AN ABSTRACT OF THE THESIS OF

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Title: Litter Decay Processes and Soil Nitrogen Availability in Native and Cheatgrass-dominated Arid Rangelands.

Abstract approved _____
David A. Pyke Kate Lajtha

As large-scale restorations of degraded rangelands are initiated, land managers need to understand how decades of dominance by the invasive annual grass, cheatgrass (*Bromus tectorum* L.), have altered ecosystem processes. One way to assess such alterations is by observing differences in decay rates, since decomposition is determined by factors such as climate, litter quality, and microbial communities. There are conflicting results as to the C:N and lignin:N ratios of cheatgrass litter and potential alterations in resulting decay rates. Evidence of altered N mineralization rates and extractable soil N as a result of long-term cheatgrass dominance is also inadequate. Our study examined differences in above-ground decay rates, litter microbial characteristics, and soil N availability in native sagebrush-bunchgrass communities and cheatgrass-dominated communities on the Snake River Plain in Idaho, USA. We predicted that cheatgrass-dominated communities would have slower decay rates due to the high lignin:N ratio of cheatgrass and altered microbial characteristics in the cheatgrass litter layer. We also predicted that soil N availability would be higher in cheatgrass-dominated communities due to late-spring mineralization after cheatgrass has senesced. Our study found no differences in decomposition rates for cheatgrass and three native bunchgrasses ($F_{3,572} = 2.46$, $p = 0.062$) over 14 months in the field. Initial lignin:N ratios of the litter did not correlate with decay results. There were also no significant differences in decomposition rates between litter decaying in cheatgrass-dominated communities and litter decaying in native communities under sagebrush (*Artemisia tridentata*) or in the interspaces ($F_{2,572} = 0.885$, $p = 0.413$). Although decay rates for the different litter communities were similar throughout the first year of decomposition, their litter microbial characteristics were different. Patterns in bacterial biomass in cheatgrass-dominated communities were related to the litter quality of cheatgrass, which had significantly higher total bacterial biomass associated with its litter than each of the native litter species. Patterns of fungal biomass were due to the dynamics of the cheatgrass litter layer in cheatgrass-dominated communities, and not the species of litter. Total fungal biomass was lower in the cheatgrass-dominated litter communities than in the native shrub communities (p =

0.023) although there were no differences in among litter species ($F_{3,202} = 1.587$, $p = 0.194$). Patterns in microbial functional diversity (Biolog) showed no indication of differences among litter communities or among litter species ($p = 0.192$ and $p = 0.561$, respectively). Functional diversity differed by sampling date ($p = 0.000$), increasing with time over the rainy season for both bacteria and fungi. Trends in litter lignin losses did not correspond with trends in fungal biomass of the litter. Lignin loss occurred as early as the first summer for one native species (*Poa secunda* J. Presl), long before fungal biomass dominance. These results lend support to the hypothesis that lignin may be lost due to breakdown by intense UVB radiation in arid ecosystems. Available NO_3 differed among communities, after accounting for time ($F_{2,233} = 6.127$, $p = 0.002$). Nitrate levels in the native soils under shrubs were lower than NO_3 levels in cheatgrass-dominated soils at every date. There were no differences in available NH_4 among communities, after accounting for site and time ($F_{2,228} = 0.41$, $p = 0.960$). The overall results of our study indicate that the years of cheatgrass dominance have had little effect on above-ground decay rates, although the microbial processes affecting these rates may have indeed changed. Availability of NH_4 in the soil has not changed, but NO_3 availability has increased. Further study into below-ground decay and ecosystem processes is recommended in order to provide a complete picture of how cheatgrass has (or has not) altered the ecosystem.

Litter Decay Processes and Soil Nitrogen Availability in Native and Cheatgrass-dominated Arid Rangelands

by
Kristen S. Harrison

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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INTRODUCTION

Bromus tectorum L. (cheatgrass) is a C_3 annual grass that was introduced to the western United States from Europe in the late 1800s (Young 1992). Since then, cheatgrass has invaded most habitats of the Intermountain West. The presence of cheatgrass as a fine fuel increases the fire frequency of the ecosystem, creating a cycle that promotes its own dominance (Billings 1992) by eliminating native competitors. There is typically an increase in available nitrogen (NO_3 and NH_4) during the first year following a fire, due to rapid increases in nitrogen (N) mineralization and condensation of volatilized N (Wan et al. 2001). These available nutrients stimulate plant growth following fire. In sagebrush ecosystems, native plants have low potential growth rates, and cannot utilize this available N for reestablishment before cheatgrass (high potential growth rate) becomes dominant (McClendon and Redente 1992). A thorough understanding of how cheatgrass dominance has altered ecosystem processes is needed before land managers attempt to restore native sagebrush/bunchgrass ecosystems.

