.69a	1.50a	6.50b	73.00ab
WA	NOCA	4.47a	sandy loam	39.07a	1.56a	7.01a	8.33a	10.33ab	69.33ab
	MORA	5.5b	loamy sand	5.60b	0.24b	3.08b	2.40a	6.80b	30.60b

All sites had relatively high SOM, ranging from 5.60 to 39.07%. Soils from NOCA had significantly higher levels of SOM than soils from EL and MORA. Both acidic pH and high OM levels are characteristic of alpine soils (Nimlos and McConnel 1965).

Total N is significantly higher at NOCA (1.56%) compared to all other sites, with no difference between EL (0.54%), HL (0.38%) or MORA (0.24%). Available N in the form of NH_4^+ ranged from 3.08 to 12.69 ppm and was significantly lower at MORA than

all other sites. Soils did not differ significantly in NO_3^-, which ranged from 1.50 to 8.33 ppm. Soil P concentrations ranged from 6.50 to 17.67 ppm, with soils from EL having significantly higher concentrations than soils from HL and MORA. Soil K concentrations ranged from 30.60 to 95.67 ppm, and soils from MORA had significantly lower K than soils from EL.

Table 2.3. Analysis of variance of %OM, total N, NH_4^+,NO_3^-, P and K for all undisturbed soils.

	%OM				Total N			
	d.f.	MS	F	P	d.f.	MS	F	P
Location	3	714.89	7.83	0.01	3	1.17	25.22	0.00
Error	9	91.31			9	0.05		

	NO_3^- (ppm)				NH_4^+ (ppm)			
	d.f.	MS	F	P	d.f.	MS	F	P
Location	3	45.96	4.20	0.04	3	28.58	0.854	0.50
Error	9	10.94			9	33.45		

	Bray P (ppm)				K (ppm)			
	d.f.	MS	F	P	d.f.	MS	F	P
Location	3	84.10	7.83	0.01	3	2908	6.53	0.01
Error	9	10.74			9	445.0		

Disturbance and restoration effects on soil parameters

Table 2.4. Mean bulk density ± 1 S.E. of the mean (g/cm^3) values measured using the irregular hole and core method for disturbed, undisturbed and restored sites.

Location	n	Bulk Density (g/cm^3)	
		Irregular hole	Core
Emerald Lake, MT			
Disturbed	3	0.78 ± 0.05	1.94 ± 0.16
Undisturbed	3	0.68 ± 0.18	0.98 ± 0.08
Heart Lake, MT			
Disturbed	2	0.70 ± 0.07	----------
Undisturbed	2	0.40 ± 0.04	----------
Restored	1	0.50	----------
NOCA, WA			
Disturbed	1	1.08	0.79
Undisturbed	3	0.43 ± 0.07	0.69 ± 0.15
Restored	2	0.59 ± 0.18	1.08 ± 0.04
MORA, WA			
Disturbed	3	0.93 ± 0.02	1.38 ± 0.08
Undisturbed	5	0.83 ± 0.08	1.27 ± 0.21
Restored	2	1.08 ± 0.19	1.52 ± 0.15

Soil moisture ranged from 72.70% (NOCA) to 6.80% (MORA) for undisturbed sites, and 69.30% (NOCA) to 11.00% (HL) for disturbed sites. Soil moisture was significantly higher overall on undisturbed (35.44%) versus disturbed (26.01%; t_8=-2.30, p=0.03) and in undisturbed vs. restored sites (19.90%; t_2=3.79, p=0.03). There was no significant difference between disturbed and restored (t_2=-0.31, p=0.40).

Bulk density (dry), measured with the soil corer, differed significantly between locations and disturbance types (Table 2.4). Differences were nearly significant between location and disturbance types with the irregular hole method (Table 2.4). Bulk density was significantly higher on disturbed versus undisturbed sites using both the soil corer (t_6=5.65, p=0.001) and the irregular hole method (t_9=3.01, p=0.01). Higher bulk density was nearly significant on restored versus undisturbed sites using both the soil corer (t_4= -1.74, p=0.08) and the irregular hole method (t_4=-1.96, p=0.06). Using the irregular hole method, mean bulk densities were 0.85 and 0 .62 g/cm^3 respectively. The corer yielded

higher bulk density measures (t_{21}=-7.80, p<0.001) compared to those measured with the irregular hole method (Table 2.3). Bulk density was nearly twice as high on undisturbed and restored soils at MORA compared to soils at NOCA and HL (Table 2.3).

Table 2.5. Analysis of variance of bulk density for both the soil coring and the irregular hole method.

Bulk Density	Soil Corer				Irregular Hole			
	d.f.	MS	F	P	d.f.	MS	F	P
Location (L)	2	0.47	101.70	0.00	3	0.18	3.74	0.09
Disturbance (D)	2	0.14	24.01	0.00	2	0.19	4.37	0.08
D x L	3	0.01	0.20	0.89	5	0.05	4.40	0.01
Error	14	0.23			16	0.01		

Soil organic matter differed significantly between both disturbance type and location (Table 2.6). Undisturbed soils had significantly higher levels of SOM (16.89%) compared to disturbed soils (10.73%,). Restored soils (13.54%) did not differ from undisturbed soils. At EL differences were least pronounced between disturbance, while NOCA had nearly two times greater SOM levels on undisturbed versus disturbed sites (39.07 vs. 20.80%). NOCA had considerably greater SOM levels then other locations (Table 2.6). With the paired t-test, SOM also differed significantly between disturbed and undisturbed sites (t_8=-2.24, p=0.03, 10.7 and 13.8%, respectively) and nearly differed between undisturbed and restored (t_4=-1.79, p=0.13, 22.8 and 13.5%, respectively; (Table 2.

Table 2.6. Mean ± 1 S.E. of the mean soil physical and chemical characteristics for all locations and disturbances types

Location	n	Soil Texture	OM %	Total N %	NH_4^+ ppm	NO_3^- ppm	Bray P ppm	K ppm
Emerald Lake, MT								
Disturbed	3	silt loam	13.07 ±1.97	0.52 ± 0.09	5.52 ± 1.25	2.33 ± 1.53	25.33 ±	135.33 ± 83.17
Undisturbed	3	silt loam	13.63 ± 2.15	0.54 ± 0.10	5.06 ± 0.36	2.67 ± 2.87	25.74	95.67 ± 24.79
							17.67 ± 4.16	
Heart Lake, MT								
Disturbed	2	silt loam	13.20 ± 4.81	0.34 ± 0.09	4.87 ± 1.50	3.5 ± 2.12	10.00 ± 8.49	112.50 ± 44.55
Undisturbed	2	silt loam	16.65 ± 2.76	0.38 ± 0.07	12.69 ±	1.50 ± 0.71	6.50 ± 2.12	73.00 ± 16.97
Restored	1	silt loam	13.50	0.47	8.85	2.00	17.00	71.00
					5.29			
NOCA, WA								
Disturbed	1	silt loam	20.80	1.26	7.63	13.00	21.00	56.00
Undisturbed	3	sandy loam	39.07 ±19.67	1.56 ± 0.42	7.01 ± 3.08	8.33 ± 11.85	10.33 ± 4.93	69.33 ± 34.02
Restored	2	sandy loam	23.35 ± 1.77	1.24 ± 0.77	7.50 ± 0.75	2.00 ± 1.41	12.00 ± 8.49	59.50 ± 3.54
MORA, WA								
Disturbed	3	loamy sand	3.4 ± 0.26	0.09 ± 0.02	2.55 ± 0.59	2.33 ± 0.58	3.33 ± 3.21	14.67 ± 3.06
Undisturbed	5	loamy sand	5.60 ± 2.80	0.24 ± 0.10	3.08 ± 0.48	2.40 ± 0.89	6.80 ± 1.48	30.60 ± 6.58
Restored	2	loamy sand	3.75 ± 1.06	0.13 ± 0.04	2.87 ± 0.07	2.50 ± 2.12	8.50 ± 2.12	18.00 ± 4.24

Table 2.4. Analysis of variance of %OM (3^{rd} root transformed), total N (4^{th} root transformed), NH_4^+,NO_3^-, P and K (All analyzed non-parametrically (NP) using the Kruskal-Wallis test) for all undisturbed soils

	%OM				Total N %				NH_4^+ (ppm) (NP)			NO_3^- (ppm) (NP)		
	d.f.	MS	F	P	d.f.	MS	F	P	d.f.	Chi-Sq	Asymp. Sig.	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	2.10	55.85	0.00	3	0.23	43.46	0.00	3	19.66	0.00	3	0.76	0.86
Disturbance (D)	2	0.19	0.19	0.05	2	0.01	1.53	0.29	2	0.15	0.93	2	1.35	0.51
D x L	5	0.04	0.56	0.73	5	0.01	1.15	0.38						
Error	16	0.06			16	0.01								

	Bray P (ppm) (NP)			K (ppm) (NP)		
	d.f.	Chi-Sq	Asymp. Sig.	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	10.73	0.01	3	20.82	0.00
Disturbance (D)	2	0.28	0.87	2	0.88	0.64
D x L						
Error						

Total N was significantly lower on disturbed vs. undisturbed site with a paired t-test (t8=-1.92, p=0.05, 0.50 and 0.42 %, respectively). Total N differed significantly only between location (Table 2.6) with total N nearly twice as high at NOCA than at other locations, similar to SOM. Plant available N in the form of $N0_3^-$ did not differ significantly between location or disturbance (Table 2.6), and ranged from 1. 5 to 8.33 ppm. NH_4^+ and P were not significantly different between disturbance or location with the non-parametric or a paired t-test, however K, differed between undisturbed and restored sites with the paired t-test (t_2=5.71, p=0.02, 49.0 and 35.7 ppm, respectively).

DISCUSSION

My first objective was to compare undisturbed soils at the 4 locations used in this study. Undisturbed soils sites were similar across locations with respect to soil texture, pH and vegetation (see site descriptions). The biggest difference between undisturbed soils was at NOCA with higher SOM and total N. SOM is a critical component of soil fertility and productivity. SOM directly effects the physical structure of soil by providing spaces for water and root penetration, and is directly related to soil microbial activity (Zabinski et al. 2002; Chapter 3). The higher total N at NOCA is likely related to increased SOM compared to other locations.

My second objective was to measure disturbance effects on soil physical and chemical characteristics. Following removal of vegetation, soil characteristics are among the most important indicators of recovery potential at a site (Chambers 1997). Recreation impacts on soils are often localized and relatively small in scale, however they tend to be

severe (Cole and Marion 1996). Bulk density is often higher on disturbed versus undisturbed soils (Monti and Mackintosh 1979, Marion and Cole 1996). Compaction leaves soils susceptible to erosion. Compaction can also inhibit vegetation establishment (Zabinski and Cole 2000) and lead to decreased seedling growth (Jordan et al. 2003) and microbial activity (Zabinski et al. 2002). Bulk density was higher in soils from disturbed sites compared to undisturbed, and while statistical analysis wasn't performed on disturbed vs. restored sites (due to lack of replication of locations with both disturbed and restored sites), data suggests restored sites, with the exception of MORA, had intermediate levels of compaction. Restored sites at MORA were former roads having higher bulk density as a result of gravel used during road construction still present in restored soils.

Soil moisture (% H_20/g soil) and SOM were significantly lower in soils from disturbed versus undisturbed sites. Soil moisture is directly related to SOM and soils with high percentages of organics have higher water holding capacities. Decreases in mineral topsoil and SOM limits water infiltration and reduces soil moisture.

Vegetation and SOM reduce surface runoff and erosion, increase infiltration and improve soil structure (Whisenant 1999). Prolonged loss of vegetative cover and SOM may initiate a positive feedback system that can accelerate site degradation (Monti and Mackintosh 1979), leading to reduced soil water, site fertility, drier surface soils with increased surface temperatures (Kevan et al. 1995, Chambers 1997), and a deterioration of soil structure (Whisenant 1999) over time (Fig 1.1).

Total N was lower on disturbed sites, which I expected given SOM patterns, as SOM and total N and are often highly correlated. These results are consistent with Zabinski et al. (2002), who found lower total N and C on recreation sites in Oregon, and Dick et al. (1988) who also found total N to be up to 37% lower on soils in Oregon disturbed by mechanized logging. Most N in soil is in organic form, which is mineralized and nitrified to form plant available N serving as a reservoir of N slowly supplying the more dynamic and much smaller inorganic (plant available) N pools (Myrold 2004). Soil N is affected by moisture, temperature and microbial activity.

Zabinski and Cole (2000) found higher plant available N, both NH_4^+ and NO_3^-, on disturbed vs. undisturbed recreation sites. Similarly, in the Beartooth Plateau disturbed borrow area soils had levels of available N that were significantly higher compared to adjacent undisturbed areas (Chambers 1997). Plant available N has many fates in the environment; it is mobile and can be leached (Myrold 2004) from a system. This suggests time of sample collection may also affect measured N concentrations.

Restoration treatments at my sites included plots with soil scarification, scarification plus compost amendment (Ekocompost ®), scarification plus soil inoculum, in the form undisturbed soil slurry mixed with stream water, and scarify plus compost and soil inoculum (HL). Other amendments included peat moss and bark chip incorporation with scarification (NOCA) and application of erosion fabric with no chemical soil amendments (i.e. fertilizer or compost) applied (MORA). Restoration at NOCA took place in the early 1970's while amendments at HL and MORA occurred in 1995. The soil treatments at HL were designed to affect the physical and chemical properties. Scarification loosens compacted soil, at least temporarily. Compost addition

adds OM and contributes to soil structure and increases nutrient availability (Zabinski and Cole 2000) and inoculum addition may increase microbial community functional diversity (Zabinski and Cole 2000), however that is not addressed in this chapter.

One of the most important aspects of a disturbance, especially in high elevation systems, is the severity of the disturbance in relationship to the soil environment (Bradshaw 1997). Alpine and subalpine ecosystems are some of the most difficult to restore following disturbance due to severe climates and limited soil resources (Macyk 2000). While climate may be the most important factor limiting restoration success in alpine and subalpine regions (Macyk 2000), other factors including soil physical and chemical characteristics, are becoming increasingly important (Marion and Cole 1996, Zabinski et al. 2002) in restoration. With this in mind, my third objective was to identify what effects restoration amendments had on soil physical and chemical characteristics in high elevation disturbed areas.

Physical and chemical soil differences are more pronounced between disturbed and undisturbed than between undisturbed and restored. I expected this due to the goal of restoration in returning disturbed systems back to pre-disturbed conditions. Bulk density on restored sites was significantly less than that of disturbed but no different than undisturbed. Soil moisture, SOM and total N were not significantly different between disturbed and restored sites. The only significant difference chemically on restored soils was soil K, which was lower on restored soil vs. undisturbed. From a restoration perspective these results are promising, scarification, originally thought to be a short term solution, may have been effective at loosening soil compaction even after a number of years. However it is likely that the integration of amendments, i.e., scarification and

compost addition, that had the most pronounced effects on soil physical and chemical parameters.

The major impacts of recreation disturbance on my sites are increased soil compaction and decreased SOM and total N. To address compaction, limited to the soil surface, scarification may be adequate. Compacted surface soils, when adequately mixed with subsurface soils, will provide better plant growth medium then subsurface soil alone (Urbanska and Chambers 2002). However the beneficial effects of soil scarification in high elevation systems may only be temporary due to heavy snow accumulation. Scarification has been a helpful in establishing vegetation initially the past (Zabinski and Cole 2000, Cole and Spilbie 2000, Urbanska and Chambers 2002) and can be a useful technique in restoration.

SOM is one of the slowest components to recover following disturbance (Chambers 1997). I recommend OM addition, either from a commercial source or a locally made slurry. A 1:1 mix of undisturbed soil and litter and water may be sufficient. Straw, peat or manure addition, along with scarification, can increase nutrient retention and decrease soil bulk density (Chamber 1997) in compacted soils. OM amendments should be added in a variety of size fractions as large pieces contribute to the physical structure of the soil, increasing pore space for water and root penetration (Zabinski and Cole 2000) and smaller pieces are more readily available for microbial breakdown. Compost, in any form, can provide a slow release of both macro and micronutrients, improve water-holding capacity (Zabinski et al. 2002) microbial function and in some cases, plant growth (Zabinski and Cole 2000).

