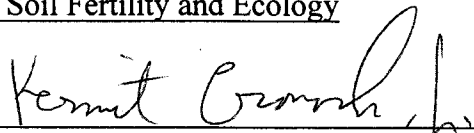


AN ABSTRACT OF THE THESIS OF

Emilie B. Grossmann for the degree of Master of Science in Forest Science. Presented on June 19, 2000. Title: Prescribed Fire in Eastern Oregon Ponderosa Pine Forests: Relationships between Soil Fertility and Ecology

Abstract approved: _____



Kermit Cromack, Jr.

I conducted two separate studies, both related to the impacts of spring and fall prescribed fire on ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.) forest soils in Eastern Oregon. The studies were either conducted at or linked to four stands of ponderosa pine, in the Malheur National Forest. Each stand received three treatments: spring prescribed burn, fall prescribed burn and no burn. For the first study, ion exchange resin bags were used to measure the relative concentrations of NO_3^- , NH_4^+ , Ca^+ , K^+ , PO_4^- , Na^+ , total P and total S in the soil solution under the three different treatments.

The second study focused on soil ecology and consisted of three projects: microarthropod feeding preference trials, microarthropod stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) as indicators of feeding habits and the role of microarthropod grazing in fungal competition. All arthropods and fungi used were either collected at the Eastern Oregon field sites or selected as representative species for ponderosa pine forest soils. Most microarthropods exhibited distinct feeding preferences in the feeding preference trials. Isotopic ratios (for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) suggested that different microarthropod species have distinct diets in the field. Isotope ratios appear to be indicators of trophic level for soil microarthropods. Fungal competition experiments indicated that microarthropod grazing can sometimes alter fungal competition and can therefore shape the fungal community.

Prescribed Fire in Eastern Oregon Ponderosa Pine Forests:
Relationships between Soil Fertility and Ecology

by

Emilie B. Grossmann

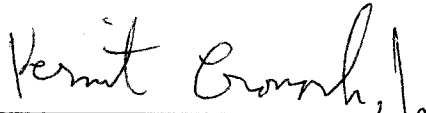
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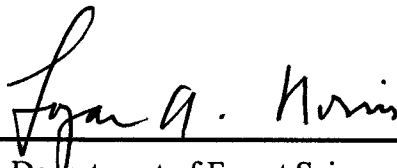
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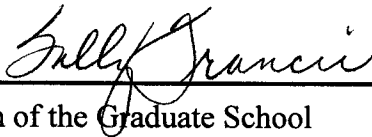
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Preface

One of the primary purposes of this project was to provide some basic science background for future applied science projects on the impacts of prescribed fires on ponderosa pine forest soils. Because of this goal, my project was associated with a US Forest Service study near Burns, Oregon, on the effects of fire on belowground organisms and processes. The part of this work described in Chapter 1 (fire's impacts on soil solution chemistry) is closely related to the Burns study. The information here rounds out the soil chemistry data (total nutrient pools) collected in Burns by Christine Niwa and Bob Peck. For the studies described in Chapter 3, I collected all of the organisms at the Burns field sites so that when that study is completed, Christine Niwa and Jane Smith will be able to use this information to help explain the implications of their findings about how microarthropod and fungal populations change with the application of spring and fall prescribed fire.

Prescribed Fire in Eastern Oregon Ponderosa Pine Forests: Relationships Between Soil Fertility and Ecology

Chapter 1. Introduction

Fire history

Fire is an important ecological force shaping the ponderosa pine forests (*Pinus ponderosa* Dougl. ex Loud.) of Eastern Oregon. Before the 1900's, fire return intervals were approximately 5-20 years (Agee 1993). These short intervals did not allow enough fuel accumulation to support a severe fire and so the fires were usually light (Agee, 1993). Mature, healthy trees usually survived (Belillas & Feller 1998). The seasonal timing of fire was usually in late summer, when the forest was at its driest.

Prior to the 1920's, light surface fires, known as 'Paiute forestry', were occasionally used as a management tool. However, this practice was discarded since it was thought to be detrimental to 'efficient fire management' (Agee 1990, 1993). In the early 1920's, fire suppression was standard management in these forests (Agee 1990, 1993). Since then, because of the Forest Service's policy of total fire suppression, those fires that escape the net of forest protection have become more severe and more intense than they once were.

Changes in the landscape aboveground

Forest fire suppression has brought about many other changes in these forests. Those changes can be seen aboveground, in forest structure and tree species composition,

as well as belowground. All of these changes have had other repercussions throughout the ponderosa pine ecosystem.

I will start by discussing some of the aboveground changes. Douglas-firs (*Pseudotsuga menziesii* (Mirb.) Franco), true firs and spruces have all increased their dominance in the ponderosa pine forests on the eastern slopes of the Cascade Mountains (Agee 1990, 1993; Lehmkuhl et al. 1994). They were present, but probably less abundant, in presettlement times than they are today. This change in species dominance is less prominent in the ponderosa pine forests further east, because the seed source for Douglas-fir is farther away.

Forest stand structure has also changed. Most historic accounts of the Eastern Oregon ponderosa pine forests describe open, park-like woods. The old pines are spaced far apart, with a grassy carpet of herbs between them. The younger stands can be denser and the youngest stands quite dense (Agee 1993). The landscape, as a whole, has a 'patchwork' pattern, with even-aged patches of ponderosa pines, but pioneers traveling through Oregon most often described the older, park-like forests. This has given the impression that the old park-like forests dominated the landscape. However, Tiedemann et al. (2000), suggest that these historical accounts of forest structure may be biased because roads are usually built along the easiest routes. The easiest routes would pass through the wide-open, older forests, not the dense, young forests. Therefore, our assumptions about the precise structure of presettlement forests may be skewed toward older forests. But, regardless of these skewed assumptions, it is still likely that forest fire suppression has caused an increase in stem density over the past eighty years. It is the extent of the change that is under debate.

This shift in species composition has changed the forest pest and disease regime of the forests. Some of the insects who have capitalized on the changes brought about by forest fire suppression include: western spruce budworm (*Choristoneura occidentalis*), Douglas-fir tussock moth, western pine beetle, mountain pine beetle and pine and fir engravers (Hessburg et al. 1994). I will elaborate on the story of the western spruce budworm. These native caterpillars were once less common in the eastside forests. They feed primarily on the young needles of true firs (*Abies* spp.), Douglas-firs and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). These trees were once less abundant on Oregon's east side, restricted to high elevations and riparian corridors. Now, because they have increased their range and dominance, more of the landscape can support large populations of budworm larvae. This has resulted in a gradual increase in the frequency and severity of spruce budworm outbreaks.

The story behind the western spruce budworm also applies to the western pine beetles and fir engraver. These arthropods have capitalized on the abundance of stressed pines growing in crowded conditions, a direct result of fire suppression.

Because of these changes in the landscape, the US Forest Service has recently changed its fire policy. They now use prescribed fire to re-introduce fire safely back into this landscape. However, there is still much to learn about how the re-introduction of fire will change the landscape, both above and belowground.

Need to study changes in the landscape belowground

In order to fully understand fire's impacts aboveground, it is important to look belowground. In this thesis, I have explored two aspects of prescribed fire's effects on

soils. The first is fire's impact on soil solution chemistry. This study is addressed in Chapter 2. In Chapter 3, I explore how fire can impact the soil biotic community, emphasizing microarthropods and fungi which are common in many coniferous forest soils.

Because it is important to interpret fire's impacts on the soil biotic community as well as simply document them, I conducted a series of laboratory studies to provide a basic science background for some common soil microarthropods in ponderosa pine forest soils. These results are described in Chapter 4.

In Chapter 5, I attempt to fit the results of Chapter 4 into the context of using prescribed fire, exploring some of the ways in which prescribed fire can potentially influence microarthropod and fungal interactions and what that might mean for the forest growing from those soils.

Chapter 2. Spring and Fall Fire in Ponderosa Pine Forest Soil: Soil Solution Chemistry

Summary

Ion exchange resin bags were used to investigate the impacts of prescribed fires set in spring or fall on the relative concentration of several soil solution ions. Four previously thinned ponderosa pine stands were used to create a randomized block field experiment, with three treatments: spring burn, fall burn and control (no burn). Resin bags were placed in the field 12 months after the fall burns and 5 months after the spring burns and left for nine months. They were collected and the ions extracted. The resulting solution was analyzed for NO_3^- , NH_4^+ , PO_4^- , total P, total S, Ca^{++} , Na^+ and K^+ . Some patterns were evident. Total S, Ca^{++} and NH_4^+ were most highly concentrated in the soil solution of the fall burned soils. Phosphate and total P measurements were higher for the burned plots than in the unburned control plots. Potassium, Na^+ and NO_3^- either showed no treatment effect or showed an inconsistent treatment effect (significant interaction term for site and treatment) between the different sites. These results were generally consistent with other research about how fire can impact soil solution chemistry.

Introduction

It is important to consider fire's impacts on soils at the same time as considering its impacts on aboveground forest health because soil fertility has a direct impact on a tree's health and thus its ability to withstand insect damage and other forest diseases. Soil fertility (N, P and S) is often low in the pumice-derived soils of Eastern Oregon (Waring et al. 1992). In the last several years, bark beetles have become a growing

problem in Eastern Oregon forests. Stressed trees are one of the primary causes of the bark beetle outbreaks that have plagued Eastern Oregon. The trees are stressed because of overcrowded conditions caused by fire suppression. The nutrient capital of the Eastern Oregon soils was never very great and with the increased stand density, competition for these nutrients has become even more intense. In some ways, this story is similar to that of the spruce budworm, described by Waring et al. (1992). Bark beetles have always been a part of the ecosystem, but when they are presented with a landscape full of stressed trees, their populations can expand unchecked by food limitations.

Fire suppression probably also changed soil fertility in the eastside ponderosa pine forests. One of the reasons why soil fertility is so low in Eastern Oregon is because periodic fire has limited nutrient buildup. Fire volatilizes several essential elements, such as C, N, P and S (Agee 1993; De Bano et al. 1998) (Table 1). Even after a fire is extinguished, more losses occur due to erosion and leaching. Since fire suppression, nutrients (especially N and S, which are more vulnerable to volatilization and leaching losses (McNabb & Cromack 1990)) have probably built up to unprecedented levels.

It follows logically that eastside ponderosa pine forest growth rates may have increased with fire suppression and thus, may be reduced by the reintroduction of fire. However, the total nutrient capital of a site does not always accurately describe soil fertility. Decomposition in these forests is slow and many of the nutrients present in the soils may be relatively unavailable for plant uptake. Covington et al. (1997) suggest that fire can enhance tree growth by freeing trees from competition through stand density reduction. They also suggest that fire speeds nutrient cycling, further reducing nutrient stress in those trees that survive the fire by transforming the remaining soil nutrients into

more available forms. Unfortunately, historic site index data is unavailable, so we do not truly know whether tree growth has increased since 1920. Still, maintenance of current forest productivity is an important management goal of the USFS today. Although some forests show an increase in growth immediately following a fire (Covington et al. 1997), it is unlikely that forest productivity will improve, in the long run, with the introduction of prescribed fires (Tiedemann et al. 2000, Busse et al. 2000).

Table 1. Response of seven soil nutrients to fire.

Nutrient	Volatilization temperature	Losses	Availability Response
N	400°F (McNabb & Cromack 1990) 200 °C (Agee 1993)	213 kg-ha ⁻¹ high:100-800 kg-ha ⁻¹	Temporarily increased
S	375 °C (Agee 1993)	13.5-19 kg-ha ⁻¹ , 30-70%	Temporarily increased
P	770 °C (Agee 1993)	55% loss within the ash layer (Giardina et al. 2000)	Temporarily increased
C	100 °C (water-repellency above 175 °C)	Highly variable	
Ca	Greater than 750 °C	Minimal	
Na	875 °C (Agee 1993)	Minimal	
K	550 °C (Agee 1993)	311 kg-ha ⁻¹ 39%	

One reason for the possibility of long-term growth reduction is the very reason Covington cites as a reason for post-fire increased forest productivity. Faster nutrient cycling results in increased concentrations of mineral nutrients within the soil solution

following fire. Although these are more available for plant uptake than nutrients bound up in soil organic matter, they are also more vulnerable to leaching. Thus, high concentrations of available nutrients, may lead to long-term depletion of the site's nutrient capital, especially if plant uptake is limited at the time of maximum availability. Therefore, the increased forest productivity sometimes observed following fire may not be a long-term trend and should not be weighed heavily when considering the impacts of prescribed fire on forest productivity. Furthermore, short-term increases in site productivity do not always occur. Landsberg et al. (1984) found that both severe and moderate burns in a ponderosa pine forest near Bend, Oregon resulted in reduced levels of foliar N and reduced annual growth. Her findings support Tiedemann et al.'s (2000) conclusions that prescribed fire should be used with caution as it may negatively impact the plant community. Busse et al. (2000), like Landsberg et al. (1984), found statistically significant reductions in tree growth after prescribed burning and attributed them to fine root mortality and crown-scorch. However, they concluded that while these growth reductions are real, they may not be important in determining long-term site productivity because they are relatively ephemeral.

The most damaging fires are intense wildfires. Along with the risk of severe damage to trees, comes the danger of soil damage. High intensity fires are more likely to remove nutrients through litter combustion and also to reduce the soil biotic community through soil heating.

In many cases, other management concerns besides growth rates may be more important, such as a stand's resistance to insect pests and wildfires. Thus, fire is a valuable management tool, despite the fact that it can sometimes negatively impact forest

growth and soil fertility. Busse et al. (2000) state that this tradeoff must be made and come to some encouraging conclusions: that it is possible to use prescribed fire, while minimizing its negative impacts on soil fertility and tree growth. Learning how to consistently limit those negative fire impacts (whether through controlling fire severity, fire season or both) is of primary importance now.