The invasion of cheatgrass into an area after fire changes the ecosystem from a perennial shrub grassland to an annual grassland. Besides the absence of shrubs, visible changes include increased litter depth and uniform litter distribution. Increased litter layers change ecosystem dynamics by decreasing the energy associated with raindrops, slowing surface water movements, absorbing water, decreasing erosion by wind, and supplying more nutrients to the soil (Moorhead et al. 1996). However, uniform distribution of cheatgrass litter across the ecosystem prevents the reestablishment of microbiotic soil crusts (Kaltenecker 1997), which provide significant levels of organic C and N to the soil (Rychert and Skujiņš 1974, Evans and Ehleringer 1993). Thus cheatgrass invasion may alter the type and amount of soil organic C and N inputs. This could subsequently alter decomposition and mineralization processes.

A significant change in the species of litter input into an ecosystem could also alter decomposition and nutrient cycling. Different litter species decompose at different rates based on their tissue litter chemistry. In general, compounds decompose in the following order from fastest to slowest: sugar, hemicellulose, cellulose, lignin, waxes, and phenols (Minderman 1968). Lignin content of litter has received considerable attention because it can be used in models that adequately predict decay rates in many ecosystems (Meentemeyer 1978; Melillo et al. 1982). However, lignin content may not be an adequate predictor for decay rates in arid ecosystems (Schaefer et al. 1985), where 50 – 75% of above-ground mass loss may be due to abiotic factors such as wind, high

temperatures, leaching, and UVB breakdown (Moorhead and Reynolds 1989). Similarly, the importance of microbial communities in above-ground litter decomposition in arid lands is unknown. There is no doubt that microarthropods play a significant role in communition and transportation of surface litter (Whitford 1996); however, little is known about the microbial communities occupying the litter layer and their relative importance in above-ground decomposition processes.

Since litter chemistry affects the rate of decomposition, it follows that any changes in litter chemistry, depth, or distribution will affect nutrient mineralization rates. Litter quality also typically influences the subsequent quality of the organic matter in the soil. Organic matter quality, together with soil microclimate factors such as moisture, temperature, and available nutrients, determine rates of N mineralization (Burke 1989). There is evidence suggesting that cheatgrass invasion decreases potential rates of N mineralization and increases N immobilization two years after invasion into a native ecosystem, due to the much higher lignin:N and C:N ratios of cheatgrass compared to perennials (Evans et al. 2001). These authors predicted continued loss of N from cheatgrass-dominated systems, due to soil crust disturbance (eliminating N fixers), N volatilization from shorter fire intervals, and immobilization due to the high lignin:N ratio of cheatgrass. However, after 40 years of cheatgrass dominance, Svejcar and Sheeley (2001) found no significant differences in N mineralization, extractable soil N, and total soil C and N compared to native sagebrush sites. These results call into question the assumption that cheatgrass prevents perennial reestablishment after fire due to its ability to alter its environment to promote its own dominance. However, since cheatgrass cannot store N in its tissues as perennials can, Svejcar and Sheeley (2001) agree that total soil N should deplete over time due to erosion and leaching. They suggest that the available N in cheatgrass-dominated systems somehow remains high while overall fertility declines.

The aim of our study was to examine decomposition processes in a cold North American desert in the Snake River Plain, Idaho, comparing native sagebrush ecosystems with those dominated by cheatgrass following fire removal of the sagebrush canopy. The goal of the study was to provide needed information on decomposition and N cycling to land managers as they attempt to restore degraded ecosystems to a pre-disturbance state. Information on decomposition processes will help land managers to make informed decisions for land reclamation after disturbance and to promote the establishment of perennials before cheatgrass can dominate.

We addressed four objectives: 1) Determine differences in above-ground mass loss among four grass litter species decaying in native sagebrush communities (under shrubs and in the interspaces) and cheatgrass-dominated communities as decomposition proceeds through different seasons of the year. Although decomposition is an extremely well studied process, very few studies have been completed in arid ecosystems (Whitford 1988; MacKay et al. 1986; Comanor and

Staffeldt 1978), and even fewer in cold deserts (Mack 1977; Murray 1975). Decomposition rates reflect the net effect of UVB radiation, moisture availability, litter quality, and microbial activity on decomposition during different times of the year. Each of these factors may vary depending on the season and the stage of decomposition; thus decay rates may be controlled by biotic influences during the wet winter months and by abiotic influences (e.g. UVB radiation) during the dry summer months. Additionally, we hypothesize that higher fuel loads in cheatgrass-dominated areas (Whisenant 1990) are the results of slower above-ground decay rates. 2) Measure the lignin content of four litter species (three native and cheatgrass) as decomposition proceeds and assess correlations with decay rates. Since above-ground mass loss may be dominated by abiotic factors such as UVB breakdown (Moorhead and Reynolds 1989, Schaefer et al. 1985), we predicted that lignin:N ratios would not adequately predict decay rates. 3) Characterize the biomass and functional diversity of microorganisms occupying litter decaying in native (shrub and interspace) and cheatgrass-dominated communities over the course of above-ground litter decomposition. We predicted that there may be differences in the functional diversity of microorganisms occupying different litter species, based on differences in litter tissue chemistry. We also expected total bacterial and fungal biomass to change over time based on seasonal moisture availability. 4) Quantify the difference in plant-available N between native (shrub and interspace) and cheatgrass-dominated soils. When moisture becomes available in autumn, microbes become active, N mineralization and nitrification occur, but NO_3 is not lost via leaching or denitrification since cheatgrass seedlings are able to use it for germination. There is another pulse of N mineralization in the spring, which continues after cheatgrass has set seed. Thus available N should accumulate over time, as moisture limits the amount of N that cheatgrass can incorporate into its tissues. Specifically, native communities should have less available NO_3 than cheatgrass-dominated communities, reflecting a "tighter," N-limited ecosystem in which most of the NH_4 produced through mineralization is quickly immobilized or lost to the atmosphere via denitrification.