Recreation sites in high elevation areas appear severely disturbed due to lack of vegetation. Disturbance affects physical and chemical characteristics of soil, most notably increased bulk density and decreased SOM and total N. Due to the heterogeneity of soil systems, both spatially and temporally, these impacts may vary in terms of severity. Scarification and organic amendments seem necessary because of the effects both have on physical structure, soil moisture, and nutrient cycling. Restoring high elevation sites is inherently difficult no matter what system one is working in and disturbance and restoration effects vary depending on both abiotic and biotic factors (Chambers 1997).

HIGH ELEVATION DISTURBANCE EFFECTS ON SOIL MICROBIAL COMMUNITIES AND ECOSYSTEM FUNCTION

Introduction

While land managers often focus efforts on vegetation cover and animal populations as indicators of ecosystem integrity, an integral component in all living systems that is often over looked is the soil. The majority of terrestrial species reside belowground and these communities play critical roles in regulating organic matter decomposition and nutrient cycling (Zeller et al. 2001), both fundamentally important in the functioning of entire ecosystems (Degens and Harris 1997). Microbial characteristics of soils can be sensitive indices of soil productivity because of the relationships between microbial diversity, plant production and ecosystem function (Doran et al. 1994). Disturbance that impacts soil properties can affect soil biota trophic structure and community composition, resulting in changes in soil nutrient dynamics and affecting plant establishment and growth (Setälä et al. 2000).

Relatively little is known about the functional diversity of microbial communities and their importance in functioning ecosystems (Degens and Harris 1997). Examining high elevation disturbed soils provides an opportunity to examine disturbance effects on microbial function and the interactions between microbial and vegetative communities, and soil chemical and physical components. Few studies have examined the effects of high elevation recreation disturbances on soil microbial

communities (Zabinski and Gannon 1997), especially in regards to comparing disturbed, undisturbed and restored soil. Understanding the roles of belowground biota and the effects of disturbance on belowground communities poses a number of challenges. Belowground species diversity is greater than any other group of organisms in any terrestrial system, with many organisms having diverse ecological roles (Allen et al. 1999). While classical approaches to studying diversity have involved the assessment of species richness and evenness, an unbiased assessment of these properties has not yet been achieved in soil microbial communities (Trevors 1998, Degens and Vojvodic'-Vukovic' 1999). Some taxonomic approaches to quantifying belowground diversity have been developed, however functional diversity may be more important for understanding effects of disturbance on soil processes than taxonomic diversity (Zak et al. 1994, Giller et al. 1997, Degens and Vojvodic'-Vukovic' 1999).

To examine the effects of recreation disturbance on soil microbial function I measured multiple soil characteristics important for plant growth and overall ecosystem sustainability, specifically, mycorrhizal infectivity potential (MIP), decomposition, soil enzyme activity, substrate induced respiration (SIR) and nitrogen (N) mineralization. This research was conducted to determine which of these measures are sensitive to disturbance and could be useful for future assessment of disturbance and restoration effects on other soil communities. I chose four different geographic locations with varying disturbance types, ranging from camp sites to social trails to restored roads. By examining different locations and disturbance types I can identify factors most severely

impacted, those amended successfully through restoration, and relationships between physical, chemical and biological soil characteristics affected by disturbance.

Mycorrhizal Infectivity Potential (MIP)

Mutualistic interactions are widely distributed in mountain biomes (Urbanska and Chambers 2000). Some of the most important mutualisms involve mycorrhizal fungi and many species of plants, and these symbiosis are often, but not always, mutualistic (Brundrett 1991). The fungus colonizes plant roots and receives carbon from the host plant, and in exchange increases the nutrient status, potentially increases water uptake under drought conditions, and protects the host plant from pathogens. Mycorrhizae also have ecosystem-level effects, stabilizing soils, increasing soil aggregation (Smith and Read 1997), as a result of fungal hyphal networks that extend from the plant roots into the soil, and restoring nutrient cycles (Miller and Jastrow 1992). Holtmeier (2003) considers mycorrhiza as an important edaphic-biotic factor in soil formation, increasing soil stability and aggregation (Smith and Read 1997), as a result of fungal hyphal networks that extend from the plant roots into the soil however, relatively little is known regarding the importance of mycorrhizal function in alpine and subalpine areas (Korner 2003). While decreased infectivity, and in general a lower abundance of mycorrhizae, are found at higher altitudes, arbuscular mycorrhizae (AM) do occur in alpine areas (Allen et al. 1987, Korner 2003). Mycorrhizal abundance generally declines with altitude (Korner 2003) and the distribution and importance of mycorrhizae is not well known for alpine ecosystems (Allen et al. 1987). However, an abundance of AM have been found in Austrian alpine ecosystems and on Mt St. Helen's (Read and Haselwandter 1981,

Allen et al. 1984). Cripps and Eddington (2005) found 68 % of the 53 species of vascular plants examined on the Beartooth Plateau, MT were mycorrhizal, 25 of which were AM fungi. Allen et al. (1987) also documented abundant mycorrhizal fungi in the roots of plants in the Beartooth Mountains, MT (approx. 3000 m). While present in high elevation systems, its remains uncertain whether plants at high altitudes become independent of mutualistic associations given the low plant cover, slow growth and short growing seasons (Korner 2003). Local soil conditions, including soil parent material, and drainage and nutrient status may also influence mycorrhizae abundance (Lesica and Antibus 1986).

Mycorrhizae are important in the recovery of disturbed ecosystems (Allen et al. 1987) and mycorrhizal inoculum is marketed as a soil amendment in disturbed areas to promote vegetative growth in environmentally stressful conditions. Mycorrhizal relationships are often involved in the establishment of vegetation and the development of soil systems (Miller and Jastrow 1992), but it is relatively unknown whether fungal communities recover in alpine habitats exposed to disturbance or whether plant access to the appropriate microbial communities speeds up revegetation (Cripps and Eddington 2005). Mycorrhizal fungi may respond negatively to disturbances such as fire, agricultural practices and mining activities, reflected by reduction in levels of infection, propagule density and the establishment of hyphal and myceilial systems (Cairney and Meharg 1999).

Miller and Jastrow (1992) identify a number of conditions in which mycorrhizal management can become increasingly important in ecosystem restoration which include cold temperatures, arid or hydric moisture regimes, low mineral nutrient content soils and low densities of infective mycorrhizal propagules, all of which can be encountered in alpine and subalpine systems. Allen et al. (1987) found mycorrhizal spore counts and percent infection were lower in revegetated mine areas soil compared to undisturbed soil however, 1 year later spore numbers and infectivity was similar between disturbed and undisturbed soils but AM fungal diversity was low.

Mycorrhizal infectivity potential is a measure of the relative number of fungal propagules in field soils. I hypothesized that MIP would decline with disturbance because live plants are absent on disturbed soils. I expected restored sites, especially those with vegetation present, would exhibit MIP greater then disturbed sites and lower or comparable to undisturbed soils.

Decomposition

Greater than 90% of terrestrial net primary production is returned to the soil as dead plant material (Sterner and Elser 2002), which is decomposed by soil organisms on or in the soil. The decay of organic matter is critical to mineralization and nutrient cycling in ecosystems (Neher et al. 2003). Litter decomposition is vital to forest productivity (Didham 1998) and is an important component of the global carbon budget (Aerts 1997). Decomposition directly affects plant establishment and persistence by facilitating two major ecosystem functions – the mineralization of essential elements and the formation of soil organic matter (SOM). Both determine the regulation of nutrients,

and have large influences on net ecosystem nutrient storage (Swift et al. 1979, Hobbie and Vitousek 1999) in terrestrial systems.

Decomposition rates are regulated by litter quality, climate, and soil physical, chemical and biotic components (Meentemeyer 1978). A large variability exists among decomposition studies with respect to litter quality, climate, and soil faunal influences (Prescott 2005). Some studies have correlated decomposition rates most strongly to mean annual temperature (Moore et al. 1999), while others determined average precipitation was more important (Prescott et al. 2004). In addition, decomposition rates also differ between ecosystem and disturbance types (Neher et al. 2003). Difficulties aside, decomposition processes still serve as an integrating variable for evaluating ecosystem function.

To account for differences in plant species and litter compositions across ecosystems, I measured decomposition *in situ* using standardized substrates (Neher et al. 2003), a predominantly cellulose substrate and a predominantly lignin substrate. These represent the labile and recalcitrant compounds that are ubiquitous in plant litter. Because decomposition serves as an integrator of the collective activities of organisms within the soil food web, differences in rates could signal either a change in soil communities or an altered condition of biotic and abiotic resources (Neher et al. 2003) between disturbance types. Due to altered organic matter (i.e., decreased vegetative cover) with increased disturbance and a potential decrease in microbial activity on recreation impacted sites (Zabinski and Gannon 1997), I hypothesized that decomposition rates will differ, although arguments could be made for either an increase or decrease in rates, between disturbed, undisturbed and restored soils.

Soil Enzymes

Extracellular soil enzymes contribute to the mineralization of soil organic matter to supply N and phosphorous (P) to plants and microbes (Boerner and Brinkman 2003), and can be an indication of soil productivity (Kiss et al. 1975, Burns 1982) or an indirect measure of soil microbial biomass (Ladd 1978, Burns 1982). The activity of any particular enzyme in soil is a composite of activities associated with various biotic and abiotic components, e.g., proliferating and latent cells, cells debris, and clay and organic colloids (Burns 1982). Soil enzymes are believed to be primarily of microbial origin (Ladd 1978), but also originate from plants and animals (Tabataai 1998). Enzyme activities may be indicative of the effects of chemical disturbances (Burns 1982) and a measure of overall microbial activity over long periods of time (Kourtev et al. 2002). The functional capacity of the soil microbial community, measured by soil enzyme activity, varies among soils dominated by differing plant communities (Waldrop et al. 2000, Kourtev et al. 2002). Land management practices can affect soil enzyme activity (Bandick and Dick 1999) with decreases in enzyme activity in cultivated fields compared to grasslands. Boerner and Brinkman (2003) found decreased acid phosphatase and β-glucosidase activities in soils recently exposed to fire, however, little is known regarding the differences between disturbed, undisturbed and restored soils, especially in high elevation systems.

I monitored the activities of eight enzymes involved in the cycling of carbon (C), N, phosphorous (P) and SOM (Kourtev et al., 2002; Table 2.1). This suite of enzymes represent the responses of a diverse microbial assemblage to a wide range of substrate types (Boerner and Brinkman 2003) and more importantly, provide insight into the

effects of altered organic matter and nutrient availabilities on disturbed, undisturbed and restored soil on soil microbial community dynamics.

Due to a general loss of vegetation and exposed mineral soil on recreation sites (Cole 1987, Cole 1995), the positive relationship between root turnover, rhizosphere exudates and microbial activity (Kourtev et al. 2002), and a general decrease in microbial activity on recreation sites (Zabinski and Gannon 1997), I hypothesized that enzyme activity will decline with disturbance and will increase on sites where vegetation has been established, with the highest activities expressed on undisturbed sites.

Substrate Induced Respiration (SIR)

The relationship between biodiversity and ecosystem function is of increasing importance in ecology (Griffiths et al. 2000), however relatively little is known about the role of soil microbial diversity in the functioning of soils. One important benefit of microbial diversity to soil functioning may be providing a greater resistance to disturbance (Degens et al. 2001). Soil microbes are far less individualistic than higher organisms, exhibiting extremely high biodiversity in just1 gram of soil (Ohtonen et al. 1997, Degens et al. 2001). Soil biota account for a vast range of activities including: nutrient transformations, decomposition, plant growth promotion and/or suppression, and the modification of soil physical processes (Wardle et al. 2002, Degens et al. 2001).

While ecosystem function increases with higher species diversity (Tilman and Downing 1997, Naeem et al. 1997), recent evidence suggests that the functional characteristics of species are equally, if not more, important than the number of species for maintaining critical ecosystem processes (Grime 1997, Griffiths et al. 2000, Wardle

2002). Microbial functional diversity has been measured using carbon utilization profiles in high elevation systems (Zabinski and Gannon 1997). Catabolic diversity is assessed by incubating soil suspensions in Biolog® microtiter plates containing tetrozolium salts, to detect microbial growth when exposed to 95 standard carbon substrates. However, it is unclear whether this technique provides an accurate assessment of the functional diversity of the whole soil community. Incubations are short (24-48 h) after inoculation and generally, less than 1% of microorganisms in soils are culturable (Degens and Harris 1997), and the environment in agar plates and microtiter wells are far from representative of *in situ* soil conditions.

The SIR method may effectively capture the activities of a wider range of microorganisms then alternative physiological methods (i.e., Biolog®). SIR method has also proven useful in previous studies examining the effects of exotic plant species on soil microbial communities (Kortev et al. 2002). SIR measures patterns of *in situ* catabolic potential of soil microbial communities and can be used as a basis for assessing microbial functional diversity. SIR respiratory profiles model the Biolog® approach using multiple substrates with the idea that species have different capacities to metabolize a range of simple, organic substrates (sugars, amino acids, fats, etc.). An approach measuring *in situ* catabolic diversity is likely to provide a more accurate measure of microbial diversity than can be obtained from using Biolog® approach. The response of soil communities to such a range of substrates is an indicator of the diversity of the organisms present and the potential functional characteristics (Kourtev et al. 2002) of the community as a whole. The patterns of substrate utilization when soils are exposed to 26 different organic substrates reflects the functional state of the soil community and appears

to be indicative of the environmental conditions in soils influencing the metabolic state of different groups of organisms (Degens 1998).

I measured the respiratory responses of fresh soil samples, over 4-hour incubations, to 26 organic substrates comprising a range of amino acids, carbohydrates, organic acids, amines and amides (Table 3.2). This method is a measure of the catabolic diversity of relatively intact microbial communities (Degens and Harris 1997). This incubation time is characteristic of the initial microbial community in the soil before growth of organisms occurs on the added substrates (Anderson and Domsch 1978, Deegens and Harris 1997). Due to decreased vegetation and exposed mineral soil (Bell and Bliss 1973, Cole 1987, Cole 1995), the positive relationship between root turnover, rhizosphere exudates and microbial activity (Kourtev et al. 2002), and a general decrease in microbial activity on recreation sites (Zabinski and Gannon 1997) I hypothesized that the catabolic diversity, or evenness of substrate utilization would decrease with disturbance.

Nitrogen Mineralization

A soils' capacity to transform organic nitrogen in SOM to inorganic nitrogen, its nitrogen mineralization potential, is often used as an index of the nitrogen available to plants in terrestrial ecosystems. The mineralization potential of a site often reflects site fertility and is closely related to the labile SOM pool and the activity of soil organisms (Robertson et al. 1999). I define N mineralization as the net increases in both ammonium (NH_4^+) and nitrate (NO_3^-). Nutrient cycling involves the activity of soil microbes, however, the effects of compaction and loss of vegetation nutrient cycling is in question.

Soil conditions including microbial community structure and nutrient availability have been shown to be adversely affected by recreational use (Zabinski and Cole 2000), however responses are varied, suggesting a more thorough investigation is necessary. Due to almost all of my disturbed sites being completely devoid of vegetation, I hypothesized that available N, measured as mineralizeable N over 12 mo, will be higher in disturbed soils compared to undisturbed, due to decreased plant uptake (Zabinski and Cole 2000).

METHODS

Mycorrhizal infectivity potential

Mycorrhizal infectivity potential (MIP) is a measure of infective arbuscular mycorrhizal (AM) propagules present in the soil. Methods for MIP analysis were modified from Brundrett et al. (1996). In July 2004 and 2005, three soil cores (10 cm x 10 cm) at each site were extracted, using a soil corer, sterilized between samples with 50% ethanol, and transferred directly into pre-sterilized pots, minimizing disturbance of hyphae. Pots were seeded with *Sorghum sudanese*, which grew for approximately 5 weeks. Roots were harvested, cleared of pigments in 2.5% KOH, acidified in 3% HCl for 12 hours, and stained with Trypan Blue by a modified method of Phillips and Hayman (1970). Colonization levels were quantified using magnified intersections method (McGonigle et al. 1990), quantifying AM hyphae, vesicles, arbuscules, and non-AM hyphae. Non-AM hyphae, characterized by non-AM structures including fruiting bodies, cross wasn't in the hyphae, and unique hyphal branching patterns, were also recorded.