Two ways to achieve the goal of minimizing prescribed fire's impact on soil fertility is to limit fire severity and to allow adequate recovery time before the site is burned again. The US Forest Service already attempts to limit fire severity by burning in the spring when fuels are moist, resulting in less intense fires that are easier to control, and thus, also safer and cheaper. Disasters, like the escaped prescribed fire that burned hundreds of homes in Los Alamos, New Mexico in spring 2000, are still possible, but are more easily prevented in the spring.

However, there may be some costs associated with burning in the spring. Spring is a time when fine root growth and microbial activity are at their maximum in the upper organic layer, where they are most susceptible to fire damage. Microarthropods also tend to migrate to the top soil layers, following this burst in microbial activity. This means that although spring burning may limit fire severity, the negative impacts to the soil biotic community may be greatest during the spring.

Methods

Study site

The prescribed burn study sites are located in the Malheur National Forest, Burns Ranger District, Harney County, Oregon, between 1,650 and 1,700 m above sea level.

These sites are covered with ponderosa pine forest, with gravelly loam and clay loam soils and with basalt, andesite and rhyolite bedrock. These forests are dry, with only 38 to 50 cm of annual precipitation. Most precipitation falls as snow during the winter, but summer thunderstorms can provide some moisture as well. Summer droughts can be severe. The vegetation covering the sites is primarily a ponderosa pine overstory. The herb layers vary from site to site. Trout's herb layer is dominated by elk sedge. Kidd flat's herb layer is dominated by mountain strawberry and both Driveway herb layers are dominated by Idaho fescue (Thies et al. 1999). The stands were thinned in 1994 or 1995 and are approximately 80-100 years old, with a few older individuals reaching 200 years.

The experimental plots are part of a US Forest Service study, by Walt Thies and Christine Niwa, examining the effects of spring and fall prescribed fires' effects on different ecosystem components, including the soil microarthropod community and the mycorrhizal community. The study involved a randomized block design with 4 blocks, each block encompassing three treatments: spring prescribed burn in May 1998, a fall prescribed burn in October 1997 and a control (no burn). The severity of the burns at the four study blocks is summarized in Table 2.

Table 2. Prescribed fire descriptions for the four study plots (from Thies et al. 1999).

	Change in %mineral soil exposed	Change in duff depth	Area burned	Average litter volume lost (cm ³ m ⁻²)
Kidd Flat				
Spring	+10%	-20%	50%	15
Fall	+10%	-25%	60%	22.5
Trout				
Spring	+45%	-65%	93%	90.7
Fall	+15%	-30%	85%	38.3
Driveway 14				
Spring	+20%	-50%	57%	28.5
Fall	+40%	-65%	90%	58.5
Driveway 17				
Spring	+20%	-50%	88%	44
Fall	+20%	-40%	95%	38

Ion exchange resin bags

Ion exchange resin bags were used to investigate some of the short-term impacts of fire on nutrients within the soil solution. Resin bags were constructed using a mixed bed resin providing cation and anion exchange capacity (2.1 meq g^{-1} and 2.6 meq g^{-1}) with a working density of 362 g l^{-1} . Each bag contained approximately 5 ml of resin.

After the soil was sliced with a trowel, the bags were placed into the slit, 5 cm below the mineral soil surface. They were installed in the field in October, 1998 and collected in June 1999. They were in place starting 12 months after the fall burns and 7 months after the spring burns.

After collection, the bags were frozen for later analysis. Laboratory analyses were performed by Oregon State University's Central Soil Analytical Laboratory. Ten grams of field-moist resin was extracted in 200ml 1M HCl and the solution from this extraction was then

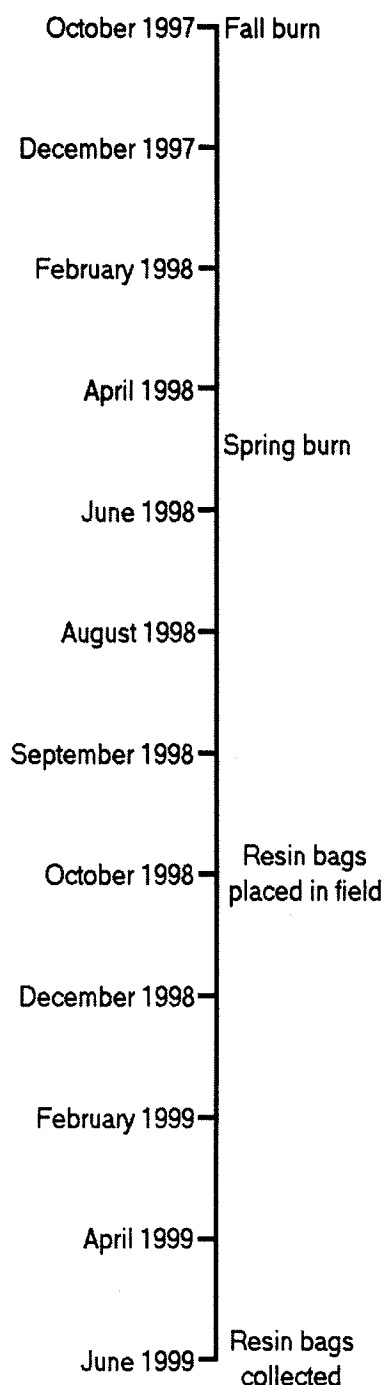


Figure 1. Time-line: Resin bag deployment and prescribed fire.

analyzed for NO_3^- , NH_4^+ , Ca^+ , Na^+ , K^+ , PO_4^+ , total P and total S. Nitrate, NH_4^+ , K^+ , Ca^+ and PO_4^+ were measured on the Central Soil Analytical Laboratory's autoanalyzer. All other ions were measured on the ICP in the same laboratory. These final data are reported as the concentration of the ions in the resin bag eluate. It is meant to give relative estimates of the quantity of ions in solution, not absolute estimates of nutrient fluxes.

Statistical methods

Statistical analyses were carried out using SAS for Windows version 6.12 (1996). Separate ANOVA models were made for each ion. The models were ion = treatment, using site as a blocking factor. The treatment effect was considered statistically significant at $\alpha = 0.05$.

Results

The response of nutrient concentration within the soil solution varied for the different ions (Figure 2). However, some general patterns did emerge from the data. One common pattern was that ion concentrations were highest in the soil solution on the fall burn plots. This pattern was seen with total S, Ca^{++} and NH_4^+ (Figure 2a,b,d, Table 3). For NO_3^- , the treatment effect was almost significant ($P = 0.0627$), suggesting that this ion may have responded to the fire treatments similarly to S, Ca^{++} and NH_4^+ . However, due to the high variability of the NO_3^- measurements, I was not quite able to definitively show this effect. The measurements for both total P and phosphate also showed elevated levels in the burn treatments, but it was not possible to distinguish between the spring and

fall burns (Figure 2e,f, Table 3). The models describing the concentration of Na^+ and K^+ did not show a significant treatment effect (Table 3).

Table 3. Models describing ion responses to prescribed fire treatments. All models use log transformed data.

Ion	df	Type III F	P-value
Sulfur*			
Treatment	2	16.66	0.0036
Error	6		
Ammonium*			
Treatment	2	16.01	0.0039
Error	6		
Nitrate			
Treatment	2	4.55	0.0627
Error	6		
Phosphate*			
Treatment	2	8.57	0.0174
Error	6		
Phosphorus*			
Treatment	2	8.02	0.0202
Error	6		
Calcium*			
Treatment	2	14.93	0.0047
Error	6		
Sodium			
Treatment	2	2.05	0.2098
Error	6		
Potassium			
Treatment	2	2.79	0.1393
Error	6		

* data logged for analysis

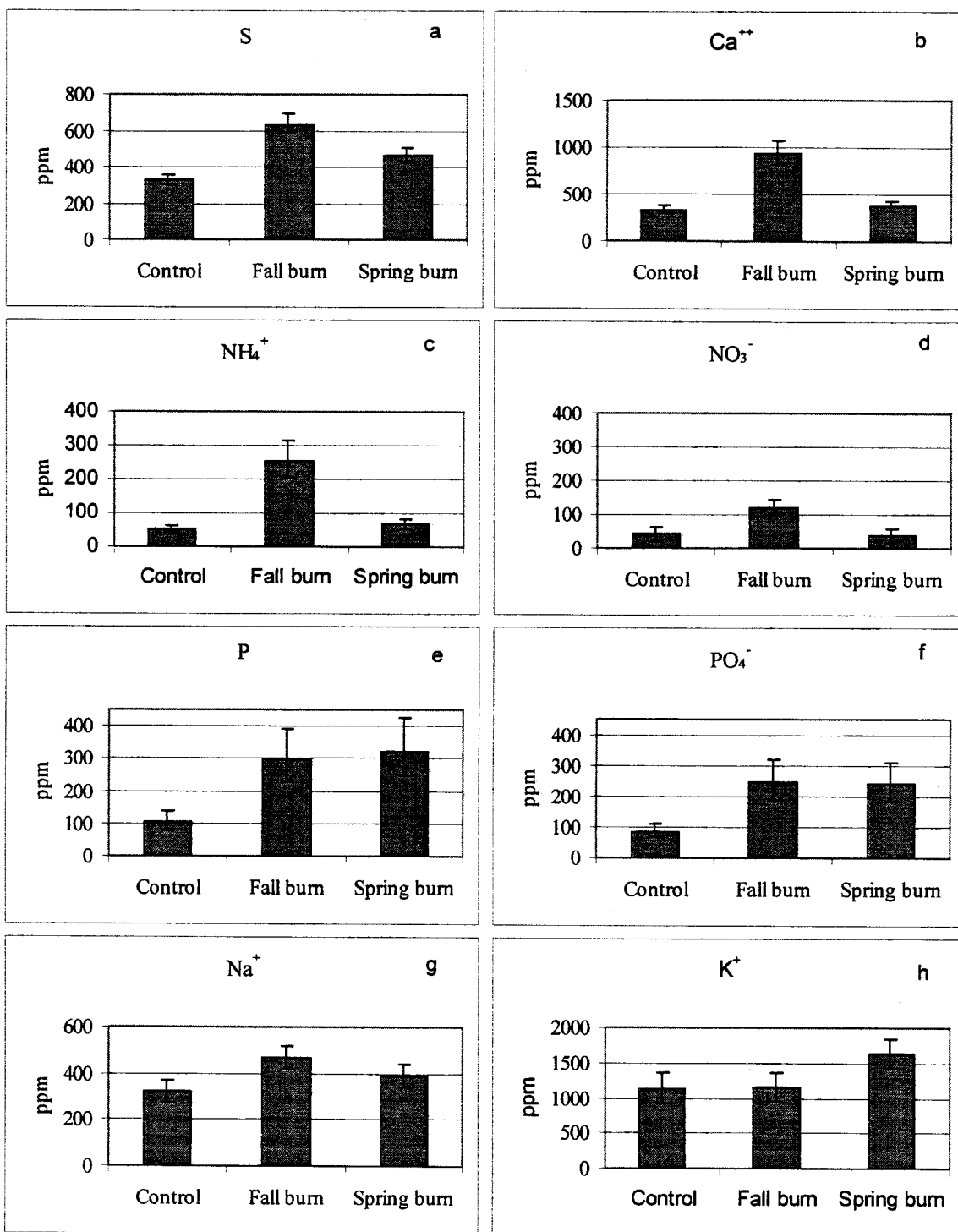


Figure 2. Mean values for ion exchange resin bag eluate. Error bars represent standard errors. Data were logged to create models and back-transformed for display.

Discussion

Many nutrients in the soil solution were more highly concentrated under the burn treatments. This is consistent with previous research (Covington & Sackett 1992). In these results, it is interesting to note the high S values for the fall burn treatments. It would be interesting to know how long the amount of S in solution remained high and whether the S in solution was subject to increased losses due to leaching or if it is quickly re-absorbed by S-limited plants or sorbed onto the surface of soil particles. It would also be interesting to know the cause of the high S concentrations. Are mineralization rates faster or is plant and microbial uptake of S slower after the fall fires? Both explanations could account for this pattern. Another possibility is that fall burns mobilize S accumulated in downed wood (Tim Schowalter, personal communication)

Calcium concentration in the soil solution was also raised significantly by the fire treatment. It would also be interesting to know the source of the additional Ca in solution. There are several possibilities, the strongest of which is Ca accumulation in the ash layer (De Bano et al. 1998). It might be a product of increased mineralization rates from residual organic matter or it might be weathered from parent material at faster rates because of increased microbial activity. Alternatively, Ca could be building up in the burned soils because fungi and plant roots are no longer taking it up since the fire may have sterilized the top few centimeters of soil.

Concentrations of both NH_4^+ and NO_3^- were higher after the fall burns. This phenomenon could be due to a variety of causes. First of all, mineralization rates could be faster in the post-burn soils. Secondly, N uptake rates could be slowed if fine roots were seriously impacted by the fire. Thirdly, it is possible that changes in the microbial

community have favored N-fixers. High rates of N fixation could also account for a buildup of NH_4^+ and NO_3^- in the soil solution.

The differences found between the spring and fall burns could be attributed to two potential causes. First of all, there could be a real difference between the effects of spring and fall fire on the cycling of S, Ca^{++} and NH_4^+ simply because of burn seasonality. This could occur if the fire's effect on the soil biotic community is in fact different between spring and fall because of something to do with the life histories of the organisms.