LITERATURE REVIEW

Ecology of Cheatgrass

There is evidence of multiple, simultaneous introductions of cheatgrass into British Columbia, Washington, Oregon, Utah, and Colorado from Europe in the late 1890's (Mack 1981, Novak et al. 1993). Cheatgrass has spread easily throughout the Intermountain West by wind, people, animals, contaminated straw, contaminated grain seed, and small rodents (Pyke and Novak 1992). Its current distribution spans the United States and much of Canada. It has severe impacts

on many ecosystems, including the arid rangelands of the Intermountain West. In this area, cheatgrass has increased the frequency of wildfires and has caused loss of native plant diversity (Billings 1992).

In a classic study, Pickford (1932) describes the process by which cheatgrass dominates an ecosystem as follows: cheatgrass introduction plus excessive grazing leads to increases in cheatgrass cover. This creates frequent wildfires, which promote the continued dominance of cheatgrass. This model has proven true since Pickford's time. Billings (1992) used this model to describe the loss of native plant diversity in pinion-juniper woodlands and sagebrush-bunchgrass ecosystems. Cheatgrass can easily dominate fire-disturbed areas, making it difficult for native grasses and sagebrush to reestablish. Thus native plant diversity is lost and the area becomes an annual grassland. As Pickford's model suggests, cheatgrass is not only found in degraded systems (e.g. over-grazed or fire-disturbed). Its competitive characteristics allow it to invade intact ecosystems as well.

The rapid spread of cheatgrass across North America suggests that adaptation and natural selection may not be the primary forces allowing cheatgrass dominance. Studies of the ecological genetics of cheatgrass suggest that it has extremely high phenotypic plasticity (i.e. the range of phenotypes that can be express by one genotype) (Rice and Mack 1991), allowing local populations to adjust to their environments and the year-to-year fluctuations within them. Since cheatgrass self-fertilizes from a genome that is a subset of its original (native) population, it is highly genetically uniform (Pyke and Novak 1992). Thus it is said to have low genetic flexibility (i.e. the range of genotypes that can be expressed). This lack of genetic flexibility combined with its high phenotypic plasticity allows cheatgrass to evade natural selection and elimination (Rice and Mack 1991).

Cheatgrass is a winter annual whose growth strategy is designed to avoid summer drought. Germination occurs in early autumn, although it can also occur anytime in the winter or spring (Mack and Pyke 1983). This is typically followed by little or no above-ground growth during the winter, and resumption of growth in early spring. Growth in fall and winter occurs mainly in the roots. In fact, cheatgrass can produce twice as many roots as bluebunch wheatgrass during this time (Aguirre and Johnson 1991). Seed production occurs in late spring, with seed dispersal and subsequent senescence in early summer.

One of the main ways that cheatgrass successfully competes with native species is through its root growth. Cheatgrass can produce longer roots than both crested wheatgrass and bluebunch wheatgrass (Arrendondo and Johnson 1999). It also has the greatest root proliferation when exposed to non-uniform high nutrient pulses, suggesting that cheatgrass root growth allows for rapid exploitation of nutrient patches (Arrendondo and Johnson 1999). Cheatgrass roots are also able to compete with the roots of native species for soil moisture. In one study, there was significantly less soil water under native species that had cheatgrass nearby versus those that did not regardless of the

age of a site after fire (Melgoza et al. 1990). This suggests that after fire, there may be less competition among natives due to the smaller number of surviving individuals and increased nutrient availability. Soil water is limiting after fire, and cheatgrass is able to out-compete natives for this water (Melgoza et al. 1990). The results of this study bolster the idea that the competitive ability of cheatgrass contributes to its post-fire dominance.

Lignin Degradation in Arid Ecosystems

The lignin content of litter has received considerable attention because it can be used in models that predict decay rates in many ecosystems (Meentemeyer 1978; Melillo et al. 1982). Models based on lignin content of litter were developed using data from mostly forested ecosystems, where soil microorganisms are responsible for the majority of the decomposition process. In ecosystems with limited soil moisture, the activity of microorganisms is hindered by very dry soils. In support of this, a study in the Chihuahuan desert found no correlations between decomposition rates and the lignin content of the litter (Schaefer et al. 1985).