Decomposition

Decomposition was measured using a mass loss method of standardized substrates containing predominately cellulose or lignin, modified from Harmon et al. (1999) and Neher et al. (2003), with field incubations. In the summer of 2003, nine replicates of screened bags (2mm fiberglass), containing one 3 cm x 8 cm rectangular cellulose museum board (Crescent, 100% cotton fiber, acid free and buffered with 2 % calcium carbonate) substrate and one identically sized balsa wood (Midwest Co., 1 mm thick) substrate were buried at 4 and 10 cm depths on each campsite at Emerald and Heart Lake, MT and 2 restored sites at NOCA with an additional 9 replicates buried at adjacent areas off the campsites, shortly after snow melt at each of the sites. In the summer of 2004 1 campsite was added at NOCA and 5 sites (2 restored roads, 2 social areas and 1 campsite) at MORA where identical screened bags filled with precision-cut disks, 2 cm in diameter were buried 4 cm below the mineral soil surface. Precision cut disks were ultimately used to ensure uniformity of weight between bags and only one depth was used after 3 mo data indicated no significant difference of mass loss between depths. All bags were buried by carefully lifting a "slice" of soil minimizing disturbance. Substrates were weighed initially before placement into litterbags. The 2 mm litterbag mesh size was selected to allow for colonization by meso- and microfauna. Field incubations and litter bag retrieval was staggered for 3, 12, 15 and 24 months, with three replicates from each site extracted at each time. Intact litterbags were transported to the lab in sealed Zip Loc® bags. Litter bags were cut open in the lab, disks were removed, placed in separate envelopes, labeled, and dried for 48 hours at 60° C. Dry disks were removed from envelopes, gently brushed free of any visible adhering soil particles, and weighed. Mass

remaining of substrate is calculated as the difference between initial and final weight and expressed as a percentage of initial weight at each collection time (Neher et al. 2003).

Three month collections were not completed at 1 site at NOCA and all 5 MORA sites in 2004, as the previous year's data showed very little mass loss after 3 mo. One set of litter bags was removed from all of the sites after 12 mo incubation, but some of the litter bags were lost before the 24 mo extraction, possibly pulled up by animals or campers. Because litter bags were placed in the ground during 2 different years, the 12 mo incubation time is a different 12 mo period for approximately half of the litter bags.

Soil Enzymes

In July 2005 three samples of moist A-horizon soil (0-10 cm), excluding the litter layer, were collected from all sites and composited in the field. The soil coring tool was sterilized with 50% ethanol between samples. Samples were transported cool for 1-3 d, depending on location, sieved through a 2 mm sieve to remove large rock and organic matter fragments, and stored at field moisture at 4° C until substrate addition. No samples were stored longer then 5 days. Five grams of fresh soil from each composited sample were diluted with 120 ml of 50 mM NaOAc buffer (pH 5) and homogenized by rapid stirring for 90 s. Stirring was continued while all aliquots were taken to minimize sedimentation (Boerner and Brinkman 2003). For each enzyme (Table 2.1), we analyzed three replicates of each sample using 2.0 ml soil slurry and 2.0 ml substrate per replicate. Soil-free blanks consisting of 2.0 ml of buffer and 2.0 ml enzyme substrate were analyzed to correct for non-enzymatic hydrolysis of substrates (Boerner and Brinkman 2003). All enzyme nomenclature follows I.U.B. (1979).

Activities assayed using p-nitrophenol (pNP) linked substrates included: pNP-phosphate for acid phosphatase (EC 3.1.3.1), pNP-glucopyranoside for β-glucosidase (EC 3.2.1.21), and pNP-glucosaminide and pNP-Beta-N,N'-diacetylchitobiose for chitinase (EC 3.2.1.14) (Table 2.1). Acid phosphatase and β-glucosidase were incubated for 1 h after substrate addition and chitinase for 2 h, both at 20° C on an orbital shaker. Leucine and glycine aminopeptidase (EC 3.4.11.x) and cellobiohydrolase (CBH, EC 3.2.191) activities were also analyzed after 1 h incubations, similar to pNP linked substrates. Phenol oxidase (EC 1.14.18.1 and 1.10.3.2) activity was measured by oxidation of L-DOPA (L-3,4-dihydroxyphenylalanine) following a 1 h incubation at 20° C. Oxidation using standardized horseradish peroxidase (Sigma) was used to calculate a L-DOPA extinction coefficient. Following incubation, samples were centrifuged for 3.5 min to separate soil, and 0.1 ml of 1.0 M NaOH was added to the supernatant to halt enzymatic activity and facilitate color development.

Table 3.1. Enzymes and substrates

ENZYME ASSAY	SUBSTRATE
1 Acid phosphatase (EC 3.1.3.1)	pNP-phosphate
2 Phenol oxidase (EC 1.10.3.2 and 1.14.18.1)	L-3,4-dihydroxyphenylalanine (L-DOPA)
3 Chitinase (EC 3.2.1.14)	pNP-acetylglucosaminide
4 Leucine aminopeptidase (EC 3.4.11.x)	Leucine p-nitroanilide
5 Glycine aminopeptidase (EC 3.4.11.x)	Glycine p-nitroanilide
6 β-glucosidase (EC 3.2.1.21)	pNP-glucopyranoside
7 Chitinase (EC 3.2.1.14)	pNP-Beta-N,N'-diacetylchitobiose
8 Cellobiohydrolase (CBH, EC 3.2.1.91)	p-nitrophenyl-β-D-cellobioside

All samples were diluted with 8.0 ml deionized water prior to spectrophotometric analysis at 415 nm (BioRad Model 3550-UV, 96 well, microplate reader, Hercules, CA). All assays followed methods of Sinsabaugh and Findlay (1995) and Boerner and Brinkman (2003).

Substrate Induced Respiration (SIR)

In July 2004 three samples of moist, A-horizon soil (10 cm x 10 cm), excluding the litter layer, were collected and composited in the field. The soil coring tool was sterilized between each sample with 50% ethanol. Samples were initially stored cool during sampling and transport, however, soils from WA warmed to air temperature during parcel transport. All samples were sieved through a 4 mm sieve to remove large rock and organic matter fragments, and stored at field moisture content in sealed Zip Loc® bags at 4° C until substrate addition. Samples were analyzed as soon as possible with no soils stored longer than 28 days. Substrates used included amino and carboxylic acids, and simple sugars that have previously been found to best distinguish between different soil types (Deegens and Harris, 1997). Substrate concentrations were similar to those detailed in Degens and Harris (1997). Two ml of each substrate was added to 1.0 g equivalent dry weight of soil (West and Sparling 1986) in Labco Exetainer® glass vials (12.5 ml), and immediately sealed with Labco airtight screw caps. Three replicate soil/substrate combinations were used to assess respiratory responses. Samples were incubated at 25º C for 4 h, as detailed in Deegens and Harris (1997). Controls of each soil sample were incubated with deionized water to determine soil basal respiratory activities. Volume CO_2 respired per gram soil per hr was calculated using:

$\mu g\ CO_2\text{-}C\ g^{-1}\ soil = ((A_{sample}*10000/B_{std})/10^3*V*K))-$ Eq. 3.1

$((A_{blank}*10000/B_{std})/10^3*V*K))$

where :

A_{sample} = Peak height (mm) of sample

A_{blank} = Peak height (mm) of blank bottle

B_{std} = Peak height (mm) of standard gas (1% CO_2)

V = Head space volume of bottle (taken as 25.24 ml without soil)

K = Conversion constant for µl to µg of CO_2-C (assuming 1 atmosphere pressure: 1.7995 µg CO_2 = 1 µl CO2 at 25°C and 1 atmosphere = 0.4908 µg CO_2-C)

Soil slurries were shaken once every 2 h during the incubation and immediately before gas sampling using a vortex mixer (West and Sparling 1986). CO_2 efflux from the soils was measured from 1 ml headspace gas, using a gas chromatograph (Varian Model CP4900 with a CO_2 pore-o-plot Q column, He carrier gas and thermal conductivity detector, Palo Alto, CA.). Respiratory response to the added substrates was calculated by subtracting CO_2 generation in the soils with blanks.

Nitrogen (N) Mineralization

Field soils were characterized for mineralization and nitrification rates using mixed bed ionic resins (Unibest, Bozeman, Montana). Polyester capsules, 2 cm in diameter, containing approximately 1 g of mixed bed ionic resin, were carefully placed, minimizing soil disturbance, below the Oa horizon and mineral soil interface. Capsules were buried in early July 2004 and retrieved in conjunction with litter bags in mid

October 2005. Resins were extracted by sequential washing in 2 M KCl and analyzed for NO_3^- and NH_4^+ by the Berthelot method and NO_3^- by the cadmium reduction method via flow injection analyzer (Mulvaney, 1996).

Table 3.2. 26 organic substrates used to assess microbial catabolic differences between soils.

ORGANIC SUBSTRATES	
Amino acids	Carboxylic acids
1 L-Arginine	14 L-Ascorbic acid
2 L-Asparagine	15 Citric acid
3 L-Cystine	16 Fumaric acid
4 DL-Histidine	17 D-Gluconic acid
5 L-Leucine	18 DL-α Hydroxybutyric acid
6 L-Lysine	19 α -Ketoglutaric acid
7 L-Phenylalanine	20 DL-Malic acid
8 L-Serine	21 Malonic acid
9 DL-Tyrosine	22 Oxalic acid
	23 Quinic acid
Amines and amides	24 Succinic acid
10 D-Glucosamide	25 L-Tartaric acid
11 Succinamide	26 Uric acid
Carbohydrates	
12 D-Glucose	
13 DL-Mannose	

Resins capsules can be effectively used to measure the bioavailability of plant nutrients, are lightweight for transport (compared with collection of mineral soil samples) and have an efficient ability to sorb and collect inorganic N with time. A 12 mo incubation time provides a yearly N pattern and estimate of net mineralization and nitrification rates.

Data Analysis

Overall patterns in MIP, decomposition, soil enzyme activity, SIR and N mineralization, in relation to location and disturbance, were analyzed using 2-way ANOVA (SPSS General Linear Model Univariate ANOVA, SPSS, Inc., Chicago, IL. Version 13.0). The model included 2-way interactions of disturbance and location, with disturbance as a fixed effect and location a random effect. Post hoc comparisons were not performed for differences between location, since location was a random effect variable in the ANOVA. Least square difference post hoc tests were used to determine which variables differed significantly with disturbance ($p < 0.10$). Differences in parameters between disturbed and undisturbed sites were analyzed at each location using paired t-tests which compare the mean of sample differences between pairs of data to the hypothetical mean (Sokal and Rohlf 1995). The 2-way ANOVA's with location random allow conclusions regarding general patterns between disturbance types over a geographical range, while the paired t-tests allow comparisons between disturbance effects considering differences within each location. Variables were transformed as necessary to pass the assumptions of ANOVA, most notably Levene's test of equality of error variances. Both MIP and decomposition rate variables were not transformed. Enzyme activities and SIR responses were transformed to pass Levene's test when necessary. The Kruskal-Wallis nonparametric test was used to compare enzyme activities and SIR responses for those variables that could not be transformed to pass the equality of variance assumption of ANOVA. Nonparametric tests were then used to examine both location and disturbance differences at a significance of asymptote significance= 0.10. When hypotheses were directional, i.e. enzyme activity will be lower

in disturbed versus undisturbed soil, a 1-tailed t-test was used. A two-tailed t-test was used when a hypothesis was non direction, i.e., decomposition rates will differ however whether rates are higher or lower on disturbed versus undisturbed sites is questionable. In some instances differences were not significant with the ANOVA but were with the paired t-test. There were no significant interaction terms with any of the ANOVA's therefore they will not be discussed.

Principle components analysis (PCA) was used separately on soil enzymes and SIR responses, including all the variables in each case. The objective of PCA is to represent a data set containing many variables with a smaller number of composite variables (components or axes) with the strongest covariation among variables emerging in the first few axes (components) (McCune and Grace 2002) . PCA ordinates the samples in a way that maximizes the variation in the samples (Kourtev et al. 2002). It is a useful technique when a data set approximates multivariate normality and variables may have linear relationships. It can reveal patterns in the data, if for example disturbed sites differ from undisturbed, based on the microbial community response to different substrates.

STUDY SITES

The Emerald Lake (EL) Basin is a subalpine system (2,714 m elevation) in the northern Gallatin Mountains in southwestern Montana (45°24'N, 111°32"W.). Mean annual precipitation at Shower Falls, Montana SNOTEL (2469 m elevation, 45°40'N, 110°95"W) is 127.76 cm (40 yr mean), mean annual temperature is 1.3 °C (6 yr mean),

and the area is snow free between July and October. The soils are moderately fine Argic Cryoborolls. Tree species include *Abies lasiocarpa*, *Pinus albicaulis*, and *Picea englmannii*. Understory vegetation consists of *Festuca idahoensis*, *Deschampsia caespitosa*, and *Vaccinium scoparium*.

In the summer of 2003 I a began study of 3 campsites on the northeastern side of the lake. The first, located in a subalpine meadow, is 11.5 m wide and 13 m long. The other two sites are predominantly forest, the first is 4 m long and 10.5 m wide and the second is 8 m wide and 9 m long. All sites are almost completely devoid of vegetation and were used as campsites throughout the study.

The Heart Lake (HL) Basin is a subalpine system (1,770 m elevation) in the northern Bitterroot Mountains in western Montana (46°57'N, 114°58"W). Mean annual precipitation is 174.50 cm (25 yr mean, Hoodo Pass, Montana SNOTEL, 1844 m elevation, 46°59'N, 115°02"W), mean annual temperature is 3.75 °C (6 yr mean, Hoodoo Pass, Montana SNOTEL), and the area is snow free between July and October. The soils are fine-grained Andic Cryocrepts. Tree species include *Abies lasiocarpa*, *Pinus contorta*, *P. albicaulis*, *P. monticola*, *Picea engelmannii* and *Tsuga mertensiana*. Understory vegetation includes *Xerophyllum tenax*, *Vaccinium globulare* and *Menziesia ferruginea*.

In the summer of 2003 I began a study at 2 sites, one of which was closed for use in 1995 and used for a study of restoration treatments (Zabinski and Cole 2000). The largest campsite is 6 m wide and 11 m long, the smaller campsite, located directly north, is 7.5 m wide and 9 m long. The largest campsite was divided into 25 1 m^2 plots in which restoration treatment were applied (Zabinski and Cole 2000). Treatments included

control plots with no amendments, plots with scarification of soil to 15 cm, scarification plus compost amendment (Ekocompost®), scarification plus soil inoculum, in the form undisturbed soil slurry mixed with stream water and incorporated to 15 cm, and scarification plus compost and soil inoculum. Revegetation on half the amended sites was by broadcast seeding and seedling transplant (Zabinski and Cole 2000). Disturbed samples were taken from control plots and restored samples were taken from scarified plots with compost and inoculum addition. Both disturbed and restored sites are nearly devoid of vegetation.

Cascade Pass is a subalpine zone (1450-1650 m elevation) in the Northern Cascade Mountains and is located in Northern Cascades National Park (NOCA), Washington (48°27'N, 121°08"W). Mean annual precipitation is 177.85 cm (29 yr mean, Park Creek Ridge, Washington SNOTEL, 1402 m elevation, 48°27'N, 120°55"W) mean annual temperature is 4.04 °C (6 yr mean. Park Creek Ridge, Washington SNOTEL). The soils are volcanic and range from hydric, silty sand loams, to fine, mixed, granitic (greus) sandy loams. Tree species include *Abies amabilis*, *Tsuga mertensiana*, *Pseudotsuga menziesii* and *Thuja plicata*. Understory vegetation includes *Sorbus americana*, *Polygonum bistorta, Polemonium spp*., *Castilleja spp*., and *Vaccinium scoparium*, which was the dominant species.