A second explanation for the differences between the spring and fall burns is the confounding factor of time since burning. This seems an unlikely hypothesis because the usual nutrient response after fire is that concentrations in solution rise rapidly and then taper off over several years. Since the fall burn happened first, the ion concentration in

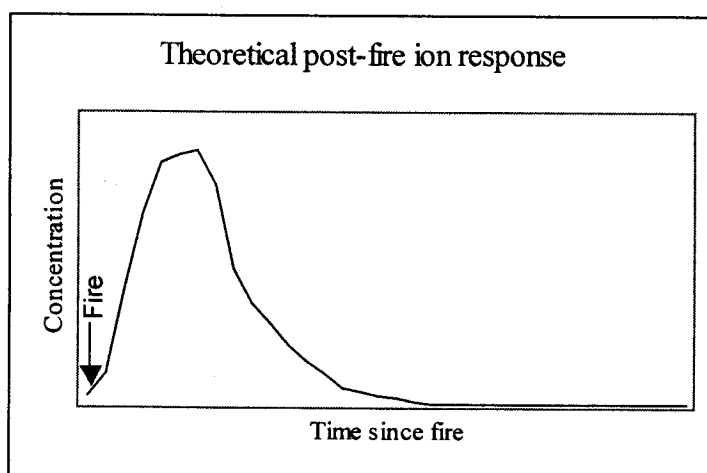


Figure 3. A theoretical curve, describing a common response of ion concentration in the soil solution after a fire. This graph applies to many, but not all ions.

the soil solution at the fall burns should have had more time to fall back to 'normal' pre-burn levels (possibly due to either leaching or uptake from recovered root systems) than for the spring burns and thus, should show lower soil solution nutrient concentrations. The trend I observed was in the opposite direction.

Figure 3 illustrates how the concentration of a theoretical ion in the soil solution will often respond to a soil disturbance, such as fire. It is possible that the resin bags sampled the soil solution either before or after this peak for the various ions under the two different fire treatments. Different ions will most likely respond to the fire on different time-scales. Nitrate usually shows the sharpest peak, while some of the slower cycling ions may show a broader, flatter peak. The results for NH_4^+ (fall burn showing a higher concentration than spring burn) make the most sense if the samples were captured at the time before the peak for the spring burn and after the peak for the fall burn. The mechanism which could account for this gradual buildup of NH_4^+ within the soil solution could be either faster nutrient cycling, with a faster-moving, bacterial-dominated soil microbial community, nitrogen fixation, slower uptake rates, due to fine root-kill, or a combination of these factors.

A third potential explanation for the differences in soil solution ion concentration between spring and fall burning is that the fall burns may have been significantly more severe than the spring burns. This does not necessarily appear to be the case. The integrated measurement of volume litter lost shows that the fall burn was more severe at the Driveway 14 and Kidd Flat sites, but was less severe at the Driveway 17 and Trout sites (Table 2).

The reasons for the differential effect of the fires in the end might also be linked to soil moisture content. The relationship between soil heating and soil moisture content is complex. In a moist soil, soil surface temperatures may be limited, as heat is removed from the soil by evaporation. However, because water has a higher heat conductance

than dry soil, scalding temperatures might be reached deeper in the soil profile in a moist soil than in a dry soil. The depth to which heat penetrates a soil may be important in interpreting how the fire influences the soils because scalding temperatures at 5cm below the soil surface may impact the soil biotic community even more than boiling or higher temperatures which do not penetrate the soil so deeply.

This latter hypothesis seems like it might account for differences in the impacts of the spring and fall prescribed fires. This hypothesis is something that would account for a seasonal effect of fire on nutrients in solution as well. In the spring, water content is normally higher. This would tend to limit litter consumption, ash deposition and also maximum soil temperatures. On the other hand, water is a good conductor of heat, and therefore, in spring, when soils are moister, the impacts on the soil biotic community may be greater, as scalding temperatures penetrate deeper into the soil. Thus, spring burns may consume less litter, deposit less nutrient-rich ash and also leave the 3-dimensional litter habitat more intact, but they may also tend to sterilize the soil more deeply than fall prescribed burns.

In the context of using prescribed burns as a management tool, if decisions are made purely on short-term nutrient availability, the fall burn appeared to give the strongest positive response. If the trees in fall-burned stands were previously limited by N or S, it is possible that the surviving trees will no longer be limited by these nutrients, presuming that their roots are not seriously injured during the fires. At least, this is true in the short-term.

In the long term, the picture is much more complex and many more factors need to be taken into account with management decisions. Whether the primary management

goal of fuel reduction was met is important to consider. Additionally, the observed rise in available nutrients is likely a short-term phenomenon, but the result of stimulating plant growth and microbial activity may be important in re-invigorating a stand.

However, long-term trends in soil fertility might be better described by total amount of nutrients present at the site. In order to make decisions that will be relevant to the time-scale of several stand rotations, long term measurements (total nutrients) must be considered (Busse et al. 1996). Because fire invariably reduces a site's total nutrient capital, this is necessary to consider. A good question might be: How are stand nutrient mineralization rates influenced in the long term? Thus, if nutrient cycling rates are higher over a long period due to periodic burning and if the reduction in total nutrient pools is relatively small, then periodic fires may improve stand productivity. However, much more research is needed before this assertion could be made.

Additionally, not all soils in the treatment plots were burned as severely as where I placed the resin bags. The actual effects of the fire should be judged in the context of burn severity (Belillias & Feller 1998). A good measure of this is the amount of mineral soil exposed by the fire. Because the soil solution in the burned plots was measured only under heavily burned soils where the mineral soil was exposed, the data need to be interpreted in light of this fact. This means that I need to consider the fact that the post-fire elevated concentrations of NH_4^+ , S, Ca^{++} , total P and phosphate probably only occurred over a portion of each stand.

The spring burn at the Trout site showed the largest change in % MSE, but the patterns of ion abundance for the Trout site do not appear different than the patterns for the other sites. Although fire intensity, at the scale of one square meter of burned soil,

might not have varied across the different sites, we can assume that the Trout spring burn may experience stronger stand-level impacts than the burns at the other sites. For example, we can assume that the total amount of NH_4^+ available for plant growth is highest in the soils of the Trout fall burn stand. Also, if leaching losses in the burned soils are important, we can assume that these losses will be greatest under the Trout spring burn.

Chapter 3. Natural and Prescribed Fire Impacts the Soil Fauna and Flora

As well as changing the nutrient concentration in the soil solution, fires may also impact the soil flora and fauna. Soil is a good insulator, protecting soil organisms from a fire's heat, but mineral soil temperatures can and do rise during a fire and the litter layer, where many organisms live, is often consumed. Raison (1979) describes how a light burn in a longleaf pine forest heats the soils:

In small fires with flames about 1m high, soil temperatures at 2.5 cm depth increased by 20°C to reach 40°C 15min after the fire had passed. Temperatures had fallen to 25°C 45 min later.

Although the heat from a fire does not penetrate very deeply into the mineral soil, it does penetrate into the top few centimeters. The litter layer and the top 5 cm of mineral soil is where the soil biotic community is most active. For mild fires like the one described above, it is likely that the deeper soil arthropods will be relatively unaffected by the fire. However, arthropods on the litter layer and on the surface of the mineral soils will experience significantly elevated temperatures.

Elevated temperatures (which may also lower relative humidity) pose a real problem to belowground arthropods. In general, soil arthropods are adapted to a habitat with relatively constant temperature and humidity. Some traits, such as well-developed lipid layers in the cuticle that are present in many aboveground arthropods, are reduced or lacking in many belowground arthropods (Villani et al. 1999). Belowground arthropods may be very sensitive to even small amounts of soil heating. Furthermore, arthropods in the litter layer may even be combusted when fire passes above.

Soil microarthropod and insect populations are, in fact, almost always reduced by fire (Ahlgren & Ahlgren 1965; Buffington 1967; Abbott, 1984; Borchers & Perry 1990; and Shaw 1997). Springett (1971) found that while populations of microarthropods in general were not reduced by fire, populations of fungivorous mites were. However, she sampled three years after the prescribed burns were implemented and therefore, the microarthropod populations had probably rebounded. This hypothesis seems logical because the fungivorous mites were at reduced levels in the burned plots, while Collembola and other mites were not. Many of the fungivorous mites are oribatid mites, which are long-lived and slow to reproduce. Additionally, even if Springett's (1971) fire did not directly reduce oribatid numbers, it is possible that it did reduce their fungal food source. Fires often shift the microbial community toward bacterial, rather than fungal dominance. Thus, the fungivorous mites in Australian forests studied by Springett (1971) may have reduced numbers for two reasons: the fire reduced their numbers, and their populations did not rebound as quickly as other components of the soil arthropod community due to their slow reproductive rates. Additionally, the surviving oribatid mites may be food-limited in a bacterially dominated post-fire soil.

Another factor limiting fire's impacts on soil arthropod populations is fire heterogeneity. Many arthropods survive fire in unburned patches of soil. The survivors may recolonize the more severely burned soil patches and may also respond to new resources made available by fire. The nanorchestid mites (which are abundant in heavily burned soils at the Burns study plots), for example, might be feeding on soil algae (Schuster & Schuster 1977) that appeared on the soil surface shortly after the prescribed fire treatments.

Mycorrhizal fungi are often reduced post-fire, due to the destruction of the forest floor (Horton et al. 1998; Stendell et al. 1999) and the Burns study was no exception. Root-tip biomass was significantly reduced in the burned plots (Jane Smith, personal communication). After a fire, mycorrhizal recolonization may occur by fire-resistant propagules. However, those ectomycorrhizal fungi with fire-resistant propagules may represent only a subset of the fungi present before the fire. Additionally, the changed conditions after the fire may favor a slightly different mycorrhizal community. Baar et al (1999) showed, in a *Pinus muricata* D. Don forest, that the relative dominance of *Rhizopogon olivaceotinctus*, versus *R. ochraceorubens* probably shifted post-fire, in favor of *R. olivaceotinctus*. However, the dominant mycorrhizal fungi, the suilloid and ascomycetous fungi, were consistently dominant before and after their fires.

Many ascomycetes fruit prolifically after a fire (El-Abayad & Webster 1968). There are many hypotheses to account for this: decreased competition from other fungi, increased available nutrients or their spores require mild heat to germinate. The morel, *Morchella* sp. is one of these post-fire Ascomycetes. The re-establishment of the soil biotic community (especially the ectomycorrhizae) following a clear-cut is extremely important to the recovery of the plant community (Ponge et al. 1998). Although fire's impacts on soils are different from clear-cutting, it is likely that this generalization holds true for both disturbance types and also holds true for other parts of the soil biotic community in addition to the ectomycorrhizae. After a severe fire, the regeneration of the soil biotic community may play a vital role in the re-establishment of a stand.

In the context of prescribed fires, applications in spring or fall may not mimic the historic summer fire regime. Environmental conditions, such as soil moisture (which

influences soil heat conductance) and the physiological state of many organisms will be different in spring and fall than in mid-summer.

There is some concern that soil organisms adapted to survive summer fires may not survive spring fires. For example, in mid-summer, many soil microarthropods migrate deeper into the soil profile in order to stay moister and cooler (Luxton 1981b; Hassall et al. 1986; MacKay et al. 1987). However, in the spring when soils are wet and fungal growth is abundant in the litter layer, microarthropods may move up to the litter layer where their food is more plentiful. Although Luxton (1981b) was studying a Danish beech woodland soil, the forces behind the vertical seasonal migrations he observed are likely to operate within the ponderosa pine forests of Eastern Oregon. Moisture (and hence, microbial growth) probably shows stronger seasonal patterns in these forests than at his study site. Thus, in mid-summer and perhaps also in early fall, microarthropods may be better protected from a fire's heat simply because they live deeper in the soil at that time of year. Additionally, moisture is a good heat conductor and so heat may penetrate deeper into the soils during a spring burn if the soils are moister then.

These possibilities are the reasons why the US Forest Service is currently studying the feasibility of fall prescribed burning. In the early fall, microarthropods and also other organisms, might be in a physiological state or a location similar to their summer state and because of this may be more likely to survive a prescribed fire.

In the context of the ponderosa pine forests in Eastern Oregon, many questions arise about how the soil biotic community is impacted by prescribed fire in different seasons. However, studies that investigate only the response of microarthropod numbers

to prescribed fire do not present the entire picture. Fire's effects on the soil biotic community are likely to be both direct and indirect. Information about population changes will be more useful when placed in the context of the soil food web and information about the functional roles of the different species.

In order to do this, we need to know more about the natural history and ecosystem functions of individual microarthropod and fungal species. This functional information may help us interpret data about what is happening to the soil community after a prescribed fire and help us judge whether the impacts of the prescribed fire on the soil community will seriously impact soil processes, including decomposition and mineralization and perhaps even assess fire's impacts on the soil's 'resistance' to pathogenic fungi. It will also help us to judge whether microarthropod populations are simply reduced by fire or whether they also respond positively or negatively to post-fire conditions.

In order to assess the ecosystem implications of a fire's impacts on the soil biotic community, it is necessary to gain an understanding of how the different components of that community interact.

Chapter 4. Microarthropod and Fungal Ecology

Summary

I investigated the roles of microarthropods in the biotic community through three different methods: feeding preference trials, natural abundances of ^{13}C and ^{15}N and an experiment in fungal competition. For the feeding preference trials, most arthropods investigated exhibited distinct preferences for some of the fungi offered. For those arthropods which did not show distinct preferences, there are several possible explanations: their preferred food was not offered, they are true generalist feeders or laboratory conditions were not conducive to feeding. Stable isotope studies suggest that many arthropods do have distinct diets in the field, although these results are preliminary. The mesostigmatid mites were enriched in both ^{13}C and in ^{15}N , as expected for a predator. *Camisia* sp. were relatively depleted in both isotopes, as expected for an individual feeding on lichens. The fungal competition studies indicated that microarthropod grazing could, in some cases, influence the outcome of fungal competition. These influences depended upon both the palatability of the fungus and its growth rate.