Several studies have gained insight on this problem. Pauli (1964) first suggested that the small amounts of soil organic matter in arid ecosystems may be due to the breakdown of lignin by ultraviolet-B (UVB) radiation. Since then, there has been a plethora of research confirming the photodegradation of lignin and other organic materials in paper and wood (Castellan et al. 1987, Gierer and Lin 1972, Leary 1968, Lewis and Fronmuller 1945, Lin and Kringstad 1970, Hon et al. 1980, Kalnins 1966). However, there have been few studies concerning the effects of UVB radiation on decomposition in terrestrial ecosystems. In one study, mass loss of shaded litter in an arid ecosystem was lower than that of exposed litter, even though the density of soil microorganisms was higher in the shaded areas (MacKay et al. 1986). Moorhead and Reynolds (1989) proposed that photochemical degradation was the primary mechanism for the rapid loss of litter in the Northern Chihuahuan desert.

Leaf litter exposed to enhanced UVB radiation has exhibited a more rapid lignin breakdown than non-exposed litter, due to photodegradation (Gehrke et al. 1995). However, overall mass loss of the enhanced UVB-exposed litter was less than non-exposed litter, due to decreased microbial activity and decreased numbers of fungi (Gehrke et al. 1995). These two counter-acting forces were confirmed in similar studies (Rozema et al. 1997; Newsham et al. 1997). Exposure to enhanced UVB during growth has also resulted in higher levels of lignin within leaf tissue (Rozema et al. 1997).

Microbial Communities

Shifts in the dominant plant species to an invasive annual may cause shifts in the soil microbial communities since different plant species contribute different carbon compounds to the soil organic matter. Cheatgrass invasion may indeed alter soil microbial communities (Kuske et al. 2002, Belnap and Phillips 2001). In one study, cheatgrass-invaded soils had higher numbers of soil fungi and a greater proportion of active bacteria (Belnap and Phillips 2001). These invaded sites had species of bacteria and fungi that were similar to sites that were invaded greater than 50 years ago, suggesting some permanent alterations of microbial communities as a result of invasion. However, others found no difference between native and cheatgrass-invaded sites in terms of microbial biomass when averaged over the landscape (Bolton et al. 1993). In a similar study of soils on the Snake River Plain, there were no significant differences in the diversity of microbial carbon source utilization in soils of native sagebrush rangelands and cheatgrass-dominated rangelands (Kaltenecker et al. 2001 unpublished report to BLM).

Measures of microbial biomass can be used to examine patterns of development of microbial communities over different seasons of the year and over progressive stages of decomposition. Microbial biomass varies seasonally due to moisture and temperature changes (Bardgett et al. 1999). In the Alaskan taiga, wet-dry cycles caused shifts in microbial biomass numbers (Schimel et al. 1999). These episodes may shift dominance from bacteria to fungi, since bacterial biomass numbers were more sensitive to such shifts than fungi. Such wet-dry cycles also occur in arid rangelands and thus may affect microbial action in decomposition. Microbial biomass ratios also vary over the course of decomposition. Fungi typically dominate early in decomposition, breaking down materials that are not yet amenable to microbial attack (Dilly et al. 2001). Bacterial numbers increase later as they become able to mineralize the degradation products of the fungi.

Nitrogen

Native sagebrush communities typically have higher total available N and P under shrubs than in the interspaces (Burke 1989, Charley and West 1977). This is the result of higher organic matter content and thus more microbial biomass under shrubs. Increased microbial biomass causes higher N mineralization rates under shrubs than in the interspaces. Cheatgrass invasion after fire may eliminate this mosaic of N availability by providing a constant, thick litter layer throughout the community. This may further allow cheatgrass to out compete native species, since cheatgrass can easily exploit available N. Perennials tend to have a greater ability to tolerate conditions of limited N than annuals like cheatgrass. In one study, decreasing the amount of available N stimulated

perennial grasses and shrubs to recover faster after disturbance (McClendon and Redente 1992). Decreasing available N was accomplished by adding a low-quality carbon source such as sucrose to the soil. Sucrose increased the decomposer biomass in the soil, thereby stimulating microbial N immobilization.

METHODS

Study Sites

The study area consisted of four locations within Wyoming big sagebrush (*Artemisia tridentata* Nutt. spp. *wyomingensis* Beetle and Young) communities of the Western Snake River Plain (between 43°00'00" and 43°30'00" north latitude and 115°45'00" and 116°30'00" west longitude) near Boise, Idaho, USA. The climate is characterized by hot, dry summers and cold, moist winters (average annual precipitation of 305 mm). The topography is gently rolling, with an elevation gradient from 855 to 1095 m and a general southwestern aspect on the landscape. Soils of all sites were similar and supported similar vegetation (Table 1) and ecological sites (ecological site as defined by USDA-NRCS 1997, www.ftw.nrcs.usda.gov\glti\NRPH.html, March 5, 2003). All climate data were obtained from the University of Idaho climate data website (inside.uidaho.edu/asp/liststations.asp, September 20, 2002). Evapotranspiration data was obtained from the Western Regional Climate Center website (www.wrcc.dri.edu/CLIMATEDATA.html, November 15, 2002).