In the summer of 2003 I began a study at 2 sites on Cascade Pass, the upper most site is 9 m wide and 10 m long and the lower site is 4m wide by 8 m long. Both sites were restored in the early 1970's. Soil amendments included peat moss and bark chip incorporation and sites were planted with *Lupinus spp*., *Phleum spp*. and *Ericaceous spp*. Vegetation on restored campsites is sparse but present. In the summer of 2004 I began

study at a third site in Pelton Basin (1445 m elevation) below the two upper sites. The Pelton Basin site is 15m wide by 30 m long. This site is almost completely devoid of vegetation. The Pelton Basin site was camped on throughout the study.

Mount Rainier (MORA) (4,392 m elevation) lies west of the Cascade Mountains, 100 miles east of the Pacific Ocean. Mean annual precipitation is 299.24 cm (Paradise, Washington SNOTEL, 1561 m elevation, 46°47'N, 121°45"W) and mean annual temperature is 4.46 °C (6 yr mean, Paradise, Washington SNOTEL). Subalpine vegetation at Mount Rainier consists of *Chamaecyparis nootkaensis*, *Tsuga mertensiana, Abies lasiocarpa, Vaccinium parvifolium, Erythronium montanum, Caltha leptosepala, Lupinus perennis, Castilleja parviflora, Xerophyllum tenax, Erythronium grandiflorum*, and *Ranunculus eschscholtzii*.

In the summer of 2004 I began study at 5 sites in 3 different locations in Mount Rainier National Park in WA. The first two disturbed sites are on Mount Rainier's south slope near the Paradise Inn (46° 47'N, 121°44"W). The upper most site (30 m wide x 50 m long), is at Glacier Vista (1,931 m elevation) and the second site (8 m wide x 20 m long) is just below, at approximately the same elevation, on the Deadhorse Creek Trail. Both are large social areas in subalpine meadows, disturbed by increased visitor concentrations and off trail travel. While restoration efforts have been made in areas near our sites, neither has been actively restored and both are devoid of vegetation.

Two restored sites are near the Sunrise Visitor Center (1,950 m elevation) in the northeast section (46°54'N, 121°38W) of the park. The first site is 20 m wide x 20 m long and the second site is 15m wide x 30 m long and both are sections of a restored road en route to the main Sunrise Camp area. Restoration work was done in 1995, and

included scarification, seedlings, and application of erosion fabric with no chemical soil amendments (i.e., fertilizer or compost) applied.

The fifth site in Mt. Rainier National Park is an active campsite near Crystal Lake (1775 m elevation), also on the northeast side of the park (46°54'N, 121°30'W). The site is 7 m wide by 10 m long and is devoid of any vegetation.

RESULTS

Mycorrhizal infectivity potential (MIP)

Mycorrhizal infectivity potential (MIP) was low at all sites and did not differ significantly between disturbed, undisturbed or restored sites (Table 3.3) with mean infectivity being 4, 5 and 3 %, respectively. MIP was significantly different between locations (Table 3.3) with the highest infectivity measured in soils from EL (Fig. 3.1). Infectivity on disturbed sites ranged from 0 (MORA and NOCA) to 9 % (HL), restored from 0 (MORA and NOCA) to 7 % (HL) and undisturbed from 0 (MORA and NOCA) to 17 % (EL).

Table 3.3 Analysis of variance of AM and non-AM MIP for all disturbances at each location

Mycorrhizal Infectivity Potential	Arbuscular Mycorrhizae				Non-Arbuscular Mycorrhizae			
	d.f.	MS	F	P	d.f.	MS	F	P
Location (L)	3	0.00	4.65	0.06	3	0.03	2.10	0.22
Disturbance (D)	2	0.01	0.25	0.79	2	0.03	2.24	0.19
D * L	5	0.00	0.63	0.68	5	0.01	1.81	0.16
Error	17	0.00			17	0.01		

Non-AM infectivity was significantly greater on undisturbed versus disturbed sites (t_8=-2.08, p=0.04), 24 and 17% respectively. Non-AM infectivity did not differ between undisturbed and restored sites (t_4=-0.73, p=0.25) and was not significantly different between location (Table 3.3), however non-AM colonization was higher than AM colonization.

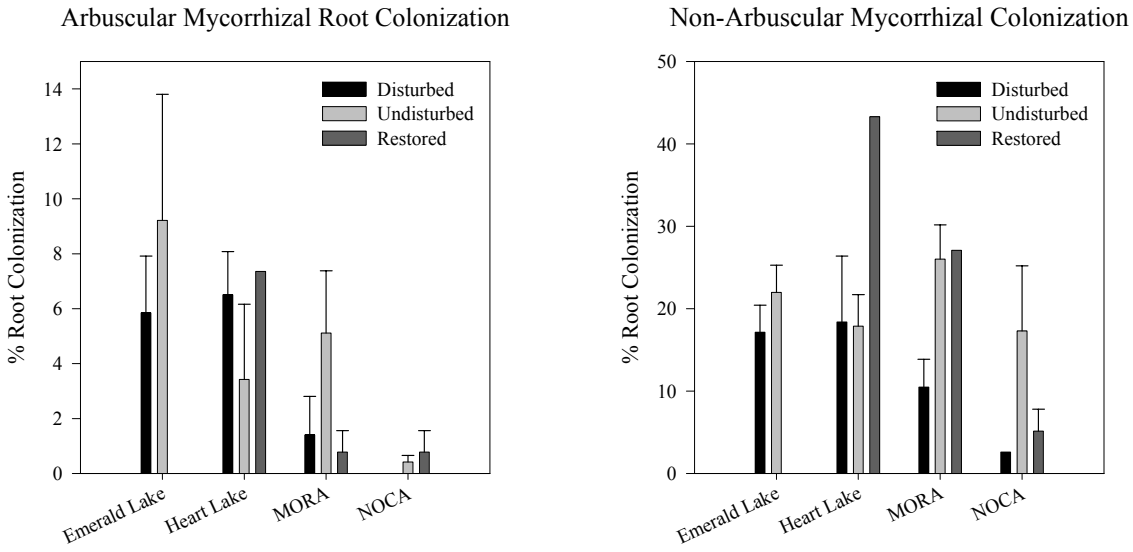


Figure 3.1. AM and non-AM root colonization. Error bars represent 1 standard error of the mean.

There was no significant disturbance by location interaction for either MIP or non-mycorrhizal infectivity potential (Table 3.3).

Decomposition

Decomposition rates after 3 mo did not differ between disturbance or location for either museum board or balsa wood (Table 3.4). Mass remaining for museum board ranged from 93% (HL, restored) to 75% (EL, undisturbed) and mass remaining for balsa

wood ranged from 98% (HL, undisturbed) to 88% (EL, undisturbed; Fig. 3.1). There were no significant disturbance by location interactions for either museum board or balsa wood (Table 3.4).

Table 3.4 Analysis of variance of decomposition rates for disturbance types over 3, 12 and 24 mo incubation times

Decomposition Rates (3 mo)	Museum Board				Balsa Wood			
	d.f.	MS	F	P	d.f.	MS	F	P
Location (L)	2	0.01	3.10	0.29	2	0.01	4.95	0.21
Disturbance (D)	2	0.01	0.19	0.84	2	0.00	2.05	0.28
D * L	2	0.01	0.29	0.76	2	0.00	0.29	0.76
Error	8	0.02			8	0.00		

Decomposition Rates (12 mo)	Museum Board				Balsa Wood			
	d.f.	MS	F	P	d.f.	MS	F	P
Location (L)	2	2.32	14.75	0.01	2	0.31	24.03	0.00
Disturbance (D)	3	0.12	0.71	0.53	3	0.01	0.56	0.60
D * L	5	0.16	1.71	0.19	5	0.01	0.75	0.60
Error	16	0.09			16	0.02		

Decomposition Rates (24 mo)	Museum Board				Balsa Wood			
	d.f.	MS	F	P	d.f.	MS	F	P
Location (L)	1	0.01	0.28	0.69	1	0.06	14.69	0.16
Disturbance (D)	2	0.01	0.58	0.64	2	0.01	0.61	0.57
D * L	1	0.02	1.09	0.34	1	0.00	0.08	0.79
Error	6	0.02			6	0.05		

I compared the 12 mo decomposition rate between the 2003 and 2004 cohorts using a t-test and because rates were higher for the 2003 cohort (61 vs. 79% museum board remaining($t=-3.62$, $p=0.001$, $t=-2.61$, $p=0.02$) and 87 and 95% for balsa wood. I did not test for differences between location at 12 mo. The paired t-test was used to

analyze between disturbance type. There was a large range in decomposition rates on both disturbed and undisturbed soils (Fig. 3.2). After 12 mo undisturbed museum board mass remaining ranged from 43 % (EL) to 92 % (MORA), restored from 71 % (NOCA) to 92 % (MORA) and undisturbed from 33 % (EL) to 88 % (MORA). Balsa wood had higher % remaining after 12 mo with disturbed ranging from 68 % (HL) to 99 % (Emerald Lake), restored from 63 % (NOCA) to 98 % (MORA) and undisturbed from 72 % (EL) to 100 % (MORA). There were no differences in decomposition rates or disturbance types for soils from HL or NOCA. After 12 mo, decomposition differed between locations (Table 3.4) and disturbance types for only museum board (t_4=-2.12, p=0.10) with undisturbed soils having less % mass remaining compared restored. There was no disturbance by location interaction for either museum board or balsa wood (Table 3.4).

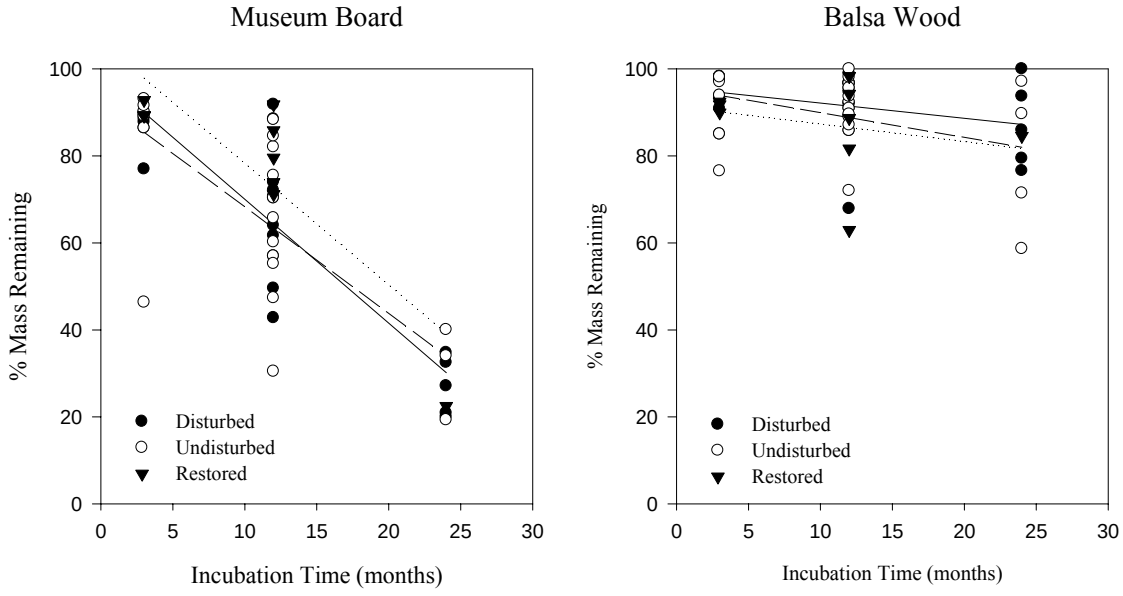


Figure 3.2. Percentage of mass remaining of substrates over time of field incubation in disturbed (dotted line, closed circles), undisturbed (solid line, open circles) and restored (dashed line, closed triangles).

Some litter bags were lost prior to the 24 mo extraction, and for one site at NOCA and five sites at MORA, the 24 mo incubation period ends July 2006. Decomposition rates after 24 mo did not differ between disturbance or location for either museum board or balsa wood (Table 3.4). Mass remaining for museum board ranged from 25% (EL, undisturbed) to 10% (HL, undisturbed) and mass remaining for balsa wood ranged from 85% (HL, restored) to 49% (EL, undisturbed; Fig. 3.1). There were no significant disturbance by location interactions for either museum board or balsa wood (Table 3.4).

Soil Enzymes

Using two-way ANOVAs of individual enzyme activities expressed as activity per gram of soil per hour, one enzyme, acid phosphatase, differed significantly between disturbance types, while five enzyme activities, acid phosphatase, phenol oxidase, glycine and leucine aminopeptidase and β-glucosidase differed between location. Both chitinase and cellobiohydrolase activities were not sensitive to disturbance or location (Table 3.5). Post hoc comparisons reveal while acid phosphatase activity (activity/g soil/ hr) is significantly higher on undisturbed versus disturbed sites ($p=0.04$) there is no difference between disturbed or undisturbed and restored soils ($p=0.43$ and 0.36, respectively).

Acid phosphatase activity was the highest at NOCA ($p<0.001$) with no difference between the other three locations. β-Glucosidase activity differed only between locations with the highest activity at NOCA. Activity was nearly different between disturbance ($p=0.142$). Leucine and glycine aminopeptidase were both significantly different between location with soils from NOCA expressing the highest activity overall.

Table 3.5 Analysis of variance of 8 enzyme activities for disturbance types at all locations expressed as activity per g of soil per hour. B-glucosidase, leucine aminopeptidse and chitinase (7) were all analyzed non-parametrically using the Kruskal Wallis Test. Phenol oxidase was square root transformed and cellobiohydrolase and chitinase (3) were cube root transformed.

	Acid Phosphatase				B-glucosidase		
	d.f.	MS	F	P	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	18.36	13.28	0.00	3	11.49	0.01
Disturbance (D)	2	5.19	3.75	0.05	2	2.84	0.24
D * L	5	0.90	0.65	0.66			
Error	16	1.38					

	Glycine aminopeptidase				Leucine aminopeptidase		
	d.f.	MS	F	P	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	3.49	6.49	0.004	3	13.39	0.004
Disturbance (D)	2	0.89	1.65	0.22	2	0.35	0.84
D * L	5	0.44	0.81	0.56			
Error	15	0.54					

	Phenol oxidase				Cellobiohydrolase			
	d.f.	MS	F	P	d.f.	MS	F	P
Location (L)	3	4.07	8.62	0.02	3	0.07	2.52	0.17
Disturbance (D)	2	0.55	1.20	0.37	2	0.00	0.01	0.99
D * L	5	0.47	1.59	0.22	5	0.03	1.10	0.40
Error	15	0.30			15	0.03		

	Chitinase (3)				Chitinase (7)		
	d.f.	MS	F	P	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	0.18	2.83	0.15	3	2.50	0.48
Disturbance (D)	2	1.40	1.40	0.32	2	0.73	0.69
D * L	5	0.06	1.45	0.26			
Error	15	0.04					

Undisturbed sites exhibited significantly higher activity then disturbed (p=0.01). Phenol oxidase activity differed significantly between location with NOCA exhibiting the

highest activity. MORA had the lowest activity with HL and EL intermediate. Phenol oxidase activity did not differ between disturbance.