Introduction

Food web

Microarthropods play many roles within the soil food web. Many are considered to be fungivorous, but there are also predaceous mites in the soil. Collembola, although primarily fungivorous, have been known to feed on roots in the absence of other food

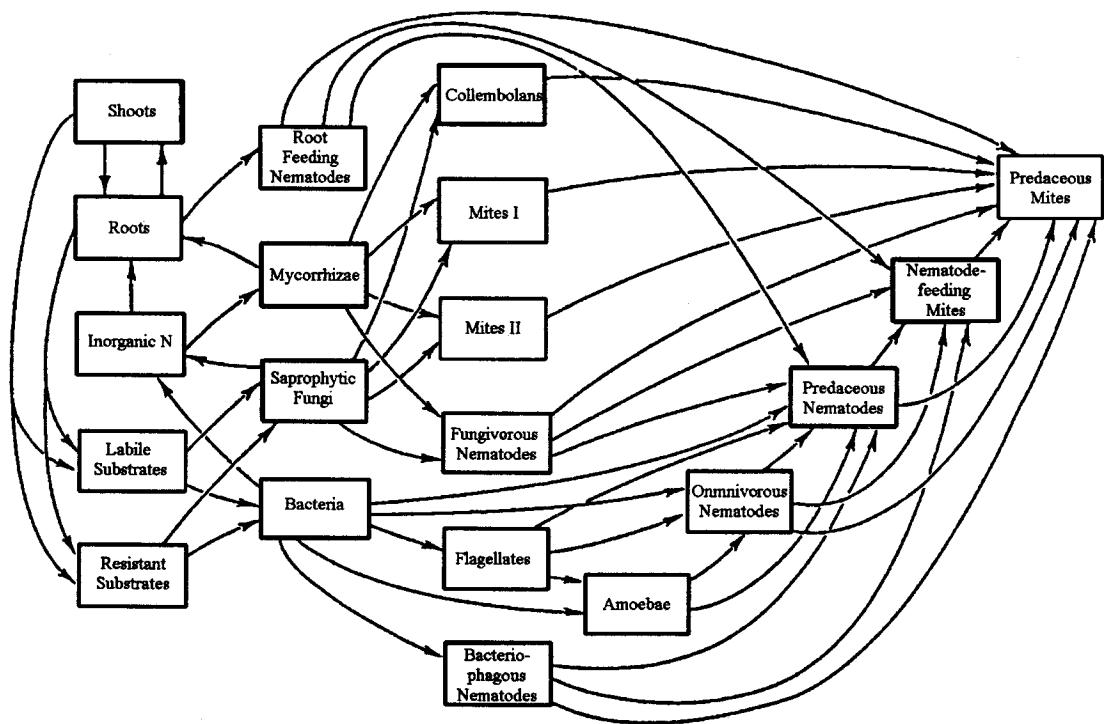


Figure 4. A simple soil food web from Elliott et al. (1988).

sources (Hopkin 1997). Studying a simple grassland soil food web (Figure 4) illustrates where microarthropods fit into the larger picture of the soil food web. In this soil food web, the fungivorous mites, nematodes and Collembola feed upon both mycorrhizal and saprotrophic fungi. In a more complex system, such as one that would be found in a

forest soil, their diets are probably more complex, including a variety of fungi in different functional groups, such as pathogens, mycorrhizal partners with plants and saprotrophs. Also, some of these fungi may be in competition with each other for resources and space within the soil. It is interesting to speculate how fungal competition may be modified by trophic interactions with different fungivores.

Trophic levels may be a useful way to simplify complex food webs. One framework often used to describe how trophic levels can be regulated in natural systems is the concept of the trophic cascade (described by Hairston et al. 1960). Trophic cascades have been elegantly shown in freshwater ecosystems (Kitchell & Carpenter 1993), but they are not easily demonstrated in complex systems such as the soil biotic community. Mikola & Setälä (1998a) failed to find evidence for trophic cascade regulation of either biomass or productivity of a microbial-based soil food web in their laboratory microcosms. Mikola & Setälä (1998b) determined that soil trophic levels interacted, although the interactions did not fit the traditional model of trophic cascades. The microbivores' biomass was limited by predation, but bacteria and fungi reacted differently to changes in higher trophic levels. One of the reasons they cited for their lack of evidence that microbivory limited their microbial community was the complexity inherent in soil food webs. Different microbes may be subject to different grazing stresses.

At one level of complexity, bacteria and fungi may belong to separate 'compartments' of the soil food web (Moore & Hunt 1988). Additionally, different fungi may experience different grazing pressures from different grazers. The phenomenally high diversity of a natural soil will probably tend to make trophic-level interactions even

less predictable than in Mikola & Setälä's (1998a,b) laboratory. Thus, the most accurate and informative representation of how the soil biotic community works may be found through species-level interactions within the soil food web.

Considering species-level interactions up and down the food web is especially important in the context of applied research. In the context of forest management, knowing the ecology and natural history of a particular fungus (perhaps a common pathogen or a mycorrhizal associate) is particularly important. If management practices alter the microarthropod and fungus community, those species interactions which shape the soil food web may also be altered. Both direct changes to the soil biotic community and indirect interactions within the food web will ultimately influence the prevalence of the fungus of interest.

Feeding preference

The feeding habits of mites and Collembola do not quite fit into the well-defined boxes shown in Figure 4. Accumulated evidence from many gut content analysis studies (Anderson & Healey 1971; Behan & Hill 1978; Takeda & Ichimura 1983; and Vegter 1983) indicates that Collembola and mites ingest a variety of 'amorphous material' along with fungal hyphae. Plant detritus, fungal hyphae, pollen, spores, mineral particles, algae and animal remains have all been found in the guts of Collembola (Takeda & Ichimura 1983). Mite diets may be equally complicated (Behan & Hill 1978). In general, dark septate fungi are more often found in microarthropod food boluses than are hyaline hyphae. There is some variation between species, however. Microarthropod feeding habits have been described as three different strategies. They have been classified as

'microphytophagous, macrophytophagous or panphytophagous' by Luxton (1972). In contrast to the field studies, it is relatively easy to demonstrate feeding preference hierarchies for different fungi in a laboratory (Mitchell & Parkinson 1976; Shaw 1988; Lartey et al. 1989; Kaneko et al. 1995 and Maraun et al. 1998). To bring these differing viewpoints together, the fungivorous microarthropods can be considered generalist microbivores, with the ability to specialize on their preferred food in times of abundance.

Various microarthropod species sometimes show slightly different food preference hierarchies, although there is often overlap between the feeding preferences of different animals (Maraun et al. 1998). In the laboratory, fungivorous microarthropods generally preferred the dark septate fungi to fungi with hyaline hyphae. The reasons for this possible preference are still unclear. It may relate to nutritional quality or to the presence of secondary chemicals (Kaneko et al. 1995). Different feeding habits (for the springtails) may also arise from different-sized mouthparts of the various animals (Chen et al. 1995). Another explanation for slightly different feeding preferences is that variations in fungal chemistry can trigger different responses by arthropods. Leonard (1984) showed that microarthropod feeding preference orders can vary, depending on the nutrient status of the media on which the fungi were grown .

Not all soil microarthropods are fungivorous, however (Walter 1988a). The precise roles of many of the soil mites are not yet well understood, but this understanding is needed. Beare et al. (1995) suggest that real advances will be made only when a broader view of the influence of biodiversity on soil functioning is found, explicitly including the 'complexity and specificity of biotic interactions in soils that regulate biogeochemical cycling'. Information about the roles of the less common

microarthropods, which do not eat fungi, is limited. Many of the mesostigmatid mites, which are also common in soils which comprise between 3 and 20% of the soil mite fauna (Petersen & Luxton 1982), are believed to be predaceous (Koehler 1995). Some mite families have never been thoroughly studied, such as members of the mite family Nanorchestidae that have only been successfully reared by two research groups (Schuster & Schuster 1977; Walter 1988a). Furthermore, not all Collembola fit well into the ecological box of fungivory. Some springtails in the family Onychiuridae will feed on roots when other food sources are absent. Others, in the Neanuridae are predaceous (Hopkin 1997). *Galumna* sp., an oribatid mite, has even been observed feeding on nematodes in the laboratory (Andrew Moldenke, personal communication).

Although laboratory studies are by far the easiest way to obtain information about microarthropod feeding, it is important to remember that feeding patterns observed in the laboratory do not necessarily correspond to feeding patterns in the field (Mitchell & Parkinson 1976).

Stable isotope natural abundance may offer a new method for studying microarthropod food sources in the field and may also reflect which parts of ingested materials are actually assimilated. Hall (1995) suggests that ^{13}C is a good tracer of food sources, while Gu et al. (1994) suggests that ^{15}N can indicate trophic levels. Isotopes have been used to determine the proportion of wood and soil in termite diets (Tayasu et al. 1997). Briones et al. (1999) used ^{13}C as a tracer to determine the food choices of Collembola. In a closed system with isotopically depleted CO_2 , measurements of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ may be able to indicate where microarthropods are feeding on a gradient between a saprotrophic or mycorrhizal fungal diet (Erik Hobbie, personal

communication). This technique has not yet been used under field conditions that lack a strong 'tracer' signal for C. The natural abundance of ^{13}C is highly variable. It is possible that the natural variation of the C isotopic signal is large enough to prevent distinction between a mycorrhizal or saprotrophic fungal diet. The natural abundance of ^{15}N is more likely to yield useful information because the ratio of 'signal' to 'noise' may be less. The combination of measurements, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is even more likely to be able to separate different microarthropod species by their diets.

It is also possible that information gained from these data may be minimal. If the measured arthropods are true generalist feeders (if they ingest and assimilate materials from a wide range of sources) interpretation of the signals will be difficult at best, because it will be difficult to establish a 'mixing line' between two or even three food sources, as did Kwak & Zedler in 1997. Even if isotopes cannot be used to deduce an animal's precise food source, $\delta^{15}\text{N}$ especially, may still provide useful information about trophic structure (Neilson et al. 1998).

Grazing impacts on the fungal/microbial community

Direct effects on fungi

When one examines the standing crop of fungal biomass and compares it to oribatid metabolism, it does not appear that oribatid mite grazing could seriously impact fungal biomass (Petersen & Luxton 1982). However, given that microarthropods preferentially graze on a subset of the fungal community, it is possible that some of them may impact their preferred food (Maraun et al. 1998). Another important thing to

consider is that some microarthropods will feed more intensely than the oribatids studied by Petersen & Luxton (1982). Some members of the Collembola often feed at higher rates and may thus impact fungi more strongly. The springtails, with a higher metabolic and reproductive rate than the oribatids, probably have a stronger potential to influence fungal growth.

Grazing may directly influence fungal growth. Whether this is a positive or negative influence depends on many factors, including: the intensity of grazing, the nutritional status of the fungi and the identity of the grazers. Bengtsson & Rundgren (1983) showed that heavy, uninterrupted grazing on *Mortierella isabellina* by the Collembolan *Onychiurus armatus*, reduced fungal respiration, while moderate, interrupted grazing increased it. Hedlund et al. (1991) found that grazing induced a change in the growth form of *Mortierella isabellina* and also changed the production of extracellular enzymes. Hanlon (1981) showed that nutrient-limited fungi were less able to respond to Collembolan grazing with compensatory growth.

Interaction/Community Effects

Understanding the impacts of microarthropod grazing on individuals within the microbial community may be important to understanding how grazing can shape that community. Microarthropod grazing can influence fungal distribution in the field, although there is still much debate about this topic. Newell (1984) showed how preferential Collembolan grazing on two basidiomycete species caused them to vertically stratify their thalli within the forest floor.

There is still some debate, however, about whether microarthropod grazing is a significant force in driving fungal succession. McLean et al. (1996) and Klironomos et al. (1992) had conflicting results. McLean et al. (1996) concluded that grazing by *Oppiella nova* and *Onychiurus subtenius* did not change the structure of a natural pine needle litter fungal community. Klironomos et al. (1992) concluded that *Folsomia candida* can speed fungal succession on decomposing spruce and fir litter by its feeding. One possible reason for the different conclusions from these two studies could be due to microcosm constructions. Klironomos et al. (1992) inoculated the sterilized soil and litter with 8 species of fungi, while McLean et al. (1996) used L layer leaf litter with a naturally occurring fungal community. It would be much easier for Klironomos et al. (1992) to detect a feeding effect in their relatively simple fungal community. It is also possible that the fungal succession observed by Klironomos et al. (1992) had already occurred within McLean et al.'s (1996) leaf litter. Klironomos et al.'s (1992) experiment was relatively short term (six weeks), suggesting that the fungal succession they observed occurred on a short time scale.

McGonigle (1995) hypothesized that biomass reduction of one fungus may leave room for a different one to colonize a substrate. Thus, microarthropod grazing can influence fungal competition. If fungi are in direct competition with one another within the soil matrix, then different levels of preferential grazing could potentially alter the competitive balance of these fungi within the soil.

Functional Effects

Microarthropod feeding differences may also result in different impacts on the various members of the microbial community. It is important to pay attention to this, because different species of fungi may play a variety of roles within the soil community, from saprotrophic decomposers to mycorrhizae to plant pathogens.

It has been shown that microarthropod grazing may disrupt mycorrhizal symbioses (Moore 1988; Schultz 1991) and can also influence the impacts of soil pathogens (Curl et al. 1988; Lartey et al. 1994). Microarthropods do play an important regulatory role in the structure and function of the soil biotic community (Elliott et al. 1988; Mikola & Setälä 1998a; Moore et al. 1988; and Parkinson 1988). However, an alternate viewpoint is that microarthropod populations may be partially regulated by the microbial community. Cromack et al. (1988), found that microarthropods were more abundant within ectomycorrhizal mats than in uncolonized forest soil. This suggests that they may have responded to the abundant microbial resources of the colonized soil.

Nutrient cycling

Although microarthropods account for only about 10% of soil respiration (Petersen & Luxton 1982), they may influence decomposition and mineralization through both direct and indirect mechanisms (Seastedt 1984). Microarthropods can contribute to decomposition directly through leaf litter comminution (break-up). Physical breakdown creates more surface area for the microbial decomposers to attack. Furthermore, it is possible that microarthropods influence the abundance and distribution of different members of the microbial community. They can disperse fungal spores as they move

throughout the soil. Depending on their feeding intensity, they can stimulate fungal compensatory growth or limit fungal growth (Hanlon 1981).

Microarthropods can influence nutrient cycling through their impacts on the microbial community as well. McGonigle (1995) emphasized that many different effects of fungivory on nutrient cycling have been demonstrated, but that much more work is needed. Mineral nutrient losses have been shown to be greater in systems with oribatid mites, than without them (Seastedt & Crossley 1980, 1983; Reddy & Venkatiah 1989; Siepel & Maaskamp 1994).