Each site consisted of a dominant vegetation pair: native and cheatgrass-dominated. Native areas were a mixture of Wyoming big sagebrush and perennial bunchgrasses that had little or no livestock use in recent history and had not burned in at least 50 years. They were a mosaic of shrub mounds with high canopy and litter cover, and interspaces with perennial bunchgrasses interspersed with biological soil crusts and bare soil. These native areas had less than 20% cheatgrass cover. Cheatgrass-dominated areas had burned within the past 20 years and had greater than 60% cheatgrass cover (Kaltenecker et al. 2001 unpublished report to BLM). Nearly 90% of the litter in cheatgrass-dominated areas consisted of cheatgrass, in contrast to the native areas, which typically had about 50% sagebrush litter, 25% perennial bunchgrass litter, and 15% annual grass litter (Kaltenecker et al. 2001 unpublished report to BLM).

Table 1. Location, elevation, ecological site descriptions, soil types, fire history, and current dominant vegetation for the four sites used in this study.

Site Name	Latitude Longitude (10'block)	Area	Legal Description	Elevation (m)	Ecological Site Description	Soil type and Map Unit	Last Known Fire(s)	Current Dominant Vegetation
Bowns Creek	43°20'00" 115°56'00"	Native	NW1/4 T1S R4E S13	1010	Loamy 10-12"	94-Lanktree-Chilcott loams, 0 to 12 % slopes. Very deep to mod. deep, well-drained. Dissected fan terraces.	unknown (>50 years)	Wyoming big sagebrush, Sandberg bluegrass, bluebunch wheatgrass
	43°20"00" 115°55'00"	Cheatgrass-Dominated	N1/2 SE1/4 T1S R4E S13	1010		27-Chilcott-Elijah silt loams, 0 to 12 % slopes. Moderately deep, well-drained. Alluvial plains, basalt plains.	1982	Cheatgrass, medusahead wildrye, Sandberg bluegrass
Mayfield	43°22'00" 115°51'00"	Native	NW1/4 SW1/4 T1S R5E S3	1095	Loamy 10-12"	94-Lanktree-Chilcott loams, 0 to 12 % slopes. Very deep to mod. deep, well-drained. Dissected fan terraces.	unknown (>50 years)	Wyoming big sagebrush, Sandberg bluegrass, bluebunch wheatgrass
	43°22'00" 115°50'00"	Cheatgrass-Dominated	SE1/4 NE1/4 T1S R5E S15	1065		94-Lanktree-Chilcott loams, 0 to 12 % slopes. Very deep to mod. deep, well-drained. Dissected fan terraces.	1985	Cheatgrass, medusahead wildrye, Sandberg bluegrass
Kuna Butte East	43°26'00" 116°26'00"	Native	NW1/4 NW1/4 T1N R1W S11	935	Loamy 8-10"	136-Power-McCain silt loams, 8 to 12 percent slopes. Very deep and well-drained. Basalt plains and low alluvial terraces.	unknown (>50 years)	Wyoming big sagebrush, Sandberg bluegrass
	43°24'00" 116°29'00"	Cheatgrass-Dominated	SE1/4 T1N R1W S4	925		158-Rock outcrop-Trevino complex, 5 to 20 % slopes. Extremely stony silt loam. Shallow and well-drained. Exposed basalt plains.	1983,1986	Cheatgrass
Nicholson Road	43°27'00" 116°27'00"	Native	NW1/4 NE1/4 T1N R1W S29	855	Loamy 8-10"	134-Power-McCain silt loams, 2 to 4 % slopes. Very deep and mod. deep, well-drained. Basalt plains and low alluvial terraces.	unknown (>50 years)	Wyoming big sagebrush, Sandberg bluegrass
	43°24'00" 116°29'00"	Cheatgrass-Dominated	NW ¼ NE1/4 T1N R1W S29	860		134-Power-McCain silt loams, 2 to 4 % slopes. Very deep and mod. deep, well-drained. Basalt plains and low alluvial terraces.	1987	Cheatgrass

Experimental Design

We used a 4x3x4x7 (site x community x litter species x sampling date) split-plot nested design. Within each site, we defined three dominant vegetation communities, two within the native sagebrush area (shrub and interspace) and one within the cheatgrass-dominated area. At each site, four 50-m transects were placed in random directions from a center point that was 50 m perpendicular from the road.

Litter decomposition and microbial measurements were made using vegetation in fiberglass mesh bags. Although the litter bag method does not provide a completely accurate measure of decomposition rates (Jensen 1974), benefits of the litter bag technique (simple mass loss measurements, penetration by rain, sun, wind, and microbes) outweigh its drawbacks and provide an index for comparing different communities. Fiberglass bags were used in this study because they allow more light to penetrate to the litter sample and withstand UV radiation better than nylon mesh (Schwemmer 1965a,b; Salvin 1968; Dunlap et al. 1969).

Mass Loss and Lignin

Litter bags contained one of four species of grass litter, three native: bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love), Sandberg bluegrass (*Poa secunda* J. Presl), and bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) and one invasive exotic annual, cheatgrass (*B. tectorum*). Leaf litter was collected from plants in the study area immediately after senescence in May and June 2001 and dried for 48 hours at 70^{o}C. All seeds and inflorescences were removed before 2 g of litter were weighed and placed in a 10-cm x 15-cm litter bag (1.5 mm mesh). Litter bags were placed at each site on 1 July 2001 and staked in pairs at random points along each transect. Each bag was randomly assigned to a removal date and an analysis procedure: mass loss, microbial functional diversity (Biolog), or microbial biomass.