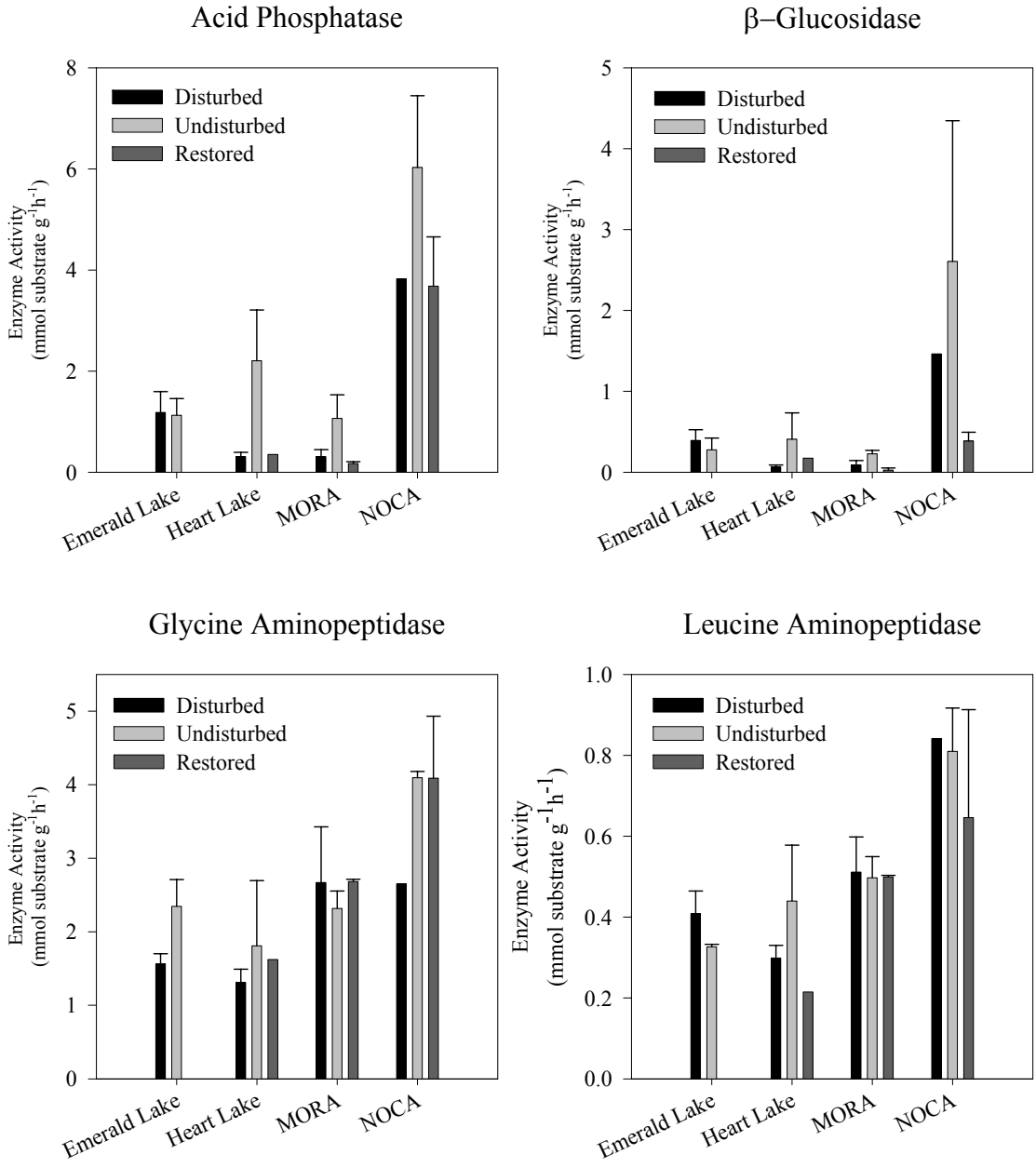


Figure 3.3. Enzyme activities in four different soils in activity/per g soil/hour for Emerald Lake, Heart Lake, Mount Rainier National Park (MORA), and North Cascades National Park (NOCA).

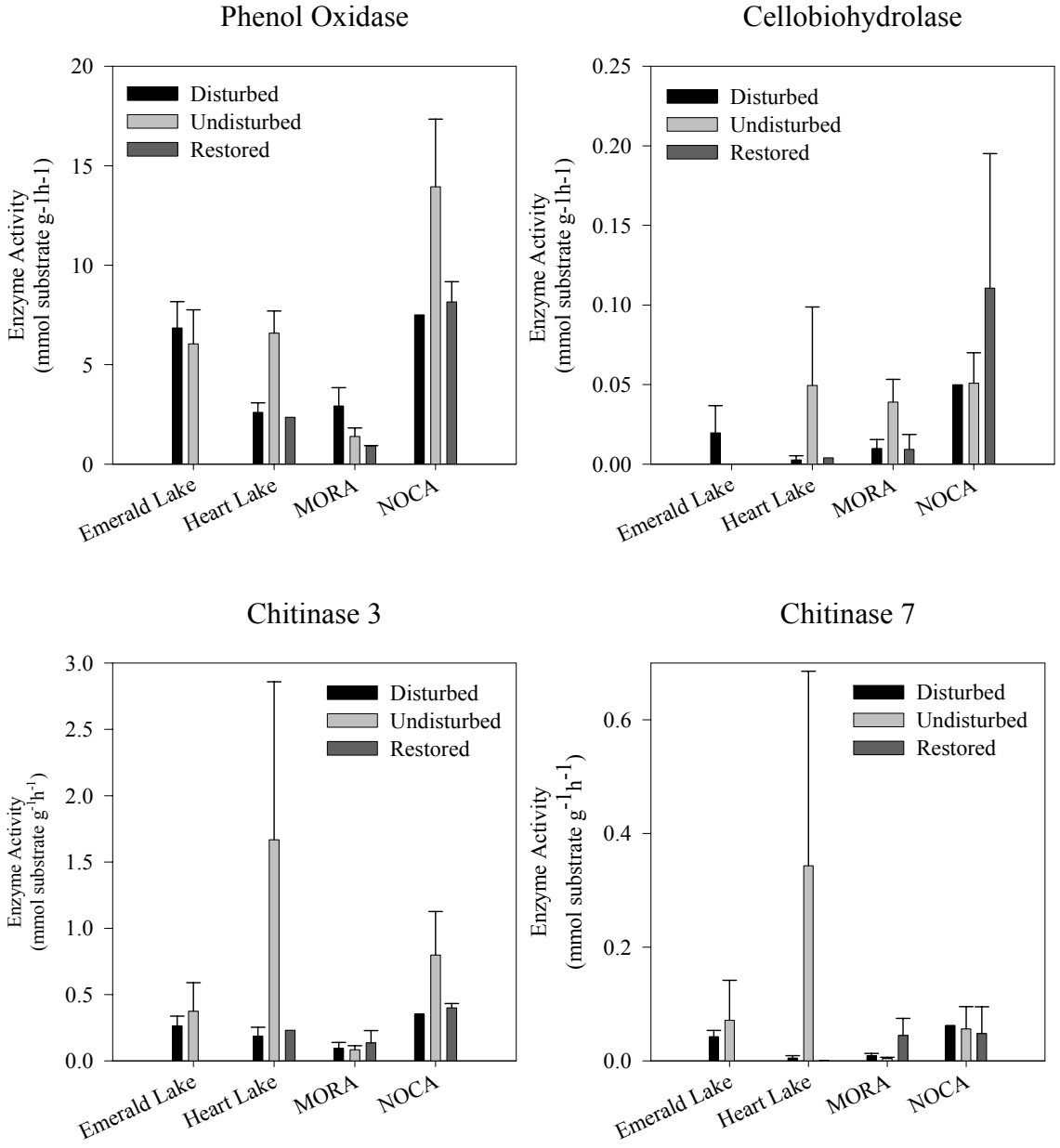


Figure 3.4. Enzyme activities in four different soils in activity of substrate/g soil/ hour for Emerald Lake, Heart Lake, Mount Rainier National Park (MORA) and North Cascades National Park (NOCA).

Cellobiohydrolase activities were low at all locations, neither location nor disturbance were significantly different. Chitinase did not differ between location or

disturbance in either assay. However, the overall trend in activity was similar between substrates with one sample from HL expressing higher activities then all other locations. There were no significant disturbance by location interactions in either analysis.

Paired t-tests comparing disturbed and undisturbed enzyme activity, expressed as activity per gram of soil per hour, also showed that acid phosphatase activity higher on undisturbed versus disturbed soils (t_8=-1.61, p=0.07). Higher activities of chitinase (3) (t_8=-1.22, p=0.13), glycine aminopeptidase (t_8=-1.27, p=0.12), β-glucosidase (t_8=-1.15, p=0.14) and cellobiohydrolase (t_8=-1.26, p=0.12) on undisturbed vs. disturbed soils were nearly significant. Other enzyme activities did not differ between disturbance type.

Because SOM levels may be an important driver for enzyme activity (Boerner and Brinkman 2003), enzyme activities were also analyzed as activity per gram organic matter per hour. Acid phophatase, leucine and glycerin aminopeptidase and cellobiohydrolase differed between location. Higher undisturbed chitinase activity was nearly significant (Table 3.5). There were no significant disturbance by location interactions. Paired t-tests comparing disturbed and undisturbed enzyme activity, expressed as activity/g OM/hour, resulted in significantly higher activities on undisturbed sites for acid phosphatase (t_8=-1.91, p=0.05), leucine (t_8=-1.50, p=0.09) and glycine aminopeptidase (t_8=-1.82, p=0.05) and cellobiohydrolase (t_8=-1.37, p=0.10). Higher activities of phenol oxidase (t_8=-1.22, p=0.13) and chitinase (3) (t_8=-1.37 p=0.11) and on undisturbed vs. disturbed soils were nearly significant.

The PCA analysis of enzyme data by location shows no strong pattern of clustering of points, either by disturbance or by location (Figure 3.5). Enzyme activity levels on undisturbed sites (open diamonds) show a wider variance, as indicated by the

distribution across both axes. Points are clustered more by location then by disturbance (Figure 3.5). The first two principle components (PC) explained 66.14% of the variation in the data.

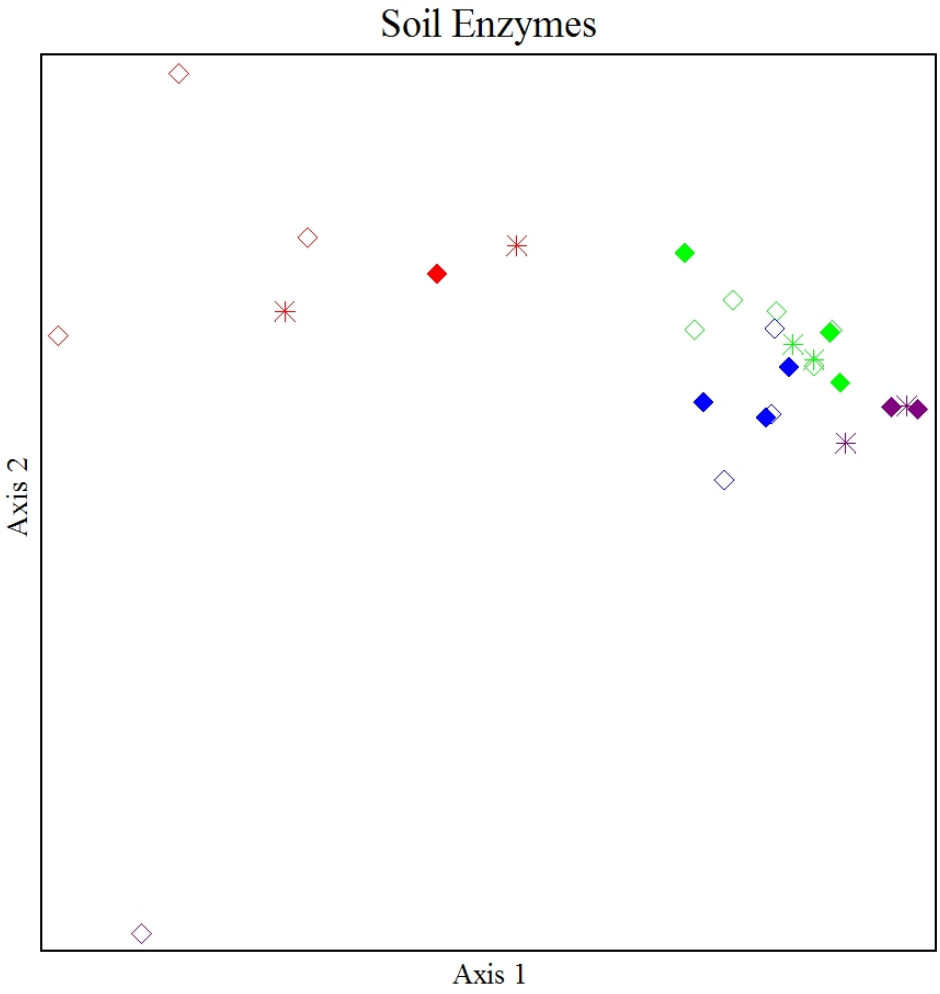


Figure 3.5. Results from principle components analysis (PCA) on soil enzyme activity. Variable are separated by location (color: red=NOCA, green=MORA, blue=EL and purple=HL) and disturbance (shape: open diamond=undisturbed, closed diamond=disturbed and asterisk=restored).

Substrate Induced Respiration (SIR)

With a two-way ANOVA twenty substrate responses differed between location, 7 of which also differed between disturbance (Table 3.6). SIR responses differed significantly for fourteen carboxylic acids, 3 amino acids, 1 carbohydrate, 1 amine and 1 aromatic substrate by location (Table 3.6). Four carboxylic acids, 1 carbohydrate and 1 amine differed significantly by disturbance (Table 3.6).

Table 3.6 Analysis of variance of 17 of the 26 substrates used that exhibited a significant disturbance or location response. To pass Levene's test of equal variance malonic acid, D-glucose and succinamide, were square root transformed, and fumaric acid, citric acid, and urocanic acid were cube root transformed. Oxalic acid, hydroxybutyric acid, tartic acid, arginine, asparagine, L-serine and mannose were all analyzed non-parametrically using the Kruskal Wallis test.

	α-ketoglutaric acid				DL-malic acid			
	d.f.	MS	F	P	d.f.	MS	F	P
Location (L)	3	$3.31x10^7$	6.10	0.00	3	$3.91x10^6$	14.21	0.00
Disturbance (D)	2	$1.40x10^6$	2.58	0.11	2	$1.25x10^6$	4.54	0.03
D * L	5	$6.02x10^5$	1.11	0.30	5	$1.97x10^5$	0.72	0.62
Error	16	$5.42x10^5$			16	$2.75x10^5$		

	Oxalic acid			Malonic acid			
	d.f.	Chi-Sq	Asymp. Sig.	d.f.	MS	F	P
Location (L)	3	16.06	0.00	3	1304.93	31.56	0.00
Disturbance (D)	2	3.09	0.21	2	4.37	0.10	0.90
D * L				5	41.34	0.74	0.60
Error				16	55.66		

	Hydroxybutyric acid			Fumaric acid			
	d.f.	Chi-Sq	Asymp. Sig.	d.f.	MS	F	P
Location (L)	3	16.46	0.00	3	132.08	26.24	0.00
Disturbance (D)	2	0.31	0.86	2	3.62	3.62	0.09
D * L				5	5.03	0.78	
Error				16	6.47		

	Uric acid				L-tartic acid		
	d.f.	MS	F	P	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	28.92	4.04	0.08	3	12.04	0.01
Disturbance (D)	2	0.21	0.02	0.98	2	1.62	0.45
D * L	5	7.16	0.33	0.89			
Error	16	21.95					

	Uric acid				L-tartic acid		
	d.f.	MS	F	P	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	28.92	4.04	0.08	3	12.04	0.01
Disturbance (D)	2	0.21	0.02	0.98	2	1.62	0.45
D * L	5	7.16	0.33	0.89			
Error	16	21.95					

	Citric acid				L-arginine		
	d.f.	MS	F	P	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	71.83	127.03	0.00	3	6.32	0.10
Disturbance (D)	2	9.39	7.59	0.00	2	0.06	0.97
D * L	5	0.56	0.08	0.99			
Error	16	7.08					

	L-asparagine			L-serine		
	d.f.	Chi-Sq	Asymp. Sig.	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	6.65	0.08	3	1.62	0.45
Disturbance (D)	2	0.92	0.63	2	10.04	0.02
D * L						
Error						

	Phenylanaline				Mannose		
	d.f.	MS	F	P	d.f.	Chi-Sq	Asymp. Sig.
Location (L)	3	$2.94x10^5$	2.42	0.10	3	10.09	0.00
Disturbance (D)	2	$5.42x10^4$	0.45	0.65	2	0.59	0.75
D * L	5	$1.21x10^5$	0.10	0.45			
Error	16	$1.21x10^5$					

	D-glucose				Succinamide			
	d.f.	MS	F	P	d.f	MS	F	P
Location (L)	3	902.49	18.67	0.00	3	993.29	25.01	0.00
Disturbance (D)	2	152.44	2.63	0.13	2	179.25	3.88	0.07
D * L	5	48.32	0.34	0.88	5	39.69	0.39	0.85
Error	16	141.82			16	102.12		

	Urocanic acid			
	d.f.	MS	F	P
Location (L)	3	28.92	4.04	0.08
Disturbance (D)	2	0.21	0.02	0.98
D * L	5	7.16	0.33	0.89
Error	16	21.95		

Paired t-tests results indicate undisturbed soils exhibit higher responses using eight of the 26 substrates and disturbed soil had a higher response in one. Carboxylic acids-- hydroxybutyric (t_8=-1.8, p=0.06), L-tartic (t_8=-1.89, p=0.09) and quinic (t_8=-2.07, p=0.04) acids, amino acids: DL-histidine (t_8=-2.17, p=0.03), L-arginine (t_8=-1.47,

p=0.09), tyrosine (t_8=-1.48, p=0.09) and L-serine (t_8=-2.20, p=0.03) and a polymer, cyclodextrin (t_8=-2.47, p=0.02)--when added to soils produced greater responses in undisturbed versus disturbed soils. One carboxylic acid, malonic acid (t_8=-2.35, p=0.02) produced a higher respiratory response on disturbed soils (Fig. 3.6).