Siepel & Maaskamp (1994) found that oribatid mites with different digestive abilities can influence decomposition rates differently. Specifically, they found that those mites that possessed chitinase released N as a waste product and stimulated mycelial growth when N was otherwise limiting. Hanlon & Anderson's (1979 a, b) work, on microarthropod and macroarthropod influences on the microflora of decomposing oak leaves, shows that the response of microbial respiration to microarthropod grazing can be complex. They found that microarthropod grazing stimulated microbial respiration at low levels, but that heavier grazing pressure decreased C mineralization rates. These authors also found that microarthropod grazing enhanced the bacterial community and diminished the fungal community. The interactions between microarthropods and the microbial community in real soils, as opposed to simplified laboratory microcosms, are probably even more complex. Seastedt et al. (1988) suggest that the interactions between microbivores, microbes and nutrient cycling are important because the mineralization rates maintained by microbivore grazing may help maintain soil fertility for plant growth in the end.

Relationship between laboratory work and the field

Because the members of the microbial community and the microarthropod community are often specific to a certain site, it is important to relate laboratory studies to particular field sites. Some studies which have done this particularly well are: the body of Luxton's work (1972, 1979, 1981 a, b and c), which focused on a Danish beech woodland soil and Mitchell & Parkinson's (1976) work in an aspen woodland soil. In order for information gained from laboratory studies to have real ecological relevance, species to be used in the laboratory should be selected based on the real soil communities from the field.

Methods

Field collections

All of the microarthropods used for the laboratory experiments were collected at the Burns field sites, (described in Chapter 2) except for some of the *Oppiella nova*, which were collected locally in Corvallis, Oregon. Collections were made at each of the four plots, at least 30 m away from the transects used by Christine Niwa and Jane Smith's groups for microarthropod and mycorrhizal community sampling. Four soil samples (top 5 cm soil plus the litter layer) were collected in each of the burn treatments, two from heavily burned patches of ground (litter consumed) and two from lightly burned patches of ground (litter scorched, but not consumed). Two samples were collected within the control treatments. These collections yielded 123 morphospecies. Species for the laboratory studies were selected based on abundance in the field and their ability to survive in laboratory cultures.

Laboratory studies

I conducted several different studies, aimed at clarifying the role of some of the microarthropod species within the belowground food web. The first and third, a feeding preference study and a fungal competition study, were aimed at describing some of the interactions between microarthropods and the fungi they feed upon. The isotope study investigated the field feeding habits of some of the species not used in the previously mentioned laboratory work. These data were used primarily to determine the trophic levels of the various microarthropods.

Feeding preference studies

The feeding preference study was a cafeteria type experiment, where 8 different types of fungi were offered to the animals in a small arena (Figure 5). The arenas were constructed in small glass petri dishes, with the bases covered with plaster of Paris, with eight wells. A barrier of parafilm was placed around the rim of the dish, underneath the lid to create a seal and prevent microarthropod escape.

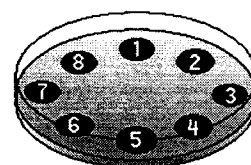


Figure 5. Feeding preference dish setup. Wells # 1-8 each contain a different fungal culture, in random order.

The fungi were grown on small plugs of agar, contained in 13 mm vial caps. These fungal mini-cultures were used so that actively growing fungi could be offered to the animals. When the fungal plug cultures and the animals were added to the dishes, the arenas were monitored for one week and the microarthropods feeding on each fungal plug were counted twice each day. After 14 observations, the experiment was terminated.

The microarthropod species used for this experiment are: *Hypogastrura* sp. (Collembola, Hypogastruridae), *Onychiurus* 1 and 2 (Collembola, Onychiuridae), *Caenobelba* sp. (Oribatida, Damaeidae), *Joshuella* sp. (Oribatida, Gymnodamaeidae), *Eremaeus* sp. (Oribatida, Eremaeidae), *Galumna* sp. (Oribatida, Galumnidae), *Oppiella nova* (Oribatida, Oppiidae), *Tectocephus* sp. (Oribatida, Tectocephidae), *Scheloribates* sp. (Oribatida, Scheloribatidae) and Nanorchestidae (Endeostigmata).

Hypogastrura sp. is a medium-sized springtail (.75 to 1.25 cm length) with a small furculum and short antennae. *Onychiurus* sp. 1 is a small species. This springtail is miniscule and has a streamlined form. Its body size and shape suggest that it is a deep soil inhabitant. *Onychiurus* sp. 2 is a relatively large springtail, between 1 and 1.5 mm in length. Its body form is less streamlined than *Onychiurus* sp. 1.

Eremaeus sp., *Galumna* sp. and *Scheloribates* sp. are all large mites (.75 – 1mm), with highly sclerotized cuticles and very dark coloring. *Tectocephus* sp. and *Oppiella nova* are both small oribatid mites, approximately 0.1 times the size of *Galumna* sp. The mite in the family Nanorchestidae is smaller than *O. nova* and has an iridescent soft body covered with short hairs. These mites jump to evade capture, making handling difficult.

The fungi used in this experiment are: *Epicoccum nigrum*, *Morchella* sp., *Fusarium* sp., *Coenococcum geophilum*, *Leptographium wagnerii*, *Trichoderma viride*, *Armillaria ostoye* and *Penicillium* sp.

Statistical analyses were conducted in SAS (1996), using a series of ANOVA models, one for each individual arthropod species. These models described how arthropod counts varied for the different fungi (count = fungi). Each animal's feeding preference order was created using the least squares means of its ANOVA model.

Stable isotope studies

The natural abundance of ^{13}C and ^{15}N in the bodies of several microarthropod species were measured by combustion and mass spectroscopy. The arthropods used for this portion of the study were collected at the Burns field site, in the control plots only, because the C and N fractionation within the soil from the fires could cause an additional confounding factor to interpretation of these data. Only some of the species collected were used in this study, due to the need for adequate mass in order to obtain N data. Those species included in this section of the study are listed in Table 4.

Measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were made at the Corvallis Environmental Protection Agency's isotope analysis facility. Samples of a minimum mass of 33 mg were used. These samples were placed in small tin cups and burned in an oven. The CO_2 and N_2 emitted from combustion were then isolated with gas chromatograph. The separated gasses were then routed through a mass spectrometer, to measure the ratios $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$. The machine was calibrated using liver, oyster and spinach standards. The data from this analysis included $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ ($\pm 0.2\text{‰}$).

Because of sample size limitations, statistical analysis was not performed. Raw data are presented graphically for evaluation in Figure 7.

Table 4. Arthropods used in stable isotope studies.

Arthropod Isotope Study Species List
<i>Galumna</i> sp.
<i>Eremaeus</i> sp.
<i>Oppiella nova</i>
<i>Gamasina</i>
<i>Scheloribates</i> sp.
<i>Camisia</i> sp.
<i>Caenobelba</i> sp.

Fungal competition studies

The potential impacts of microarthropod grazing on fungal competition were estimated in the following experiment. The experimental arenas were small glass jars, with plaster of paris in the bottom, with one well in the middle, sized to fit one of the 13 mm agar discs (Figure 6).

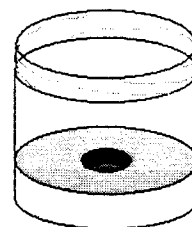


Figure 6: Culture jars for the competition experiments

Fungi for the competition studies were cultured in a similar manner as those fungi used for the feeding preference studies, except for the fact that 2 fungi were grown on each agar disc. There were 6 fungi, combined factorially to make 15 different pair combinations. These species included *Armillaria ostoye*, *Trichoderma viride*, *Leptographium wagnerii* var. *ponderosum*, *Coenococcum geophilum*, *Epicoccum nigrum* and *Morchella* sp.

Trichoderma viride and *Epicoccum nigrum* are both saprotrophic. *Leptographium wagnerii* var. *ponderosum* and *Armillaria ostoye* are both root pathogens on ponderosa pines. *Fusarium* sp. is another pathogen, causing a disease called pitch canker, in different pines (Farquhar & Petersen 1991). The morel is also generally considered a soil saprotroph. *Coenococcum geophilum* is a mycorrhizal fungus on many ponderosa pines. These fungi may interact within the soil as they compete for space and nutrients. *Trichoderma viride* has been shown to act as a biocontrol agent for *A. ostoye* (Reaves et al. 1990), a common root pathogen ponderosa pine forests. *T. viride* might even act in this manner upon other pathogenic fungi, such as *Phellinus* (Goldfarb et al. 1989).

After the fungal cultures were placed within the jar, the animals were added. Fifteen *Galumna* sp. (mites), 15 *Hypogastrura* sp.(springtails) or zero animals were

added to the jar. Each experiment ran for one week and was checked twice daily, for a total of 14 observations per culture. The arthropods feeding on each fungus were counted and the approximate percent cover of each fungus over the entire dish was estimated. Each factorial combination was replicated 4 times, except for some of the combinations involving the *Galumna* sp. For some of the *Galumna* sp. combinations, the number of replications was reduced to 3, due to limitations on the numbers of individuals available.

Statistical analyses were carried out using SAS for Windows, version 6.12 (1996). Separate ANOVA models were carried out separately for each fungal species. The variables included in the models initially were change=competing fungus, Arthropod, competing fungus*Arthropod (competing fungus being the competing species in each pair). Non-significant interaction terms (at the $\alpha = 0.1$ level) were eliminated to provide simple models where the highest level of interaction was always significant.

I also investigated whether or not arthropod feeding preference was influenced by the fungal pairings. Using the arthropod count data from the competition experiment, I built ANOVA models using the same method listed above, with the following changes: I used arthropod 'counts' as my response variable, instead of 'change'. For the *A. ostoye* count model, the data were logged for analysis and then back-transformed for display.

Results

Feeding preference

The various fungi had different levels of overall palatability. *Epicoccum nigrum* and *Morchella* sp. were the most highly preferred when considering all of the feeding preference trials together. *Fusarium* sp., *Coenococcum geophilum* and *Leptographium*

wagnerii were intermediate in their overall palatability, while *Trichoderma*, *Armillaria* and *Penicillium* were less favored. The ranking of the different fungi differed for each animal experimental group.

The feeding preference hierarchies were slightly different for the different springtails (Table 5). *Hypogastrura* sp. showed a strong preference for the plant pathogen, *Fusarium* sp. Next in line were *L. wagnerii* and *Morchella* sp., followed by *E. nigrum* and *A. ostoye*. *Trichoderma viride*., *C. geophillum* and *Penicillium* sp. were its least favorite food-choices. *Onychiurus* sp.1 most preferred *Morchella* sp. They would also feed upon *E. nigrum* and *Fusarium* sp., but hardly touched any of the other fungi offered. *Onychiurus* sp. 2 fed heavily on *E. nigrum* and fed moderately on *C. geophillum*. It was sometimes observed on *Fusarium* sp. and *Morchella* sp. and rarely or never observed on *A. ostoye*, *L. wagnerii*, *Penicillium* sp. and *T. viride*. It appears likely that if replicated feeding preference trials were conducted with this species, *Hypogastrura* sp. would show a statistical difference between its feeding levels of *E. nigrum* versus all of the other fungi. It is also possible that *C. geophillum* would be statistically preferred as well.

The oribatid mites also showed variable hierarchies (Table 5). *Oppiella nova* did not feed heavily on any fungi, but it fed the most upon *Fusarium* sp., *E. nigrum* and *Morchella* sp. It was almost never found on *A. ostoye* or *T. viride*. *Galumna* sp. fed fairly heavily upon *E. nigrum* and *L. wagnerii*. *Morchella* sp. and *A. ostoye* were intermediate, followed by *C. geophillum* and *Fusarium* sp. *Penicillium* sp. and *Trichoderma* were almost never utilized.

Joshuella sp. was not strongly attracted to any of the choices offered. It was sometimes present on *L. wagnerii*, but was almost never found upon any of the other species. I suspect that I simply did not offer the preferred food of this known fungal feeder. Fungal spores are often found in this mite's gut (Andrew Moldenke, personal communication) and most of the fungi offered were not mature enough (or perhaps were not growing on the proper media) to produce spores, except for *Penicillium* sp. and *T. viride*. However, these two fungi are rich in secondary chemicals, which may have deterred feeding. Another alternative explanation is that this is a small mite with a slow metabolism and therefore does not feed frequently.

Tectocephus sp. had a similar reaction to the fungal offerings as did *Joshuella* sp. It showed limited interest in all of the fungi. This may have been because none of the fungi that were offered were its preferred food. It has been reared successfully in the laboratory of Andrew Moldenke on *Cladosporium* sp. It was observed on all of the different fungi, except for *A. ostoye* and *Penicillium* sp.

Eremaeus sp. fed fairly heavily upon *E. nigrum*, moderately on *C. geophillum*, *Morchella* sp. and *Fusarium* sp. and lightly on *T. viride*. I could not detect a significant difference between the levels of feeding on each of these fungi, probably because of inadequate replication. Only two dishes, each containing approximately 8 *Eremaeus* sp. were used. It seems likely that *Eremaeus* sp. would show a statistical feeding preference for *E. nigrum* and *C. geophillum* with more replicates.

Scheloribates sp. fed most upon *E. nigrum* and moderately on *Fusarium* sp. and *C. geophillum*. It is likely that a statistical preference for *E. nigrum* could be shown with replication.

Table 5. Feeding preference ANOVA model coefficients and overall probability. Abbreviations: Arm = *Armillaria ostoye*, Coe = *Coenococcum geophilum*, Epi = *Epicoccum nigrum*, Fus = *Fusarium* sp., Lep = *Leptographium wagnerii*, Mor = *Morchella* sp., Pen = *Penicillium* sp., Tri = *Trichoderma viride*.