Bags were removed at seven dates over 14 months: 3 August 2001, 6 September 2001, 6 November 2001, 15 January 2002, 25 March 2002, 4 May 2002, and 10 September 2002. At each removal date, bags were dried to a constant mass at 70^{o}C and weighed. Empty bags were also placed at each site and removed on the same dates as the litter, to account for any mass loss from the decomposition of the bag itself. Percent mass loss was calculated for each litter species within each community. Since bags were not replaced back into the field, sampling date was not treated as a repeated measure in the analysis. Data was analyzed for differences among litter species and among communities in percent mass remaining using a multiple linear regression. Decay rates (k; g·yr^{-1}) were calculated using the first-order decay function (Jenny et al. 1949; Olson 1963):

$$\ln(X_t) = \ln(X_o) - kt$$

where X_o is the initial litter mass, X_t is the amount of mass remaining after time t (years), and k is the first-order decay rate constant.

Portions of litter of each species (collected for the litter bags) were ground to 1 mm in a Wiley mill and analyzed for initial percent lignin and N (Kjeldahl). During late May 2002, new litter from of each of the four species was collected and dried for 48 hours at 70^{o}C. Two grams of each litter species (unground) was placed separately into litter bags. Bags were placed at random locations within each community at each site, stratifying between shrub and interspace in the native area. These bags were collected in early September 2002 and results were used to compare percent lignin before and after the one summer of decomposition, as a representation of the decomposition during the 'first' summer.

In early May 2002 and early September 2002, some of the litter removed for mass loss measurements on those sampling dates was subsequently ground in a Wiley mill to 1 mm. These samples were analyzed for percent lignin and results were used to compare percent lignin before and after the second summer of decomposition. All percent lignin and lignin-to-N ratios were determined by the Oregon State University Forage Analysis Lab.

Microbial Communities

Litter bags were removed at four sampling dates (8 November 2001, 17 January 2002, 6 May 2002, 12 September 2002) to determine the functional diversity of carbon source utilization (Biolog) by bacterial and fungal communities (Garland and Mills 1991; Zak et al. 1994; Dobranic and Zak 1999) inhabiting the litter. Litter bags were placed in clean, unused, sealable plastic bags and kept in a cooler while being transported to the laboratory. Analyses were conducted at several sampling dates as decomposition proceeded, since substrate use changes over time as the associated plant community changes over time (Garland 1996b). Biolog uses microplates (Biolog Inc., Hayward, CA) with 96 wells, 95 each containing a different carbon substrate and one blank control. The substrates are grouped into six guilds (Table 2): polymers, carbohydrates, carboxylic acids, amines/amides, amino acids, and miscellaneous. Each GN (Gram-negative) microplate well also contains a tetrazolium violet redox dye for indication of carbon use by bacteria. Fungal communities were analyzed on SF-N (spore-forming gram-negative) microplates. These plates contain the same carbon substrates as the GN plates, but do not contain any dye; thus 1.5 mg of dimethylthiazolyl-diphenyl-tetrazolium bromide (MTT) was added to each sample designated for fungal analysis (Dobranic and Zak 1999) for indication of carbon use by fungi.

There have been numerous efforts recently to assess the functional diversity of soil microbial communities across different landscapes (Myers et al. 2001, Ellis et al. 1995, Zak et al. 1994, Staddon et al. 1997, Waldrop et al. 2000, Grayston et al. 2001). The purpose of Biolog is to

provide an estimate of the functional diversity of microorganisms. Thus it can be a good technique for examining changes in microbial communities after disturbance (Turco et al. 1994). However, functional diversity cannot be correlated with taxonomic diversity, since two different species of bacteria may be able to utilize the same carbon substrate (Staddon et al. 1997).

Table 2. Guild membership for the 95 carbon substrates in Biolog microplates

Polymers	**Carbohydrates**	**Carboxylic Acids**	**Amino Acids**
α-cyclodextrin dextrin glycogen tween 40 tween 80	N-acetyl-D-galactosamine N-acetyl-D-glucosamine adonitol L-arabinose D-arabitol cellobiose i-erythritol D-fructose L-fucose D-galactose gentiobiose α-D-glucose m-inositol α-D-lactose lactulose maltose D-mannitol D-mannose D-melibiose β-methyl D-glucoside D-psicose D-raffinose L-rhamnose D-sorbitol sucrose D-trehalose turanose xylitol methyl pyruvate mono-methyl succinate	acetic acid cis-aconitic acid citric acid formic acid D-galactonic acid lactone D-galacturonic acid D-gluconic acid D-glucosaminic acid D-gulcuronic acid α-hydroxybutyric acid β-hydroxybutyric acid γ-hydroxybutyric acid *p*-hydroxyphenylacetic acid itaconic acid α-keto butyric acid α-keto glutaric acid α-keto valeric acid D,L-lactic acid malonic acid propionic acid quinic acid D-saccharic acid sebacic acid succinic acid	D-alanine L-alanine L-alanyl-glycine L-asparagine L-aspartic acid L-glutamic acid glycyl-L-aspartic acid glycyl-L-glutamic acid L-histidine hydroxy L-proline L-leucine L-ornithine L-phenylalanine L-proline L-pyroglutamic acid D-serine L-serine L-threonine D,L-carnitine γ-amino butyric acid
Amines/Amides succinamic acid glucuronamide alaninamide phenylethylamine putrescine 2-amino ethanol			
Miscellaneous urocanic acid inosine uridine thymidine 2,3 butanediol glycerol D,L-α-glycerol phosphate glucose-1-phosphate glucose-6-phosphate bromosuccinic acid			