The PCA analysis of the SIR responses again shows a similar pattern as the soil enzyme data (Fig. 3.6). Undisturbed sites show the widest spread across the two axis, and there is very little clustering of points by either disturbance or location. The first two principle components (PC) explained 82.38% of the variation in the data.

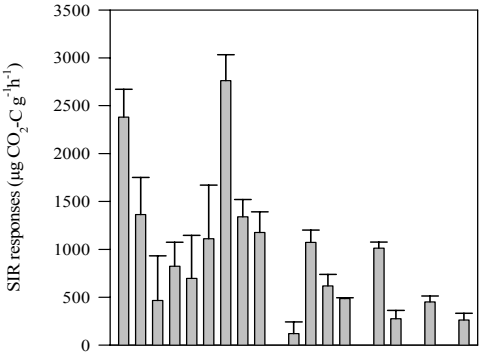
Nitrogen Mineralization

Total available N, measured as the sum of available NH_4^+ and NO_3^- (µg per capsule), was significantly higher on disturbed versus undisturbed soils (t_6=-3.32, p=0.01, 253.89 and 101.07, respectively). Disturbed soil had significantly higher NH_4^+ (t_{df}=-1.81, p=0.06, 62.18 vs. 25.18 µg) and NO_3^- (t_6=-2.68, p=0.018, 191.72 vs. 75.89 µg) than undisturbed.

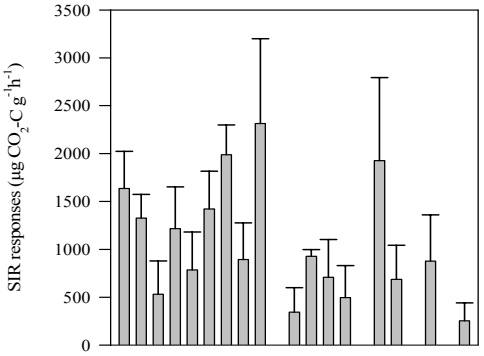
Table 3.2. Total mineralizable N (mean ± 1 SE) measured with ionic resin capsules (UNIBEST, USA), reported in µg/capsule, for each location and disturbance type. NA signifies a lack of a restored treatment at Emerald Lake and inability to locate capsules at Heart Lake.

Location	Disturbed Total N (µg/capsule)	Undisturbed Total N (µg/capsule)	Restored Total N (µg/capsule)
Emerald Lake	242.91±119.36 (n = 3)	44.43±34.23 (n=3)	—
Heart Lake	45.51± 32.31 (n=2)	na	14.88 (n=1)
NOCA	74.12±6.23 (n=2)	169.06±123.54 (n=3)	216.19±108.57 (n=5)
MORA	129.58±39.01 (n=8)	45.74±14.31 (n=5)	435.84±185.07 (n=6)

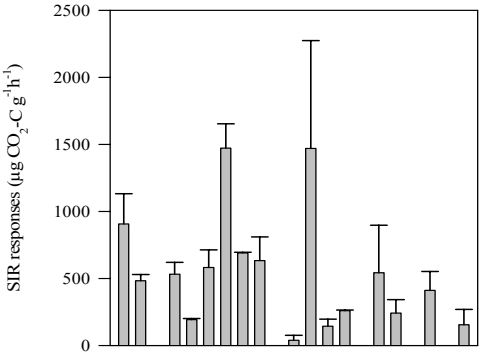
Heart Lake, MT Undisturbed



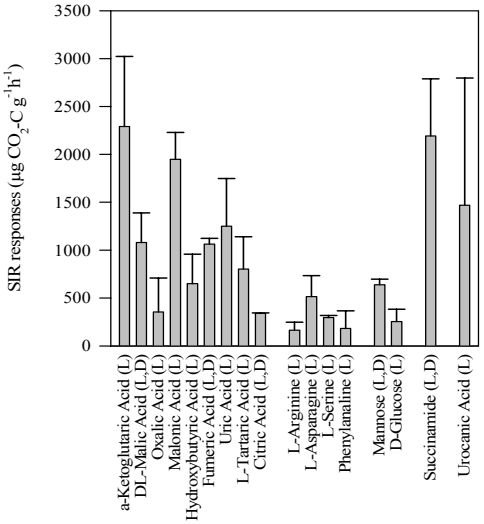
Emerald Lake, MT Undisturbed



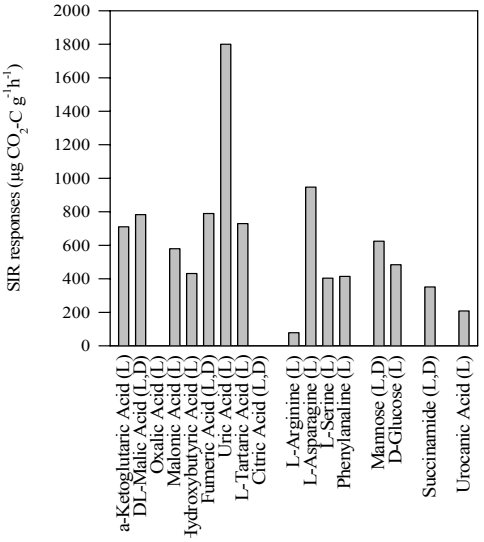
Heart Lake, MT Disturbed



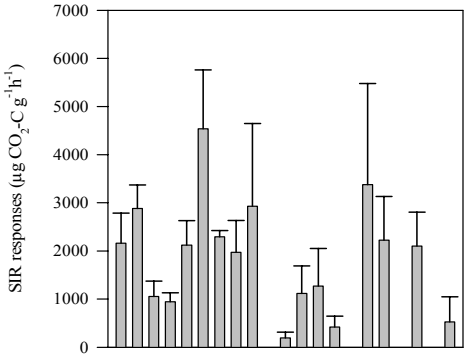
Emerald Lake, MT Disturbed



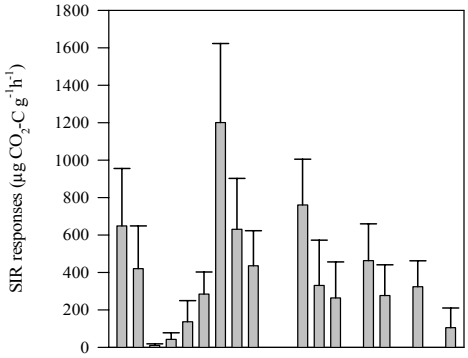
Heart Lake, MT Restored



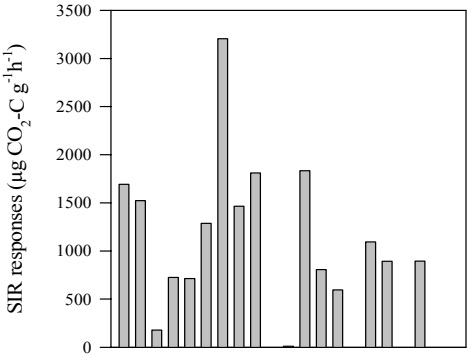
NOCA, WA Undisturbed



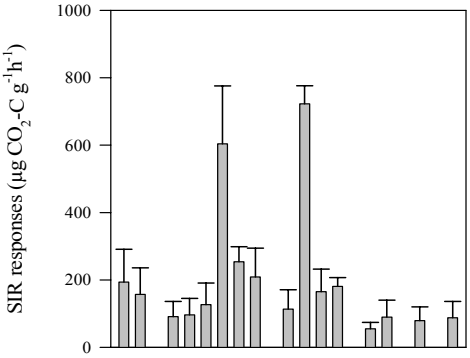
MORA, WA Undisturbed



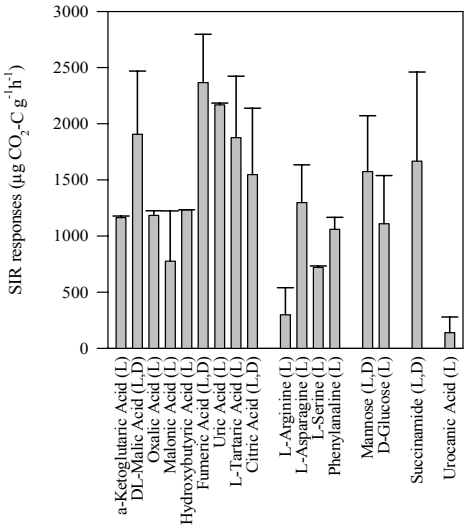
NOCA, WA Disturbed



MORA, WA Disturbed



NOCA, WA Restored



MORA, WA Restored

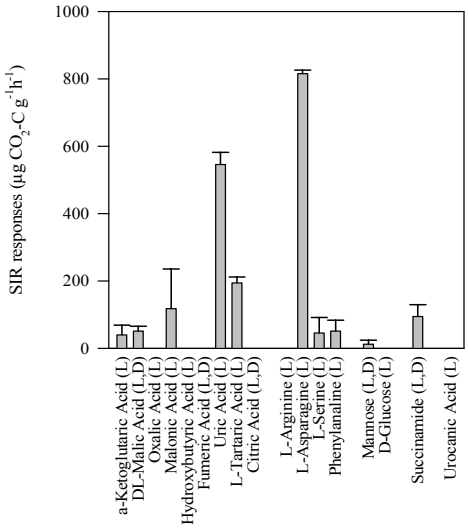


Fig. 3.6. (pages 70-71) SIR responses for analysis of variance of 17 of the 26 substrates used that exhibited a significant disturbance or location response at all locations. Significant differences are located in parenthesis for location (L) and disturbance (D).

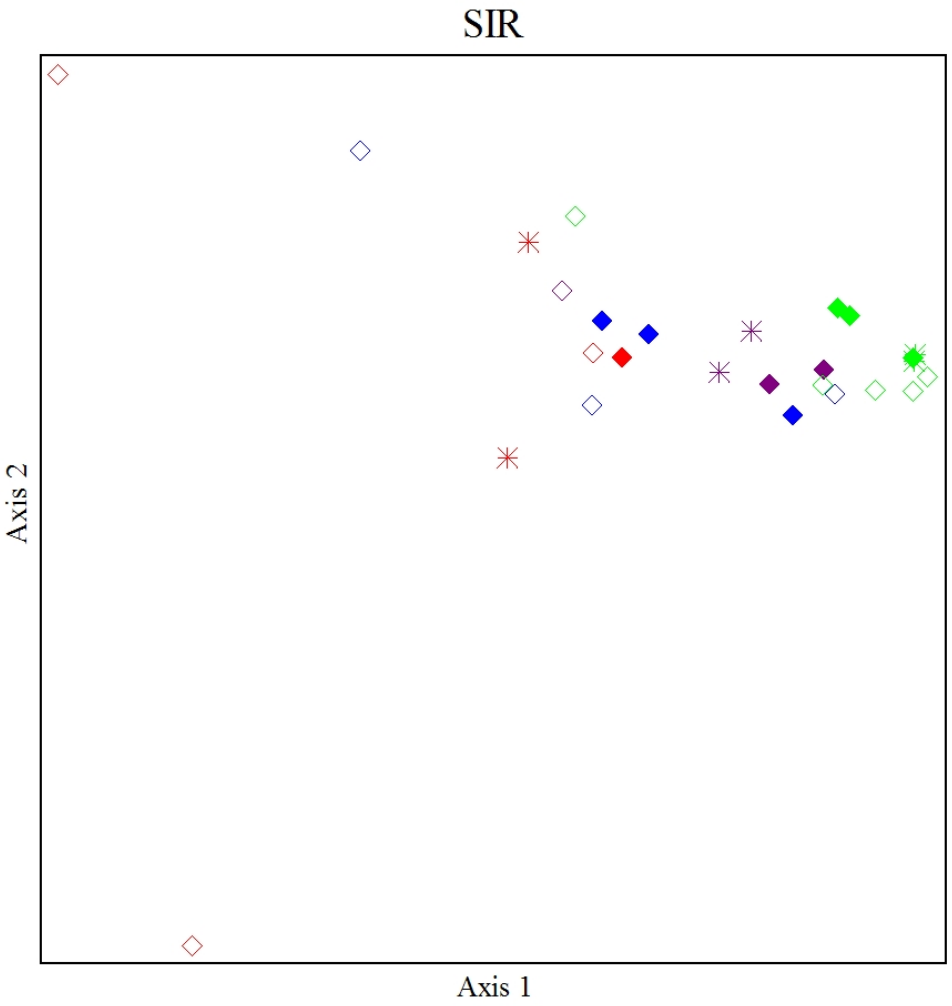


Figure 3.7. Results from principle components analysis (PCA) on substrate induced respiration (SIR) responses. Variable are separated by location (color: red=NOCA, green=MORA, blue=EL and purple=HL) and disturbance (shape: open diamond=undisturbed, closed diamond=disturbed and asterisk=restored).

DISCUSSION

Mycorrhizal Infectivity Potential

Mycorrhizal fungi are an integral part of the soil microbiota, with almost all families of vascular plants containing species that form at least one type of mycorrhizae (Newman and Reddell 1987). The relative abundance of AM fungal propagules was low at all locations, regardless of disturbance type. This is likely a result of a lack of AM plant species. *Vaccinium* species dominate the undisturbed understory at most of the sites. *Vaccinium*, and other ericaceous plant species, form a specific symbiosis, called ericoid mycorrhizae (Goulart et al. 1993). Ericoid mycorrhizae are often more prominent in higher altitude systems (Smith and Read 1997), and unlike AM fungi which influence P uptake, ericoid mycorrhizae may be most important in the uptake of N (Goulart et al. 1993). Ericoid mycorrhizae stain differently, produce finer hyphae (Smith and Read 1997) and do not form a mycorrhize with grass species, so they would not show up in my MIP assays.

Disturbance may cause a reduction or loss of mycorrhizal fungi (Allen et al. 1984, Allen et al. 1987). Recreation-impacted sites are devoid of vegetation, eliminating host plant roots and contributing to an overall lack of infective propagaules. However, I did not measure disturbance effects on AM propagules, in part because mycorrhizal infectivity rates were so low on undisturbed soils. It is questionable whether a shortage of mineral nutrients at high altitudes explains the small size and slow growth of alpine plants (Korner 2003), it could explain a deficiency in plant-fungal symbiosis. In an already limiting environment a plant may abstain from forming mycorrhizae in order to

conserve C for its own vegetative production. Plants are already slow growing, and relatively small in these systems, making biomass and C transfer more important then P uptake, for instance. MIP may be an indicator of disturbance intensity, especially in systems where colonization rates are higher, such as meadows and grasslands.

While AM infectivity was low, non-AM fungal colonization occurred in up to 43% (HL, restored) of the root intersections. Non-AM fungi may affect plant growth by some of same mechanisms as AM fungi, in terms of soils properties. While not as important in nutrient and water uptake, non-AM fungi may increase soil water infiltration and contribute to SOM. Non-AM fungi may also interact with other organisms in the soil, either as parasitic pathogens, damaging host species, or non parasitic saprobes, obtaining nutrients from the degradation of non-living SOM.

Mycorrhizae are an important consideration for revegetation since plant survival, growth and community composition can be affected by AM (van der Heijden et al. 1998). Mycorrhizae have been shown to benefit vegetative growth in reclaimed mine waste (Stahl et al. 1988, Moynahan et al. 2002). Native AM fungi effectively forming mycorrhizae in severely disturbed soils may increase seedling growth and establishment, especially when surface soils are mixed with subsurface soils that may contain little or no mycorrhizal inoculum (Allen and Allen 1980, Stahl et al 1988). However there is little information about their effects on restoring recreation disturbed soils in high elevation systems.