Overall		<i>Hypogastrura</i> sp.		<i>Onychiurus</i> sp.1		<i>Onychiurus</i> sp. 2	
Fungus	Coeff.	Fungus	Coeff.	Fungus	Coeff.	Fungus	Obs.
Epi	0.117	Fus	2.005	Mor	0.295	Epi	4.522
Mor	0.101	Lep	0.630	Epi	0.190	Coe	1.130
Fus	0.065	Mor	0.605	Fus	0.145	Fus	0.348
Coe	0.053	Epi	0.375	Coe	0.090	Mor	0.217
Lep	0.040	Arm	0.265	Lep	0.060	Arm	0.043
Tri	0.014	Tri	0.150	Tri	0.050	Lep	0.043
Arm	0.010	Coe	0.120	Arm	0.025	Pen	0.043
Pen	0.003	Pen	0.115	Pen	0.005	Tri	0.000
n = 32, P = 0.0001 *		n = 5, P = 0.0001 (0.165)		n = 5, P = 0.0014 (0.045)		n = 1 **	

<i>Oppiella nova</i>		Nanorchestidae		<i>Galumna</i> sp.		<i>Joshuella</i> sp.	
Fungus	Coeff.	Fungus	Coeff.	Fungus	Coeff.	Fungus	Coeff.
Fus	0.389	Coe	0.469	Epi	2.183	Lep	0.117
Epi	0.342	Mor	0.400	Lep	1.733	Arm	0.056
Mor	0.252	Tri	0.281	Mor	0.583	Epi	0.017
Coe	0.049	Lep	0.175	Arm	0.225	Fus	0.014
Lep	0.035	Arm	0.163	Coe	0.192	Coe	0.011
Pen	0.025	Epi	0.019	Fus	0.175	Mor	0.008
Arm	0.015	Fus	0.006	Pen	0.008	Tri	0.006
Tri	0.007	Pen	0.000	Tri	0.008	Pen	0.005
n = 5, P = 0.0364 *		n = 4, P = 0.211 (0.155)		n = 3, P = 0.0001 (0.088)		n = 3, P = 0.9109 *	

<i>Eremaeus</i> sp.		<i>Tectocephus</i> sp.		<i>Scheloribates</i> sp.		<i>Caenobelba</i> sp.	
Fungus	Coeff.	Fungus	Coeff.	Fungus	Obs.	Fungus	Obs.
Epi	1.643	Fus	0.150	Epi	1.275	Epi	0.778
Coe	0.815	Lep	0.088	Fus	0.625	Pen	0.444
Mor	0.685	Mor	0.075	Coe	0.250	Arm	0.333
Fus	0.542	Epi	0.063	Mor	0.175	Lep	0.222
Tri	0.161	Coe	0.050	Tri	0.075	Mor	0.111
Lep	0.071	Tri	0.025	Arm	0.000	Tri	0.111
Pen	0.071	Arm	0.000	Lep	0.000	Coe	0.056
Arm	0.042	Pen	0.000	Pen	0.000	Fus	0.000
n = 2, P = 0.175 (0.381)		n = 2, P = 0.7273 (0.063)		n = 1 **		n = 1 **	

* No standard error listed because data were logged for analysis. Back-transformed model coefficients are presented here.

** No standard errors or P-values listed because n=1.

Caenobelba sp. also fed most upon *E. nigrum* and moderately on some of the other fungi. One interesting trend to note with this arthropod was that it was fairly frequently found on *Penicillium* sp. This was the only species that showed *Penicillium* sp. towards the top of its feeding preference hierarchy. *Armillaria ostoye* was also fairly high on the list, which was unusual. Perhaps this indicates that *Caenobelba* sp. avoids competition by specializing on fungi with secondary chemicals that repel other microarthropods.

From the data collected, the Nanorchestid mite appeared to prefer *C. geophillum* and *Morchella* sp. and to also use *T. viride*, *L. wagnerii* and *A. ostoye* occasionally. However, no statistical differences are evident due to a larger standard error. It was impossible to ascertain whether these mites were actually feeding under a dissecting microscope because of their small size. Therefore, these data simply indicate mite presence or absence, not necessarily feeding. Their suggested preference for *C. geophillum* may have been due more to its fluffy structure, rather than its palatability. This structure provided good cover for this poorly-protected mite. Also, it was difficult to ascertain whether these mites were alive or dead. Multiple observations were sometimes made of the same mite in the same place on the same fungus. Therefore, the 'count' is not necessarily indicative of multiple feeding episodes. Due to the lack of movement, it seems unlikely that these mites were actively feeding. If they were actively feeding, they may have been sucking down the cellular contents of the hyphae instead of macerating them, as some of the larger oribatids do. Schuster & Schuster (1977) suggested that mites in this family are probably fluid feeders (probably on algae) because of the structure of their mouthparts.

Stable isotopes

The individual microarthropods appeared to have different characteristic isotopic signals, especially for N (Figure 7). This may suggest that they occupy different positions on the decomposer food chain. Those animals that are richer in ^{15}N (the gamasid mites and the *Oppiella nova*) may tend to feed either on other animals in the decomposer community or on fungi that have assimilated a substrate that is also relatively rich in ^{15}N .

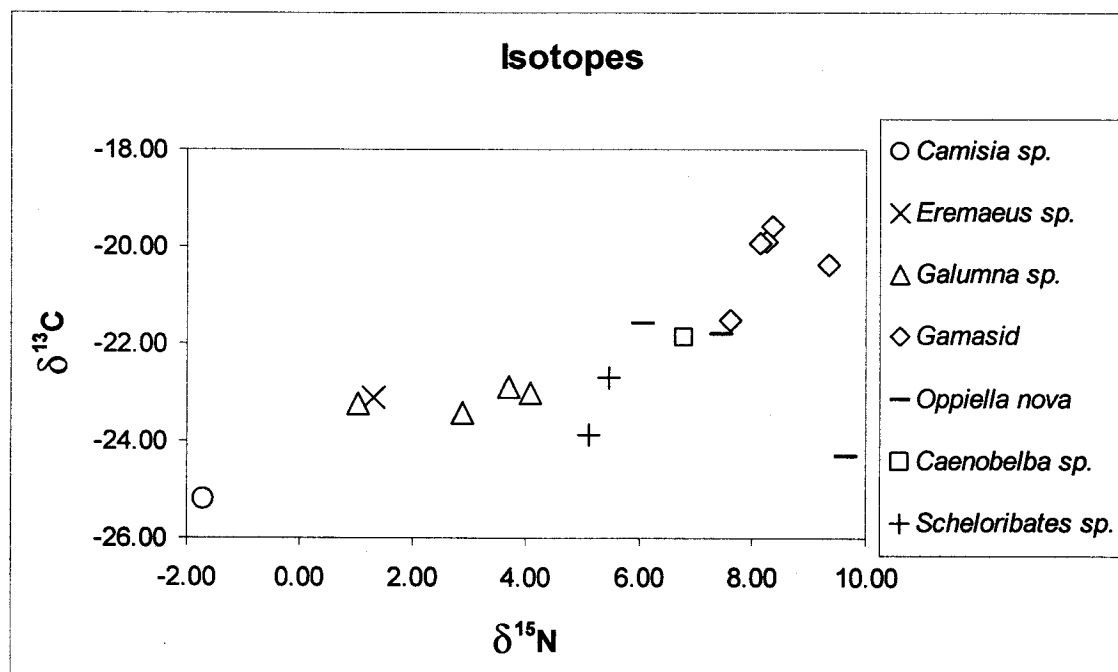


Figure 7. Stable isotope signals of the different microarthropods.

As expected, the information for C was much less clearly defined. The spread of the ^{13}C isotopic signal was less than for the ^{15}N isotopic signal (Figure 7). Therefore, it was more difficult to separate out the different arthropods using only C, because the

signal yielded lower resolution. The gamasid mites had the highest $\delta^{13}\text{C}$ value. *Oppiella nova* showed a wide range of signals, while *Galumna* sp. was consistent in its $\delta^{13}\text{C}$ measurements.

When plotted in two dimensions, the C and N signals for the different microarthropods sort out fairly clearly. *Camisia* sp. showed the lowest values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, while the gamasid mites had the highest. All of the other mites fell somewhere in between. It is difficult to pinpoint the exact location of *O. nova* along the line because of its wide range in C signals.

Fungal competition

Change in cover

All models describing the change in cover of each fungus, except for *Trichoderma viride*, included an interaction term: competing fungus*arthropod (Table 6). This interaction term indicates that the change in size of the fungal thallus depended on both the identity of the competing fungi and also on the presence/absence or identity of the microarthropods. It also means that the impact of the various arthropod treatments was different, depending on the identity of the fungal competitor. For *T. viride*, the interaction term was dropped, leaving both of the main effects, indicating that *T. viride* interacted differently with different fungi and also experienced somewhat lower growth in the presence of grazers (Table 6).

Table 6. ANOVA models for competition experiment.

Fungus	df	Type III F	P-value
<i>Armillaria ostoye</i>			
Competing fungus	4	2.36	0.0672
Arthropod	2	5.81	0.0057
Competing fungus X Arthropod	8	1.86	0.0898
Error	31		
<i>Coenococcum geophilum</i>			
Competing fungus	4	18.77	0.0001
Arthropod	2	9.88	0.0003
Competing fungus X Arthropod	8	5.77	0.0001
Error	31		
<i>Epicoccum nigrum</i>			
Competing fungus	4	5.11	0.0012
Arthropod	2	13.17	0.0001
Competing fungus X Arthropod	8	3.27	0.0035
Error	49		
<i>Morchella</i> sp.*			
Competing fungus	4	1.07	0.3768
Arthropod	2	1.71	0.1883
Competing fungus X Arthropod	8	2.46	0.021
Error	53		
<i>Leptographium wagnerii</i>			
Competing fungus	2	112.82	0.0001
Arthropod	2	3.44	0.0408
Competing fungus X Arthropod	8	8.04	0.0001
Error	30		
<i>Trichoderma viride</i>			
Competing fungus	4	80.02	0.0001
Arthropod	2	3.8	0.027
Error	64		

*data logged for analysis.

Several patterns are evident from these analyses. The first pattern is that the fungus did not change much from beginning to end, regardless of the presence, absence or identity of the microarthropods. The competing fungus also did not negatively impact the growth of these fungi. This pattern is commonly seen with the slow-growing,

unpalatable fungi, especially *A. ostoye* and *C. geophillum* (Figure 8c,d). The second pattern to note is that the presence of grazers resulted in a reduced fungal thallus, compared with the control. This pattern was especially evident with *Morchella* sp. and *E. nigrum*, two of the fungi that were among the more preferred fungi in the feeding preference experiments. In this case, fungal thallus reduction was mostly caused by microarthropod grazing, not competition. In other cases, it was evident that competition limited fungal growth.

A related pattern here is that the presence of microarthropods seems to lessen competitive inhibition between some fungi. This is most evident for the pairing of *C. geophillum* and *E. nigrum*. The fungal thallus of *C. geophillum* did not diminish as much in the presence of arthropod grazers (Figure 8c), while the fungal thallus of *E. nigrum* did not grow as much in the presence of those grazers (Figure 8b).

In the case of *L. wagnerii*, competition posed the most serious threat to its growth. It was an exceptionally poor competitor with both *E. nigrum* and *T. viride* (Figure 8a). In the case of its pairing with *E. nigrum*, the presence of grazers lessened competitive inhibition to some extent. In the case of its pairing with *T. viride*, neither arthropod changed the outcome. *Leptographium wagnerii* was always virtually eliminated (overgrown) by the end of the week. *Morchella* sp. was also a poor competitor when paired with *E. nigrum* and *T. viride*. Grazing by *Galumna* sp. slightly lessened competition effects with *E. nigrum*, while springtail grazing did not.

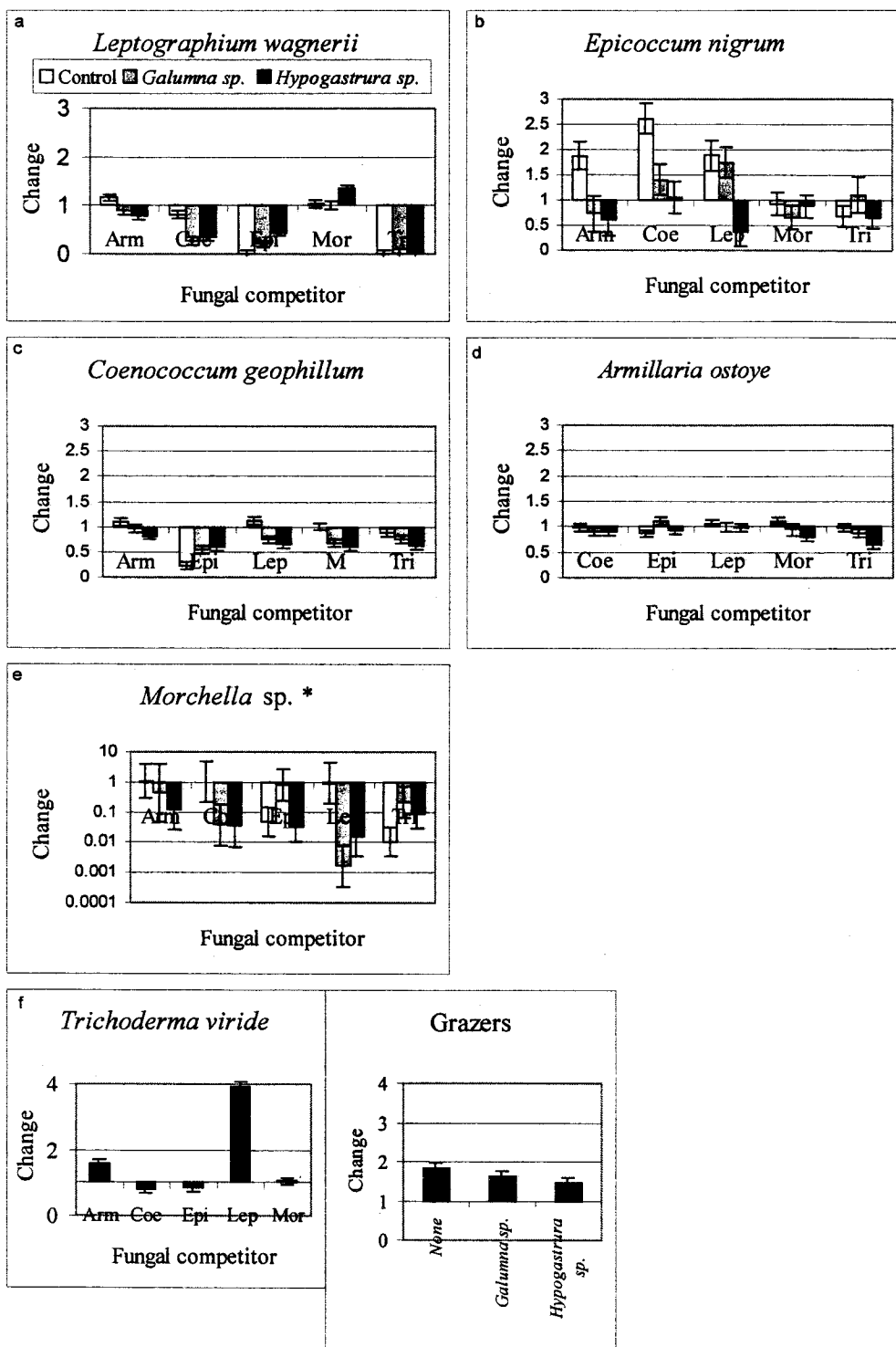


Figure 8. ANOVA model parameter results for competition experiment. Abbreviations: Arm = *Armillaria ostoye*, Coe = *Coenococcum geophilum*, Epi = *Epicoccum nigrum*, Lep = *Leptographium wagnerii*, Mor = *Morchella* sp., Tri = *Trichoderma viride*.