Litter samples were prepared for the GN and SF-N microplates using the protocol outlined by Dobranic and Zak (1999), with the following modifications. Litter samples were air-dried in a laminar flow hood and then ground in a commercial coffee grinder. The ground plant material was washed through a 250 μm and a 150 μm sieve using sterile deionized water. The coffee grinder and

sieves were washed thoroughly and sterilized with 95% ethanol between each sample. Plant material collected on the 150 μm sieve was washed off and combined with the rest of the filtrate. The filtrate was suction filtered until dry. Eighteen milligrams of filtrate was added to 150 μL of a 0.1% agar solution. Each microplate well was inoculated with 100 μL of the solution using a 12-channel micropipette. A microplate reader (Bio-tek Powerwave$_x$340, Winooski, VT) was used to take an initial reading (A_{595}) of well color development (WCD) for each well on each plate. Plates were incubated for 5 days at 23^{o}C, taking a WCD reading after every 24 hours. The overall well color development (OWCD) for each carbon substrate from each sample was taken from the A_{595} reading after 72 hours (as indicated by Haack et al. 1995, Lindstrom et al. 1998). A matrix of microplates versus the OWCD for the 95 microbe groups (carbon substrates) was created.

One criticism associated with Biolog is that inoculum cell density is correlated with the rate of color development (Haack et al. 1995). Our methods attempted to equalize inoculum densities, however, we did not have the means to check the accuracy of our technique. Therefore, to adjust for any possible differences in inoculum densities, the OWCD of each substrate for each microplate was divided by the average well color development (AWCD) of the entire plate, as indicated by Garland and Mills (1991). Using this relativization produces sufficiently similar Principle Components Analysis (PCA) results to those obtained using an inoculum-independent kinetic model (Lindstrom et al. 1998).

After relativization, negative values were converted to zero, since a negative WCD is not biologically meaningful. Values less than 0.1 were also converted to zero, since only values greater than 0.1 exhibit color development. In bacterial analyses, an outlier analysis revealed a sample unit with a Euclidean distance that was greater than 2 standard deviations from the mean (su588 = 2.98 sd). Our notes revealed a pipetting error for that microplate and so it was eliminated from the analysis. In the fungal analysis, one sample unit (su328 = 6.74 sd) was removed from analysis due to contamination in the blank well.

Principle Components Analysis (PCA) was used to create ordinations of sample units (microplates) in species (carbon substrates) space, using PC-ORD (McCune and Mefford 1999). PCA was deemed an appropriate method based on the suitability of a linear model of relationships between substrates. Relationships among substrates in the same guild (Table 2) were linear and relationships among species in different substrate guilds approached linearity (data not shown). The cross-products matrix used was a correlation matrix containing Pearson correlation coefficients. The significance of the principal components was determined by comparing the eigenvalues to the eigenvalues of a broken-stick model (Jackson 1993).

A multi-response permutation procedure (MRPP) was used (PC-ORD) to analyze differences among groups. MRPP is a non-parametric, multivariate technique for evaluating differences among groups (similar to MANOVA). Grouping variables were defined *a priori* by

treatment levels in the experimental design (4 sites x 3 communities x 4 litter species x 4 sampling dates). For example, "site" was one grouping variable containing four groups (locations). The distance matrix was calculated using Euclidean distance measures. Microbial communities within litter communities, litter species, and sampling dates were also compared using 4 diversity measures: richness (S), evenness (E), Shannon's diversity index (H) and Simpson's diversity index (D'). Diversity summaries were analyzed for significance using ANOVA.

To assess bacterial and fungal densities found on litter, portions of the litter from our mass loss bags were analyzed for total bacterial biomass and total fungal biomass by Soil Foodweb Inc. (Corvallis, OR). Biomass was determined using differential interference contrast direct microscopy (Ingham and Klein 1982, 1984; Ingham et al. 1999). The ratio of total fungal biomass to total bacterial biomass was also analyzed to determine the point during the decomposition process that microbes associated with litter switch from bacterial to fungal dominance. Litter from each species and each community was analyzed at five occasions over 14 months: 8 September 2001, 8 November 2001, 17 January 2002, 6 May 2002, 12 September 2002.