Cripps and Eddington (2005) suggest the prevalence and diversity of mycorrhizal symbiosis could also be indicators of the health and sustainability of plant communities, however my results suggest a more thorough inventory of mycorrhizal species may be

necessary to determine which species are present and their responses to recreation disturbance. Depending on plant communities present, severity of disturbance and soil chemical and physical properties, mycorrhizal fungi may already be present or not imperative to establishing vegetative communities on these soils due to their already low abundance in undisturbed soils.

While a positive correlation between AM fungal colonization and increased plant diversity has been documented (van der Heijden et al. 1998), others have been unable to identify any effect of soil inoculation on both AM and ectomycorrhizal colonization (Hedlund and Gormsen 2002). It has also been suggested that mycorrhizae are especially beneficial in the reclamation of arid regions (Allen and Allen 1980), however mycorrhizal grass species are often dominant in these systems in undisturbed soils. My data suggests that AM species may not be the most severely impacted characteristic following disturbance. AM may not be present in high elevation in abundance even in undisturbed systems. The question of whether mycorrhizal fungi are negatively impacted by recreation disturbance in high elevation areas may be answered more thoroughly by investigating other mycorrhizal relationships, most notably, ericoid mycorrhizae. While disturbed soils are devoid of host plant and AM infective propagules, perhaps this is not the case for other fungal species. My data suggests AM inoculum would not be the most efficient restoration amendment in these scenarios, due to lack of AM plant species and the low abundance of AM already present in undisturbed soils.

Decomposition

Decomposition is the second largest flux in the global cycling of organic matter, next to primary production itself (Sterner and Elser 2002), and is an important component of the global carbon budget (Aerts 1997). Decomposition is critical to mineralization and nutrient cycling in ecosystems. The decomposition of plant litter influences build up of SOM, release of nutrients for plant growth, and flux of CO_2 from soils (Wardle et al. 2003). Because decomposition serves as an integrator of the collective activities of organisms within the soil food web, it may be a potential indicator of soil condition (Neher et al. 2003), reflecting the impacts of disturbance on soil microbial communities. The rate of decomposition is a function of many characteristics and processes, including chemical composition or quality of the organic material, temperature, moisture and the composition of the decomposer community. Decomposition rates may signal either a change in decomposer communities or a shift in the condition of biotic or abiotic resources at a site (Neher et al. 2003).

Mass remaining generally decreased linearly through time regardless of location or disturbance. Decomposition on my sites did not differ significantly between disturbance, however some litter bags lost up to half their mass after 12 mo. Neher et al. (2003) found disturbance affects the decomposition of balsa wood but not museum board. In agricultural and wetland soils, museum board decomposition is greater initially in disturbed vs. undisturbed soils. However disturbance has no effect on decomposition of museum board in forest soils (Neher et al. 2003). At my sites, decay rates of museum board overall were greater then balsa wood, similar to Neher et al. (2003). Museum board is predominantly cellulose, a labile substrate, which is the main carbohydrate

constituent of plant call walls and is decomposed by a wide variety of microorganisms (Paul and Clark 1996). Balsa wood is predominantly lignin, an aromatic compound, one of the most resistant compounds in plant litter that only specialized organisms can breakdown (Neher et al. 2003). I hypothesized the museum board would reflect differences in decomposition initially while balsa wood would reflect differences as time elapsed.

Decomposition rates varied greatly at all sites and were not affected by disturbance at my sites. Decomposition may not be as sensitive an indicator to disturbance in my systems as previously suggested. Variation in environmental factors, including soil moisture, temperature and available minerals (Kowalenko et al. 1978), may be driving decomposition rates instead of disturbance regimes. Meentemeyer (1978) attributes the combined climatic energy and litter moisture as the basic regulators for the rates of decomposition. Moore et al. (1999) found decomposition to be most strongly correlated to mean annual temperature in Canada while in British Columbia, Prescott et al. (2004) found average precipitation to be most important. From an ecosystem perspective the process of litter decay is critical for maintaining site fertility and productivity. My results suggest decomposition rates after 3, 12 and 24 mo are not sensitive to recreation disturbance, or are too heterogeneous to be quantified over a relatively short period of time. Decomposer communities may be present in soils regardless of recreation impacts and considering decomposition rates when designing restoration protocol may be unnecessary.

Soil Enzymes

The functional capacity of the soil microbial community is reflected in the activities of soil enzymes involved in the release of N, P and C to the soil solution (Kourtev et al. 2002, Boerner and Brinkman 2003). All biochemical reactions are catalyzed by enzymes and nutrient cycling in soils involves biochemical processes mediated by microbes and soil animals (Tabatabai 1982). Many factors affect enzyme activities in soils including disturbance, soil amendments, and seasonal environmental variability (Tabatabai 1982, Moorhead et al. 1996). Aon and Colaneri (2001) suggest enzymatic activities are potential indicators of soil stress to management practices and that the perturbation of the sensors may provide insight into soil degradation compared to other slowly changing soil properties, such as SOM and decomposition. They found strong correlation between total nitrogen and soil moisture and enzyme activities. While enzyme activities in agricultural systems follow these patterns, responses to disturbance in alpine and subalpine systems are unknown.

I monitored the activities of eight enzymes involved in the release of C, N and P and those and the degradation of SOM (Kourtev et al. 2002). I hypothesized enzyme activity would be lower on disturbed sites due to lack of vegetation, reduced SOM and soil moisture and increased compaction. Previous studies indicate that compacted soils exhibit reduced microbial activity due to decreased pore space and reduced soil moisture, however these studies measured only a few microbial properties including carbon utilization (Zabinski and Gannon 1997) and acid phosphatase activity (Dick et al. 1988). Soil compaction is generally thought to decrease soil respiration and enzyme activity (Jordan et al. 2003).

I expected lower activities of both acid phosphatase and β-glucosidase due to reduced SOM on disturbed soils, however acid phosphatase (activity substrate/g soil/hr) was the only enzyme that differed significantly between disturbance, with undisturbed soils having higher activity the disturbed soils (ANOVA and paired t-test). Higher activities (activity substrate/g soil/hr) of chitinase (3), glycine aminopeptidase, β-glucosisdase and cellobiohydrolase were nearly significant on undisturbed vs. disturbed soils (paired t-test). This is consistent with Dick et al.'s (1988) findings of decreased acid phophatase activity in disturbed soils in west-central Oregon. Reduced enzyme activity could indicate altered SOM quality (Boerner and Brinkman 2003) and/or reduced microbial biomass (Nannipieri et al. 1993). Acid phosphatase is important in soil organic P mineralization and plant nutrition (Tabatabai 1982) and is strongly correlated with the rate of release of both inorganic N and P to the soil solution (Boerner and Brinkman 2003). Acid phosphatase shows optimum activity and is predominant in acidic soils. The levels of acid phosphatase activity I observed were an order of magnitude greater then activities reported in temperate forest systems in Ohio by Boerner and Brinkman (2003) and in low elevation forest soils in New Jersey by Kourtev et al. (2002). There was no difference between disturbed and restored soils.

When enzyme activity was corrected for SOM, by calculating it activity/g OM/hr, there were no significant differences between disturbed and undisturbed soils. Higher chitinase (3) activity was nearly significant on undisturbed vs. disturbed soils, similar when reported as activity/g soil/hr (ANOVA). Paired t-tests comparing disturbed and undisturbed enzyme activity, expressed as activity/g OM/hr, however, resulted in significantly higher activities on undisturbed sites for acid phosphatase, leucine and

glycine aminopeptidase and cellobiohydrolase. Higher activities of phenol oxidase and chitinase (3) and on undisturbed vs. disturbed soils were nearly significant.

There are location differences between acid phosphatase, β-glucosidase, leucine and glycine aminopeptidase and cellobiohydrolase (ANOVA). Acid phosphatase and glycine amino peptidase activity are highest overall at NOCA where the highest level of SOM was also observed.

Strong correlations have been made between changes in microbial biomass and acid phophatase activity (Nannipieri et al. 1983, Kandeler and Eder 1993). Dick et al. (1998) showed soil phosphatase activity is reduced in compacted forest sites in Oregon while microbial biomass carbon is unaffected or decreased depending on environmental factors. Tillage of compacted soil has been effective at increasing phophatase activity (Dick et al. 1988) by improving aeration and water infiltration. Jordan et al. (2003) also showed soil compaction decreased acid phosphatase activity. Boerner and Brinkman (2003) found fire disturbance lowered acid phophatase activity, however because SOM was not reduced significantly they attributed reduced activities to OM quality rather than quantity. Nannipieri et al. (1983) initially linked increased phosphatase activity with increased microbial biomass, however, while microbial biomass has increases initially when treated with organic substrates, eventually activity in treated soil decreased to the level of the untreated control soil. While not measured directly, I expect microbial biomass may be reduced in disturbed soils due to strong correlations between it and enzyme activity illustrated by Nannipierie et al. (1983) and Kandeler and Eder (1993). Also, it appears activity is related to SOM, as activity of 6 out of 8 enzymes were highest at NOCA, although not all were significant (Fig 3.4).

Glucosidases are widely distributed in nature and have long been detected in soils. β-glucosidase is the third enzyme in the chain of three which breakdown labile cellulose and other carbohydrate polymers (Boerner and Brinkman 2003) and is widely distributed in fungi and is a dominant glucosidase present in soils. The hydrolysis products of β-glucosidase are believed to be important energy sources for microorganisms in soils (Tabatabai 1982). Bandick and Dick (1999) suggest β-glucosidase assays are useful in reflecting soil management effects. Caldwell et al. (1999) found β-glucosidase activity is the most sensitive indicator of vegetation disturbance in lowland Costa Rican soils, however they contest soil type may have accentuated the vegetation treatment with greater activity reduction in acidic, highly weathered soils. Glucosidase activity may reflect differences in SOM residues present. β-Glucosidase differed between location (activity/g soil/hr), with the highest activities measured in undisturbed soils from NOCA. β-Glucosidase activities did not differ between disturbance suggesting the communities responsible for its role in the C cycle are either present in soils in similar abundance and/or are less susceptible to perturbation at my sites.

I also examined the activity of other enzymes important in the cycling of C and N and the breakdown of SOM. While the activities of these enzymes did not differ significantly between disturbance, I discuss their importance briefly. Chitinase (chitobiase) is the second enzyme in the chain of three which breakdown chitin and release C and N rich compounds (Boerner and Brinkman 2003). Niemi et al. (2005) found chitinase activity to be strongly affected by the time of sampling, with the lowest activities measured during the summer. Increased chitinase activity may indicate a fungal based mineralizer community vs. one dominated by bacterial communities. I

measured chitinase activity with 2 substrates, both exhibiting a similar trend in activities however neither were significantly different between disturbance or location, although paired t-tests resulted in nearly significant higher activity in undisturbed soils, likely due to the high response observed at HL (Fig. 3.4). The levels I measured were an order of magnitude higher then those measured by Vepsalainen et al. (2001) and Kourtev et al. (2002), potentially indicative of a fungal dominated system or reflective of the time of sampling with chitinase activities often higher in the spring (Vepsalainen et al. 2001), when I sampled. I found low MIP in all soils, disturbed and undisturbed, while not necessarily indicative of a non fungal based community, could suppress differences in disturbance types.

Phenol oxidase plays an important role in incorporating phenolic compounds into humus components (Skujins 1976). Phenol oxidase is one of many enzymes involved in the degradation of lignin (Boerner and Brinkman 2003). Both a decreased β-glucosidase and acid phosphatase activity and increased phenol oxidase actually could indicate a soil system dominated by recalcitrant organic matter forms, and a reduction in organic matter quality (Boerner and Brinkman 2003). While this may be expected in high elevation systems, I did not observe a significant increase in phenol oxidase activity, however on undisturbed sites increased activities were observed (activity/g OM/ hr) but not significantly.

Cellobiohydrolase is involved in the degradation of cellulose, chitin and polyphenolic substances. Niemi et al. (2005) found cellobiohydrolase is sensitive to soil compaction and low SOM, and to be most abundant in surface soils. Paired t-tests

resulted in cellobiohydrolase activity being significantly higher on undisturbed sites when expressed as activity/g OM/ hr and nearly significant when expressed as activity/g soil/hr.

Aminopeptidases are N-related enzymes and their activity is inversely proportional to N availability (Kourtev et al. 2002), suggesting I may observe a change in activity due to recreation disturbance effects on soil N. Both leucine and glycine aminopeptidase differed significantly by location, as did SOM. The highest activities were recorded in soils from NORA, which had the highest OM levels. Both were significantly reduced in disturbed soils when analyzed as activity/g OM/hr and (Table 3.5) glycine aminopeptidase was nearly significant using a paired t-test expressed in activity/g soil/hr. Aminopeptidase activity depends strongly on the time of sampling, with the greatest activities at the end of the summer season (Vepsalainen et al. 2001) potentially concealing differences between disturbance types.

The lack of significant differences between disturbance in the activity of most enzymes may suggest the organisms responsible for the production of these enzymes, and the activities of the enzymes themselves, are less susceptible to disturbance. Enzyme activities are highly correlated and depend strongly on SOM breakdown. This is evident when activities are expressed per g OM, and become even more apparent when analyzed using the paired t-test. While most were not significantly higher in undisturbed soil when analyzed with the ANOVA four were nearly significant when expressed as activity/g OM/hr. The reduced SOM on disturbed sites is reflected in reduced enzyme activity. This is in agreement with numerous other studies (Niemi et al. 2005, Tabatabai 1990, Degens et al. 2000) that suggest enzyme activity is driven by SOM. Boerner and

Brinkman (2003) suggest that OM quality may be more influential on enzyme activity than SOM itself, however I did not directly measure SOM C and N ratios.

Dust from roads, oil drill pads and other construction activities reduced enzyme activities in tundra systems in Alaska, while altering soil physical-chemical characteristics, and potentially decomposition and nutrient mineralization processes (Moorhead et al. 1996). Enzyme activity was higher in continuous grass fields versus cultivated fields and in cultivated fields, activities were highest in areas where cover crops or organic residues were added as compared to treatments without organic amendments (Bandick and Dick 1999). Soil microorganisms play key roles in determining the structure and function of plant communities (Wardle 2002) and understanding soil function is required to provide strategies and approaches for land resource manager to promote long term ecosystem sustainability (Aon and Colaneri 2001).

Some aspects of microbial function are negatively affected by recreation disturbance and changes in soil properties such as decreased porosity, aeration, and water infiltration (Dick et al. 1988). Enzyme activity may be related to OM quality, which I didn't measure, but I did see little difference in soil nutrients between disturbance and decomposition. Enzyme activity measurements have been increasingly used to investigate changes in microbial functions due to disturbance (Dick 199, Vepsalainen et al. 2001). My results indicate enzyme activity can be used to examine elements of the SOM decomposition and relationships between enzyme activities, decomposition processes, and belowground nutrient dynamics (Moorhead et al. 1993). However, enzyme responses may be confounded by time of sampling (Tabatabai 1982, Moorhead

et al. 1996,Vepsalainen et al. 2001). Decomposition rates were relatively insensitive to recreation disturbance, however this may have more to do with to short an incubation, slow decomposition in alpine systems in general and abiotic factors I did not measure. Principle components analysis for soil enzymes separated substrates more clearly by location then by disturbance (Fig. 3.6). This is supported by evidence that microbial communities differ depending on plant species.

Substrate Induced Respiration (SIR)

SIR was the second physiological method used to asses the catabolic diversity of soil microbial communities in disturbed, undisturbed and restored soils. Organic substrates were chosen from 4 major chemical groups (Table 3.3), previously screened for concentration and incubation times by Degens and Harris (1997). Microbial community response differed for 17 of the substrates between location, and 5 substrates between disturbance types. Response to the carboxylic acid group was most sensitive with 14 substrates from that group differing by location, 3 of which also differed by disturbance type. Similar to enzyme assays, SIR responses separated soils by location more effectively than by disturbance (Figure 3.6). Paired t-tests indicate undisturbed sites showed higher respiration than disturbed sites for the majority of substrates differing by disturbance (carboxylic acids: hydroxybutyric acid, L-tartaric acid, quinic acid; amino acids: DL-histidine, L-arginine, DL-tyrosine, L-serine and a polymer, cyclodextrin), disturbed sites were greater than undisturbed for one substrate (malonic acid) and greater than restored for one substrate (ketoglutaric acid). Degens and Harris (1997) found the highest and most variable response to carboxylic acid additions in soils under different

agricultural management. However, due to the large number of t-tests conducted to compare the 26 different substrates tested, the power of this analysis is questionable and the discussion will only include the results obtained from the ANOVA.