* Data logged for analysis and back-transformed for display.

Trichoderma viride's growth was determined overwhelmingly by its relative ability to out-compete the other fungus. There was no statistically significant interaction term in its model (Table 7). This was probably caused by its ability to totally take over *L. wagnerii*. Although it also grew well against *A. ostoye*, its growth in these dishes was not paired with a loss in the area of *A. ostoye*. Against the various other fungi, its thallus was either slightly reduced or did not change from zero (Figure 8f).

In some cases, the impacts of grazing were different between *Galumna* sp. and *Hypogastrura* sp. This was especially evident in the pairing of *E. nigrum* and *L. wagnerii*. *Epicoccum nigrum*'s thallus was reduced in the presence of *Hypogastrura* sp., but was not reduced in the presence of *Galumna* sp. (Figure 8b). This might be accounted for by the different feeding preferences or perhaps the different feeding habits of the two arthropods. A similar trend was observed with *Morchella* sp. paired with *E. nigrum*. *Epicoccum nigrum* almost disappeared in the presence of *Hypogastrura* sp. and also in the control dishes (Figure 8e). However, when *Galumna* sp. was present, *Morchella* sp. persisted throughout the experiment.

Another pattern I observed in this experiment was that grazing lessened the impacts of competition for the less preferred species. This was shown by *C. geophillum*, *Morchella* sp. and *L. wagnerii* in certain pairings (Figure 8a,c,e). The reverse trend was also seen. Grazing could decrease the competitive superiority of some of the more preferred species. The latter pattern was shown primarily with *E. nigrum*'s interactions. Sometimes the grazing action of the microarthropods would not change the competitive balance of the fungi. In fact, sometimes they would create clear space on the agar, free of fungi.

In the case of *T. viride*, the effects of grazing were overshadowed by its competitive interactions. This is probably why there

was no interaction term in the original *T. viride* model. The original model was

primarily driven by *T. viride*'s dominance over *L. wagnerii*. *Leptographium wagnerii* was always overgrown by *T. viride* at the end of the experiment. However, when the rate of change of *T. viride* cover was modeled, an interaction term emerged (Table 7). This interaction term was manifested primarily in the interaction of *T. viride*'s competition with *C. geophilum* (Figure 9). *Trichoderma viride* completely lost its ability to compete with *C. geophilum* when *Hypogastrura* sp. was present. Its rate of change was negative instead of positive or zero.

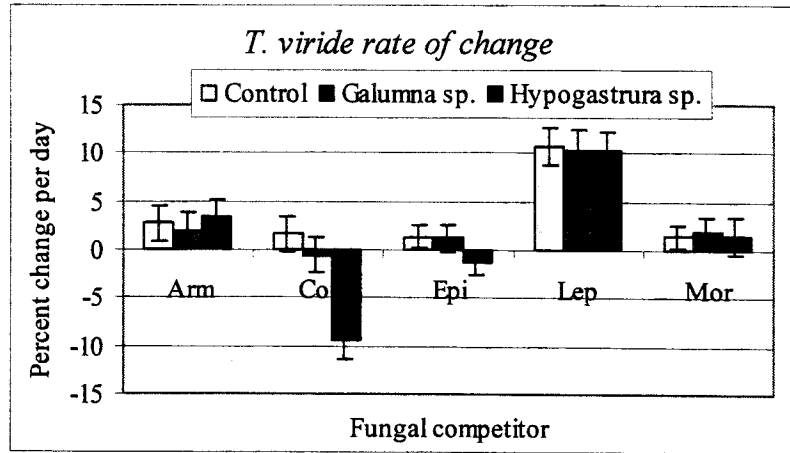


Figure 9. *Trichoderma viride* rate of change model
Abbreviations: Arm = *Armillaria ostoye*, Coe = *Coenococcum geophilum*, Epi = *Epicoccum nigrum*, Lep = *Leptographium wagnerii*, Mor = *Morchella* sp., Tri = *Trichoderma viride*.

Table 7. Model effects for *Trichoderma viride* rate of change model

<i>Trichoderma viride</i>	Df	Type III F	Pr > F
Competing fungus	4	20.52	0.0001
Arthropod	2	3.44	0.0382
Competing fungus X Arthropod	8	2.06	0.0536

Counts

The fungi could be ranked according to feeding preference within the fungal competition experiments as well. These rankings were not always consistent with those from the simple feeding preference experiments. Because there is a three-way interaction term in the combined model, it is evident that arthropod feeding was influenced by all of the variables (the identity of the fungus, the identity of its competitor and the identity of the feeding arthropod) (Table 9). Looking at the models for the individual fungi, we can see that arthropod feeding depended on

Table 8. Models describing arthropod counts.

Fungus	DF	Type III F	Pr > F
<i>T. viride</i>			
Competing fungus	4	5.09	0.0019
Arthropod	1	3.65	.0630
Error	38		
<i>Morchella</i> sp.			
Competing fungus	4	3.29	0.0186
Error	42		
<i>E. nigrum</i>			
Competing fungus	4	5.55	0.0013
Arthropod	1	25.52	<.0001
Competing fungus*Arthropod	4	3.1	0.0264
Error	29		
<i>L. wagnerii</i>			
Competing fungus	4	42.67	<0.0001
Error	28		
<i>C. geophilum</i>			
B	4	15.57	<.0001
Arthropod	1	67.51	<.0001
Competing fungus*Arthropod	4	3.8	0.013
Error	21		
<i>A. ostoye</i> *			
Competing fungus	4	3.10	0.0307
Arthropod	1	12.09	0.0016
Error	24		
Combined			
Arthropod	1	49.96	<.0001
A*Arthropod	5	9.53	<.0001
Competing fungus*Arthropod	6	0.7	0.6513
A*Competing fungus*Arthropod	18	2.02	0.0102
Error	174		

* data logged for analysis

different factors for the various fungi. Sometimes, an interaction of the identity of the competing fungus and the identity of the microarthropod predicted the number of animals counted upon each fungi.

It is interesting to note the heavy feeding upon *L. wagnerii* when it was paired with the morel, because that heavy feeding does not correspond with a diminished percent cover of *L. wagnerii* (Figure 8a, Figure 10b). It appeared that the arthropods also fed heavily on *Morchella* sp. (Figure 8e, Figure 10a). Therefore, although *L. wagnerii* experienced grazing pressure, it was also simultaneously experiencing competitive

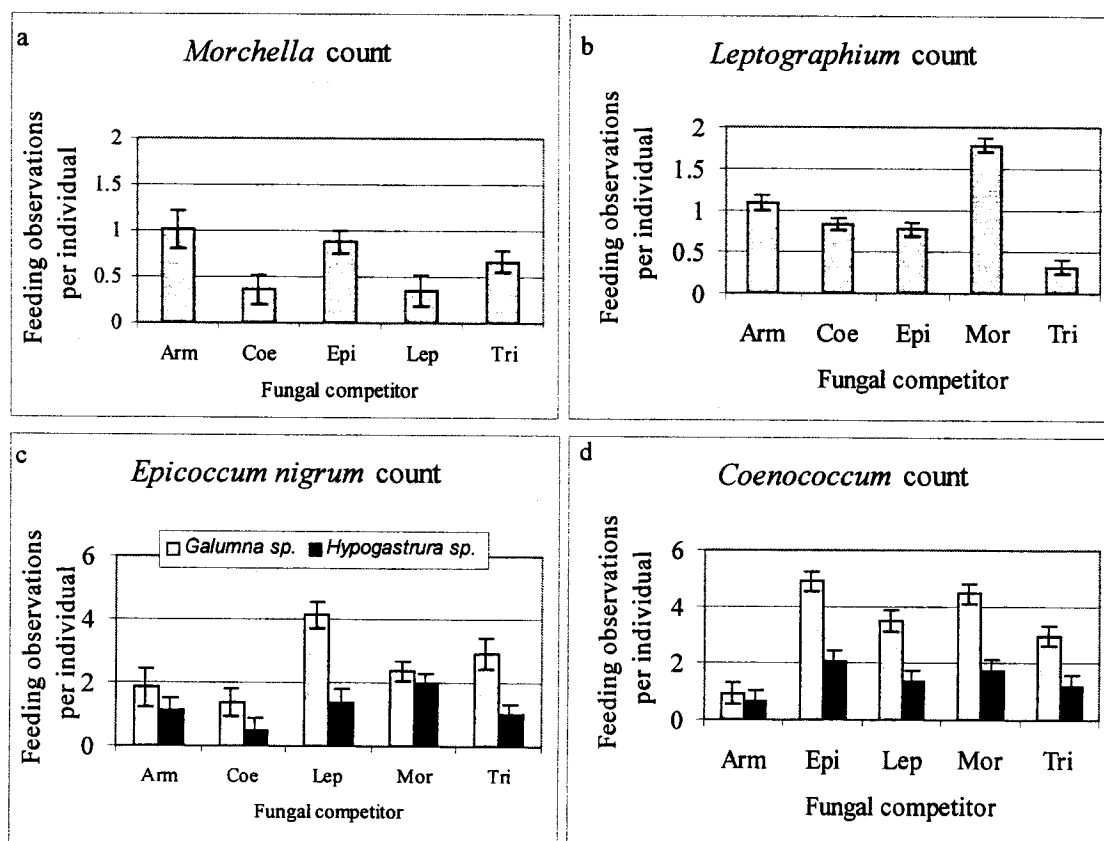


Figure 10. Arthropod counts from competition experiments. Abbreviations: Arm = *Armillaria ostoye*, Coe = *Coenococcum geophilum*, Epi = *Epicoccum nigrum*, Lep = *Leptographium wagnerii*, Mor = *Morchella* sp., Tri = *Trichoderma viride*.

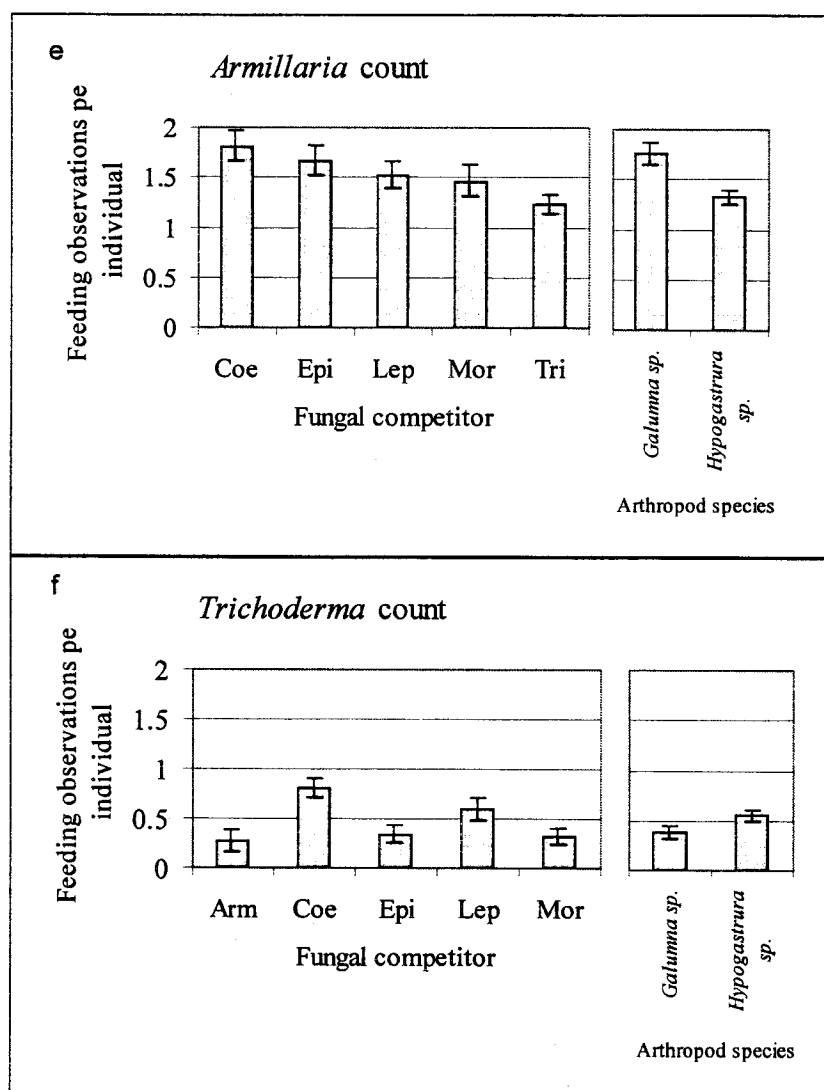


Figure 10, Continued.

release. *Morchella* sp. did not have strong grazing pressures according to the count data (Figure 10a), although its cover did drop in the presence of grazers (Figure 8e).

These counts were not entirely inconsistent with the initial feeding preference trials. *Epicoccum nigrum* was often heavily fed upon, as was *L. wagnerii* (Figure 10 b,c). *Coenococcum geophilum* also often had arthropods present on it. However, it is likely that this reflects oviposition by *Galumna* sp., not feeding.

Discussion

Feeding preference

The 'overall' results for the feeding preference trial do not necessarily reflect the feeding patterns of a true soil microarthropod community. The relative abundance of the study organisms was selected primarily by my ability to collect sufficient numbers of them in the field and to keep them alive in laboratory cultures long enough to work with them. The overall feeding preference of a real soil microarthropod community will reflect the microarthropod community composition in the field. This microarthropod community structure may change a lot from microsite to microsite in the forest floor.

Species dominance is important to consider when hypothesizing how a microarthropod community might impact a fungal community. For example, if *Hypogastrura* sp. is exceptionally abundant, then it seems likely that *Fusarium* sp. will be limited. If *Fusarium* sp. is not available, then perhaps *L. wagnerii* or *Morchella* sp. will be impacted heavily. On the other hand, if *Galumna* sp. is dominant, perhaps *Fusarium* sp. may persist while *E. nigrum* is impacted heavily by grazing pressures. If the microarthropod community is small or if it is highly diverse and the populations of all the various microarthropods with different feeding preferences are well-balanced, then competition within the soil fungal community might not be changed by grazing pressures.

Some of the various microarthropods used have a stronger potential to impact fungal populations than others. They might have higher metabolic rates and have to feed more. This difference can be seen between *Hypogastrura* sp. (relatively high feeding rates) and some of the other microarthropods, like the slow-moving *Joshuella* sp. This is

compounded by the high reproductive rate of *Hypogastrura* sp. In some of the field samples, *Hypogastrura* sp. was extremely abundant. However, its distribution (in both space and time) was patchy. In patches of soil with high densities of voraciously feeding springtails, the palatable fungi may be strongly impacted. *Oppiella nova* was also relatively abundant and its numbers were more evenly distributed. However, due to its small size and the fact that negative impacts on fungal colony growth were not visually detectable in the feeding preference experiments where it was present, it seems unlikely that this arthropod will negatively impact fungal growth, unless it is extremely abundant. Further research, measuring ingestion rates of the different microarthropods, might yield better estimates of each microarthropod species' potential to impact fungi.

Another interesting point to think about from the feeding preference trials is that these types of trials may help to explain some of the diversity of fungivores within the forest floor. Maraun et al (1998) guessed that this might be the case, but his results did not support the hypothesis. In my feeding preference trials, some resource partitioning was apparent, although feeding preference orders were consistent between many species. The exception was *Caenobelba* sp. It was the only arthropod which fed upon *Penicillium* sp. and *A. ostoye* (feeding coefficient >.3).

Unfortunately, my data are not directly comparable with Kaneko et al.'s 1995 study, as we did not use the same fungal taxa within our experiments. *Oppiella nova*'s preference for the dark septate fungi over those with hyaline hyphae was not shown in my experiment. *Fusarium* sp. (light-colored) was ranked near the top, while *A. ostoye* (dark-colored) was rarely touched. *Oppiella nova*'s preference for *A. ostoye* and *Fusarium* sp. was also reflected in the overall rankings.

Stable isotopes

The stable isotope data do indicate that the microarthropods collected for this analysis showed distinct isotopic signals for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, suggesting that they had distinct diets in the field. This is good information to pair up with the feeding preference data because it lends support to the hypothesis that these microarthropods do partition resources below ground. Microarthropods with similar laboratory feeding preferences may modify their feeding habits in the complex world of the field. Whether microarthropod isotopic ratios can be used to make definitive statements about microarthropod feeding habits requires more study. More background work and a larger-scale study are both needed. However, initial results are promising.

It still remains to be seen whether it is possible to determine, from isotopic ratios, whether mycorrhizal or saprotrophic fungi dominate a microarthropod's diet. From my data, the C signal variability is too large for this trend to appear. Additionally, microarthropod diets are complex, including pathogenic fungi (*Fusarium* sp. and *L. wagnerii* in this study) which obtain their C from plants, as do the mycorrhizal fungi, but do not pass N to their plant hosts. The different strategies of obtaining and passing on nutrients exhibited by different fungi will each result in a different signal for the fungal thallus. Microarthropods may also assimilate some bacterial C or N or occasionally feed on other animals, further confusing their signal. Thus, a two or even a three-end mixing model to explain microarthropod isotopic ratios is probably inappropriate.

One trend that can be seen fairly well is that the gamasid mites have a relatively distinct, high signal for both C and N isotopes (Figure 7). Their higher ^{15}N signal indicates that they are assimilating N higher up along the food chain than the other

arthropods studied. This is consistent with the hypothesis that they tend to be predatory (Walter 1988a), rather than microbivorous. At the other end of the spectrum, *Camisia* sp.'s signal is very low (Figure 7). Although this is a single sample, it was made up of 8 individual mites, so this signal probably is not just an error. Many *Camisia* sp. are lichen-feeders (André & Voegtlin 1981), so they may be obtaining their C and N from relatively unfractionated sources.

Fungal competition

An interesting example of how microarthropod feeding can influence competition is seen with *Morchella* sp. paired with *E. nigrum*. The presence of *Galumna* sp. allowed *Morchella* sp. to persist throughout the experiment. In this case, the heavily feeding *Galumna* sp. probably fed more heavily on *E. nigrum*, thus freeing *Morchella* sp. from excessive competition. However, as was the case with the above-discussed pairings, the count data do not support this theory. It is possible that *Morchella* sp. is more able to respond to mild grazing with a compensatory response than is *E. nigrum*. This could explain why *E. nigrum*'s competitive ability was reduced, despite the fact that it experienced the same amount of grazing as did *Morchella* sp.

There are two explanations for the fact that some of the fungi (especially *A. ostoye* and *C. geophillum*) did not change their cover markedly through the course of the experiment. First of all, their ungrazed growth rates were fairly slow and they were not inhibited by competition with other fungi (with the exception of *C. geophillum* paired with *E. nigrum*). One potential reason that these fungi were not inhibited by competition may be the fact that they were always well established in the fungal plug culture before

the competing fungus was introduced. Because of their slow growth rates, I had to let them establish well in advance of the competitors in order to approximate a 50:50 starting ratio for the fungal pairs in the competition experiments. In a natural environment, competition might be an important factor in determining their growth as they initially colonize a substrate. The second explanation is that *A. ostoye* and *C. geophillum* did not appear to be heavily impacted by grazing. This is confirmed by the fact that they were not heavily fed upon in the feeding preference trials either. Their feeding coefficients were generally below 0.3 observations/animal. On the other hand, when these data were paired with the animal counts for the competition experiments, the picture becomes more confusing. *Coenococcum geophillum* exhibited relatively high *Galumna* sp. counts, which suggests that it was under heavy grazing pressure. However, this might not have been the case in reality, because *Galumna* sp. females appeared to prefer using *C. geophillum* as an oviposition site, hiding their eggs within the fluffy thallus.

One pattern that I did not observe was an overcompensatory growth response to feeding pressure. There are two major reasons which could explain why this was the case. First of all, it is likely that the grazing intensity experienced by the fungi was too high for overcompensation. Secondly, it is also likely that different fungi have various responses to grazing impacts, just as different fungi have various palatability levels. The fungus that has been shown to exhibit a compensatory growth response to microarthropod grazing is *Mortierella isabellina* (Bengtsson & Rundgren 1983; Hedlund et al. 1991), which I did not use in the experiments. It is possible that the fungi I used simply do not exhibit overcompensatory growth in response to microarthropod feeding.

Another pattern which was surprisingly absent, was competitive inhibition of *A. ostoye* by *T. viride*. This interaction between *A. ostoye* and *Trichoderma* sp. has been observed before (Reaves et al. 1993). It is possible that the variety of *Trichoderma* I used does not have the ability to inhibit *A. ostoye*, although it did consistently out-compete *L. wagnerii*, another soil pathogen.

Hypogastrura sp. grazing appeared to impact fungal growth much more strongly than did *Galumna* sp. grazing. This could not be explained by the arthropod counts from the competition experiments. In the feeding preference trials, *Hypogastrura* sp. and *Galumna* sp. exhibited similar maximum feeding rates per individual, but their feeding preference orders were different. Thus, *Galumna* sp. had a feeding rate of 2.1 for *E. nigrum*, while *Hypogastrura* sp. had a feeding rate of 0.375 for *E. nigrum*. They also showed different feeding rates for *L. wagnerii* (0.630 for *Hypogastrura* sp. and 1.733 for *Galumna* sp.) Comparing this information to the outcome of the fungal competition experiments between *E. nigrum* and *L. wagnerii*, the picture does not make sense. A direct measurement of biomass consumption might be more valuable in the end.

Relating the percent change of the fungal thalli with feeding pressure was also problematic in some of the other fungal combinations, especially the pairing of *E. nigrum* and *L. wagnerii*. The springtails reduced *E. nigrum*'s cover more than the mites did. This is counterintuitive when paired with the arthropod count data. More mites than springtails were found upon *E. nigrum* and yet the springtail treatment showed the strongest growth reduction. Returning to the feeding preference data does not answer this question. *Hypogastrura* sp. had a much lower feeding rate on *E. nigrum* than did *Galumna* sp.

The arthropod counts may not accurately indicate feeding activity for two reasons. First of all, mouthparts were difficult to see through the microscope, so the presence of an arthropod on a given fungus might not indicate an actual feeding episode. Secondly, the observations may have been too infrequent to correlate well with the amount of biomass ingested.

In some cases, however, arthropod observations may be better correlated with feeding activity. Feeding was definitely observed under high magnification in the feeding preference and competition experiments. It is possible that there is an inherent difference in the ways in which *Galumna* sp. and *Hypogastrura* sp. feed. Perhaps *Hypogastrura* sp. is more destructive than *Galumna* sp. or alternatively, the saliva of *Galumna* sp. might induce a compensatory growth response in *E. nigrum*, while the saliva of *Hypogastrura* sp. does not.

Chapter 5. Conclusions

It is my hope that the two studies (Chapter 2 and Chapter 4) may help to build an understanding of how prescribed fire impacts soils. This information alone will not dictate whether or not prescribed fire is a wise management choice. Understanding how fire impacts soils will help managers make the best decisions when weighing their different objectives.

Many management goals besides soil solution chemistry and microarthropod ecology are important to consider when deciding whether or when to burn a specific stand. Today, concerns about restoring ecosystem integrity (reducing over crowding in stands, creating landscape conditions which are less susceptible to insect outbreaks and reducing fuel-loading) may outweigh the potential costs to soil fertility and plant growth. Until we fully understand all aspects of how fire interacts with the ponderosa pine ecosystem, it is difficult to weigh the various management options.

Tiedemann et al. (2000) suggest that the management goal of returning the ponderosa pine forests to 'presettlement conditions' may not be in our best interests. First of all, they emphasize that our perception of what 'presettlement conditions' are is biased towards the old, wide-open forests with a frequent fire return interval. Second of all, they maintain that all the gains in soil fertility and site productivity from the last 90 years of fire suppression will be lost. Busse et al. (2000) on the other hand, suggest that extremely low-intensity prescribed fires will result in minimal, short-lived reductions in tree growth. However, the fires in Busse et al.'s (2000) study only reduced woody fuels

by 50%. This amount of fuel reduction might not be enough to abate fire hazard. More intense fires may result in real reductions in plant growth. Understanding the intensity thresholds past which a fire becomes damaging to soils is important to understand in order to weigh the potential costs and benefits of prescribed fire.

In the end, planning burns to minimize nutrient losses is important. This includes nutrient losses during the fire (nutrient volatilization through duff combustion) and also post-fire losses (erosion and leaching). From my soil solution data, it appears that the possibility of nutrient losses due to leaching might be less in the spring burns. Whether or not leaching losses are a problem will depend on nutrient uptake rates, both by the microbial community and the plant community.

Busse et al. (2000) suggested that the amount of the O-layer which was burned was the best predictor for reduced PAI (periodic annual increment). From the burn descriptions, it appears that impacts to tree growth may not follow a seasonal pattern, as the amount of litter lost was extremely variable between the different plots. At the Driveway 14 site, the fall impacts were probably greatest, because they lost the greatest litter volume. At the Trout site, the spring burn impacts were probably greatest, while at the Kidd Flat and Driveway 17 sites, the spring and fall burn impacts were very similar. This suggests that applying a prescribed burn during spring or fall may not be the best method to minimize soil impacts. As the other studies at the Burns sites come to an end, we will know whether seasonality was more or less important for the fire's impacts on trees, soil microarthropods and mycorrhizal fungi than burn intensity.

Assessing the impacts of fire on the soil biotic community is very important. The studies I present here are to be used to help interpret fire's direct impacts and to help

form hypotheses about fire's potential indirect impacts. For example, suppose a spring prescribed fire virtually eliminated all *Hypogastrura* sp. from the soil. We could infer that the outcome of fungal competition in those soils might be slightly different, especially between *E. nigrum* and other fungi. For example, competition between *E. nigrum* and *C. geophillum* may have a different outcome. In a soil with fewer springtails, *C. geophillum* would be more strongly limited by competition.

Further research is necessary in order to determine whether competition between *E. nigrum* and *C. geophillum* could influence the effectiveness of mycorrhizal fungi in their symbiotic association (it is definitely possible that the two fungi are not in competition in the field), but my research here outlines a path to investigate some of the more subtle (but still important) effects of fire on the workings of the soil biotic community.

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