Soils from MORA had lower activity than the other locations, while soils from NOCA had the highest responses recorded. While the SIR technique I employed has previously been useful in distinguishing changes in catabolic diversity over short periods of time, as well as large differences developed over many years (Degens and Harris 1997), this was tested in agricultural systems. It appears in my systems, while undisturbed soils exhibit higher responses for a number of enzymes, the technique was most effective at distinguishing between location differences and moderately effective at distinguishing between disturbance type.

Small changes in microbial communities between disturbed, undisturbed and restored high elevation soils could potentially be detected using a larger range of substrates in the assay. Degens and Harris (1997) suggest using less than 36 substrates may compromise the capacity to detect differences in catabolic diversity between soils. This was not possible due to the large number of samples and the relatively short period of time between sample collection and incubation, using more substrates may have compromised the integrity of some of the samples. Stronger response differences between location then between disturbance suggest that physical and chemical soil properties between soils types probably have a greater influence on SIR then differences in SOM and disturbance (Degens and Harris 1997).

Decreases in the diversity of soil organisms may cause declines in the resistance of soils to disturbance (Brussard et al. 1997, Degens and Harris 1997). Degens et al.

(2001) found soils with reduced catabolic evenness (uniformity of substrate uses) were more susceptible to disturbance than soils with greater catabolic evenness Restoration of disturbed systems requires a stable and productive soil with a self-sustaining plant/soil system in which nutrient release rates are adequate for sufficient plant growth (Bentham et al. 1992). Harris and Birch (1989) followed changes in soil at sites reclaimed after opencast mining by enzyme assay and measuring nitrifying potential, and found increases in both over time. Degens and Harris (1997) saw an overall decline in SIR responses with greater cropping intensity which was also reflected by a general decrease in microbial biomass. Zabinski and Gannon (1997) compared carbon utilization profiles between heavily impacted subalpine campsites and adjacent undisturbed area and found decreased functional diversity on impacted versus non-impacted. Degens et al. (2000) saw greater catabolic evenness in soils under pasture compared to soils under cropping which they attribute mainly to a depletion of organic C, possibly due to a reduction in quality of OM in those soils. Previous research has demonstrated that the quality of soil can in fact be assessed by measuring characteristics of the microbial communities present and these measurements enable us to characterize the state of degradation and effects of management aimed at restoring ecosystem structure and function (Harris 2003). Bentham et al. (1992) concluded that the size, activity and composition of the soil community are characteristic of habitat type and changes occurring within the communities of restored soils, with time, also appear to be consistent with habitat type. It is however also possible that catabolic diversity may be a more stable property of microbial communities (Degen and Vojvodic-Vukovic 1999), suggesting it is less sensitive to impacts associated with recreation. Still the implications of decreased

catabolic evenness is relatively unknown (Degens et al. 1999), especially in high elevation soils. It does however show potential as an indicator of disturbance effects on soil communities, suggested by differences between a number of undisturbed and disturbed soils at my sites.

Nitrogen-mineralization

Nitrogen (N) is often the main nutrient limiting plant growth (Hart et al. 1986). In natural ecosystems, most N absorbed by plants becomes available through the decomposition of OM (Chapin et al. 2002). A soil's capacity to transform organic N to inorganic N, its nitrogen mineralization potential, is often used as an index of the N available to plants in terrestrial ecosystems. In ecosystems of cold climates the majority of organically bound plant nutrients are incorporated in SOM (Makarov et al. 2003). Soil organic matter increases with altitude, commonly reaching a peak in montane forests and lower alpine zones due, in part, to reduced microbial activity (Korner 2003) and lower decomposition rates. Therefore, despite the relatively large amounts of total N, the concentration of available inorganic N is relatively low and N availability is a major factor regulating primary plant production and community composition in ecosystems in cold climates (Makarov et al. 2003).

One of the most significant changes in resource dynamics caused by anthropogenic activity is the alteration of the N cycle (Vitousek 1994, Evens and Belnap 1999). N cycle alteration can cause changes in soil quality in turn affecting vegetative communities and ecosystem sustainability. The mineralization potential of a site often reflects site fertility and is closely related to the labile soil organic matter pool and the

activity of soil organisms (Robertson et al. 1999). Nutrient mineralization is largely regulated by soil organisms (Tamm 1991). Soil conditions including microbial community structure, nutrient availability have been shown to be adversely affected by recreational use (Zabinski and Cole 2000), however responses are varied.

Nitrogen mineralization was significantly higher on disturbed versus undisturbed soils at my sites, as I hypothesized. Decreased rates of N mineralization have been reported in compacted agricultural soils (Whilser et al. 1965). While soil compaction can decrease microbial activity, and soil N due to less immobilization by microbial populations (Jordan et al. 2003), my results do not support these findings. Disturbed sites in my systems exhibit higher available N, possibly due to lower plant cover and decreased plant uptake in these soils.

Kaye and Hart (1998) found restoration treatments including thinning and removal of trees, native plant litter incorporation and a prescribed burning increased N mineralization by 2-3 times that of non restored soils. While restoration can increase the rate of N mineralization, it may not be a parameter that needs to be addressed directly at the sites I studied. While microbial communities are potentially impacted by recreation disturbance, N mineralization does not seem to be. My results suggest that while significant decreases in SOM have occurred in recreation areas where soils have been trampled (Marion and Cole 1996, Grieve 2001) or compacted, this is not reflected in mineralizable N over a 12 mo period at my sites.

Differences in microbial communities and ecosystem processes differed more by location than by disturbance, suggesting recreation disturbance effects are not as severe on some ecosystem components as originally hypothesized. The parameters not affected

by disturbance were MIP and decomposition. MIP was low everywhere, regardless of disturbance or location, likely due to lack of AM plant species present at these sites. Decomposition rates varied by disturbance and location, however no significant patterns were observed. Prescott (2005) suggests insights into nutrient cycling and C storage in ecosystems are more likely to arise from measuring the mass and nutrient storage of annual litter inputs than by measuring early rates of decay. The effects of litter morphology and chemistry, and abiotic (temperature and moisture) and biotic factors (biological trophic levels present to aid in organic matter breakdown) make decomposition an important but difficult process to reestablish following a disturbance (Coleman 2001).

Disturbance significantly affected both enzyme activity and SIR responses. Recreation effects varied, with a subset of the total number of substrates affected. Enzyme assays proved to be more useful in distinguishing between disturbed and undisturbed sites. Both soil enzyme activities and SIR responses appeared to separate soils by geographic location more effectively than by disturbance. Nitrogen mineralization was higher on disturbed sites, likely due to lack of plant uptake on disturbed sites.

Microbial communities play integral roles in developing self sustaining communities, however it is still questionable whether or not they need to be considered in restoration practices in high elevation systems. Native soil slurry addition and the incorporation of soil plugs may facilitate microbial dispersion from undisturbed soils. Mixing undisturbed topsoil with mineral soil from disturbed sites may also increase microbial activity and propagule availability. Nutrient availability for plants is not an

issue on these disturbed sites, N mineralization is greater on disturbed sites suggesting the N needed for plant growth is available and, once plants are established, is available for plant uptake. Monitoring MIP and decomposition in these systems is not a big concern. Both were not significantly affected by disturbance. MIP was low and decomposition varied widely between location, disturbance type and substrate. Enzyme assays did reflect disturbance impacts and may be a useful tool for assessing recreation and other impacts on microbial communities. Depending on SOM inputs and abiotic factors at different sites substrates should be chosen carefully, however one may not need a large set of substrates to obtain useful information regarding microbial function. Acid phosphatase, β-glucosidase and chitinase are three enzymes that have been shown to respond to disturbance and are essential in the cycling of nutrients in many terrestrial systems. Measuring SIR responses is tedious and the usefulness of its measure in disturbed alpine systems is still in question. A larger set of substrates and soil samples may lead to more significant differences between disturbance types. Nitrogen mineralization is crucial for developing sustainable plant communities, and mineralization rates is simple to measure and relatively inexpensive. Information pertaining to mineralization rates over a growing season on disturbed sites could alleviate the expenses associated with unnecessary fertilizer application.

While microbial communities are affected by disturbance, often negatively, with unimpacted areas nearby, the scale of recreation disturbances is relatively small, and there is a large amount of heterogeneity belowground. Perhaps functional components of high elevation soil systems are adversely affected, as previously suggested, such as soil enzymes and SIR, while other components are more resistant. The rigorous nature of

alpine environments, coupled with the impacts of disturbance and often limited chemical and biological processes, pose a number of challenges when restoring high elevation soils. In general, my study shows that soil processes are mostly intact on recreation impacted soils.

CONCLUSIONS

Mountain environments belong to some of the most endangered ecosystems in the world (Broll and Keplin) and are highly valued for livestock forage, mineral and timber assets and recreation opportunities (Urbanska and Chambers 2000), as well as serving as vital watersheds, unique plant and animal habitat, and long-term global carbon and nutrient storage (Urbanska and Chambers 2000, Prichard et al. 2000). Recreation use in alpine and subalpine regions is rapidly increasing (Macyk 2000), and these areas will undoubtedly receive increased pressure as human populations and activities continue to expand (Chambers 1997). Increased use is particularly notable on severely disturbed sites, and results in major ecological changes, including reduced soil organic matter (SOM), vegetation loss and increased soil compaction and erosion (Cole 1986, Zabinski and Gannon 1997). Studying recreation impacts in high elevation areas presents a useful opportunity to study disturbed effects on soil physical, chemical and biological components on a feasible scale.

I examined the effects of recreation disturbance on the physical, chemical and biological components of soils in high elevation systems in Montana and Washington. I hypothesized: 1) recreation disturbance would impact soil physical characteristics by decreasing SOM and soil moisture and increasing soil bulk density; 2) soil chemical properties would differ on undisturbed, disturbed and restored sites, specifically, total N would be higher on undisturbed sites, however the direction of the other changes were unclear; 3) soil microbial function would be affected, specifically, MIP would decline with disturbance because live plants are absent on disturbed soils, decomposition rates

would differ, although arguments could be made for either an increase or decrease in rates, between disturbed, undisturbed and restored soils, and enzyme activity and microbial catabolic diversity, or evenness of substrate utilization would decrease with disturbance. Lastly, I hypothesized mineralizeable N would be higher in disturbed soils compared to undisturbed, due to decreased plant uptake.

Disturbed sites had decreased soil moisture, SOM and total N and increased compaction, indicated by significantly higher bulk densities. NO_3^-, NH_4^+ and P were not affected by disturbance while K was higher on disturbed sites. Differences in microbial processes were more apparent between location then by disturbance type. MIP was low regardless of disturbance or location, likely due to a overall lack of AM plant species present at my sites. Non-AM infectivity was higher on undisturbed soils, however the ecological significance of this is unclear. Decomposition rates differed by location but not by disturbance for the 3, 12 and 24 mo incubation times. Enzyme activity was significantly lower on disturbed sites for one substrate, acid phosphatase and nearly significant for 4 when expressed as activity/g soil/hr. Activity was significantly lower for 5 substrates and nearly significant for 2 when expressed as activity/g OM/hr. This may suggest enzyme activity may be more closely related to OM quality and not quantity, a variable I did not measure. SIR responses were lower on disturbed sites for 6 substrates; 4 carboxylic acids, 1 carbohydrate and 1 amine. N mineralization rates were higher on disturbed vs. undisturbed sites.

All of the disturbed sites I studied were devoid, or nearly devoid, of vegetation and soils visually appeared heavily impacted. Some of my results support the assumption that soil processes will be impacted on such disturbed sites while other processes seem

unaffected. Recreation disturbance had more severe effects on SOM, bulk density total N then other chemical and microbial functional characteristics. Perhaps from a microbial perspective these sites are not as severely degraded as originally thought. All my disturbed sites are relatively small (tens of meters) and surrounded by intact, undisturbed systems. So, while visually these sites appear heavily impacted, and in regard to some chemical and physical characteristics, this is true, impacts may be less severe on below ground communities.

Physical and chemical soil differences are more pronounced between disturbed and undisturbed than between undisturbed and restored. Bulk density on restored sites was significantly less than that of disturbed but no different than undisturbed. Soil moisture, SOM and total N were not significantly different between disturbed and restored sites. The only significant difference chemically, on restored soils, was soil K, which was lower on restored soil vs. undisturbed.

From a restoration perspective these results have a number of implications. To address compaction scarification may be adequate. However the beneficial effects of soil scarification in high elevation systems may only be temporary, due to heavy snow accumulation during winter seasons. To address decreased SOM and total N, OM additions may be necessary. OM additions can increase nutrient retention and decrease soil bulk density, however, SOM is one of the slowest components to recover following disturbance (Chambers 1997). Regardless, OM amendments should be added in a variety of size fractions, larger sizes to contribute to both soil physical structure, and smaller sizes to facilitate microbial breakdown. It is likely that the integration of amendments,

i.e., scarification and compost addition, will have the most pronounced effects on restoring soil physical and chemical parameters.

While microbial communities are affected by disturbance, most often negatively, effects varied with disturbance and by location. The scale of the disturbances I studied is relatively small, however there is a large amount of heterogeneity belowground. Perhaps some functional components of high elevation soils are adversely affected, as previously suggested, such as soil enzymes and SIR responses, while other components are more resistant to recreation impacts. Whatever the case, disturbance affects both physical and chemical characteristics of soil. Recreation impacts included loss of vegetation, decreased SOM, increased soil bulk density and a potential shift in below ground communities. Due to the heterogeneity of soil systems, both spatially and temporally, these impacts may vary in terms of severity.

Ecosystems have attributes that can be categorized into 2 main components, structure and function (Bradshaw 1997). A number of hypothetical pathways, or "trajectories", may exist that a disturbed system can follow during restoration (Bradshaw 1997, Zedler and Callaway 1999) (Fig. 1.2). In many systems ecosystem structure and function may recover more quickly in intact areas with less severe damages (Zedler and Callaway 1999). This could be true for recreation sites, which are relatively small in size, and surrounded by intact, undisturbed systems. Conversely, it is likely that restoration outcomes are nonlinear and are affected by abiotic and biotic factors. In high elevation systems climate may be the driving force. Restoration of certain ecosystem attributes, completely or partially, may be possible but it is more difficult to completely achieve original ecosystem structure and function (Bradshaw 1997). My results suggest that

ecosystem components, including soil physiochemical and biological components, i.e., bulk density, SOM, mycorrhizae, decomposition and microbial functional diversity (enzyme activity and SIR) are decoupled, responding differently, and individualistically, to disturbance. Perhaps some components can be returned to original conditions, others may not, and still others may exceed pre-disturbed condition. My research points out that ecosystem function is the result of many processes, some of which are not affected by disturbance, some of which recover following restoration, and some which do not recover. What effects these responses have on ecosystems function as a whole are still unclear.

While it is well know that lands disturbed by anthropogenic causes decreased in biodiversity, it is less well appreciated that there are also changes in nutrient cycling (Allen et al. 2002) due to altered soil microbial communities. Further research is needed to develop a better understanding of disturbance effects in high elevation systems. Some techniques developed for restoring alpine and subalpine systems appear successful, at least initially (Chamber et al. 1990, Zabinski and Cole 2000). Methods for restoring the structure and function similar to pre disturbance or adjacent native ecosystems are still poorly developed for areas with limited soil resources (Chambers 1997). Long term studies on restoration effects of restoration amendments on ecosystem function, such as decomposition, successional trajectories, and microbial system function after disturbance are still lacking. It is clear however that recreation disturbance negatively affects some high elevation ecosystem components while having little impacts on others. When restoring recreation impacted sites in high elevations areas, it is important to realize that

different components may not respond concurrently and instead, may respond differently to both disturbance and restoration.

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