Microbial biomass data were log-transformed and analyzed using a linear mixed-effects model (LME) that included site as a random effect (S-Plus 2000). Making site a random effect accounted for variation due to rain events on two of the collection dates. Parameters were estimated using the restricted maximum likelihood method (REML). As there are no formal tests for model comparisons using linear mixed effects, models were compared for adequacy based on their Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and log-restricted likelihood (logLIK). Models with a smaller AIC, BIC, and a larger logLik were deemed a better fit to the data. We began with a fit to the richest model, including all interactions + $days^2$ + $days^3$. We then proceeded with a backwards elimination of fixed effects parameters until a parsimonious inferential model was obtained to answer the questions of interest. Parameters were eliminated one at a time based on non-significant p-values ($p \geq 0.05$).

There were two outliers whose total bacterial biomass were an order of magnitude higher than the other values. There was no evidence to warrant their removal, and so the analysis was performed with and without these outliers. Removing the outliers resulted in a better fit of the model to the data. For total fungal biomass, two outliers were identified with zero total fungal biomass, both from the January 02 sampling date. There was no significant reason to exclude the outliers, and so analysis was performed with and without the outliers.

Random litter samples were collected from each community at each date to compare results for litter decaying in the field to litter decaying in our litter bags. For random litter samples, there was no January 2002 sampling date; instead there was a March 2002 sampling date. There was no distinction among litter species for the random litter samples. The analysis proceeded in the same

way as before, beginning with a fit to the richest model, followed by a backwards elimination of fixed effect parameters.

Nitrogen

Resin capsules (Skogley 1994) were used to estimate N availability. Resin capsules are preferable to resin bags (Binkley and Matson 1983) because they have a uniform surface area, simplifying comparisons between samples. They also allow for capture of both cations and anions simultaneously and independently in the soil (Skogley and Dobermann 1996). Results from the capsules give an adequate measure of the bioavailability of NH_4 and NO_3 because they are sensitive to initial ion concentrations in the soil, as well as ion diffusion rates through the soil and nutrient release rates from solid phases (Skogley and Dobermann 1996). These are the same factors that control the availability of nutrients to plants and microbes. Total mineral nitrogen content, as measured using ion-exchange resins, is significantly correlated to N mineralization rates as determined by laboratory methods Lajtha (1988).

All capsules were placed within the soil in the zone of greatest root activity for grasses at random locations along five transects within each native and cheatgrass-dominated area. A soil core (10 cm length) was removed by pounding a 2.5 cm (inside diameter) polyvinyl chloride tube into the soil at a 45^o angle. This placed the capsules about 7 cm beneath an intact soil surface. The soil core was replaced after the resin capsule was placed at the bottom of the hole. Within native areas, resin capsule locations were stratified, using separate randomized placements under shrubs and under interspaces. Capsules were placed in the field on 1 July 2001 and were collected for soil NO_3 and NH_4 analysis at six dates: 7 September 2001, 7 November 2001, 16 January 2002, 26 March 2002, 5 May 2002, and 11 September 2002. Frozen soils prevented complete recovery of all the resin capsules during the January collection date. The rest of the capsules scheduled for this date were removed at the end of March after soils thawed.

Ammonium and NO_3 were extracted from capsules according to protocol from UNIBEST Inc. (www.unibest.us, August 3, 2001). The extracts were neutralized prior to analysis of NO_3 and NH_4 content using various dilutions of NaOH. Samples were kept frozen until analysis (UNIBEST, Inc. Laboratories, Pasco, WA) using a segmented flow analyzer. Ammonium concentrations were determined using the salicylic method and NO_3 was determined by hydrazine reduction. The resin adsorption quantity (RAQ) was calculated for both NO_3 and NH_4 and used to create nutrient accumulation curves (Doberman et al. 1994). The RAQ was calculated according to the following formula:

$$RAQ = cV/MA$$

where c is the concentration of the nutrient in the extract (mg/L), V is the volume of the extract (mL), M is the molar mass of the nutrient (g/mole), and A is the surface area of the resin capsule ($11.4cm^2$). Since neutralization diluted our samples, we recalculated each value for c (obtained from analysis) based on the amount that sample was diluted. The RAQs for NO_3 and NH_4 were log-transformed and analyzed for differences among communities over time using a multiple linear regression.

RESULTS

Mass Loss and Lignin

Grass litter decomposition after 14 months was similar among locations dominated by native plants (interspace or shrub) and annual grasses, regardless of litter species (accounting for time, $F_{2,572} = 0.885$, $p = 0.413$). The estimated difference in percent mass remaining between each community was less than 1% (Figure 1). There was a weakly significant difference in percent mass remaining among litter species (Figure 2), after accounting for community and time ($F_{3,572} = 2.46$, $p = 0.062$). The percent mass remaining for *E. elymoides* was 1.754% greater than *P. secunda* (95% C.I. = 3.187 to 0.321, p = 0.017) and the percent mass remaining for *P. spicata* was 1.677% greater than *P. secunda* (95% C.I. = 3.129 to 0.225, p = 0.024). Percent litter mass remaining for each species at the end of the study ranged from 61.0 % for *B. tectorum* to 63.5 % for *E. elymoides*.

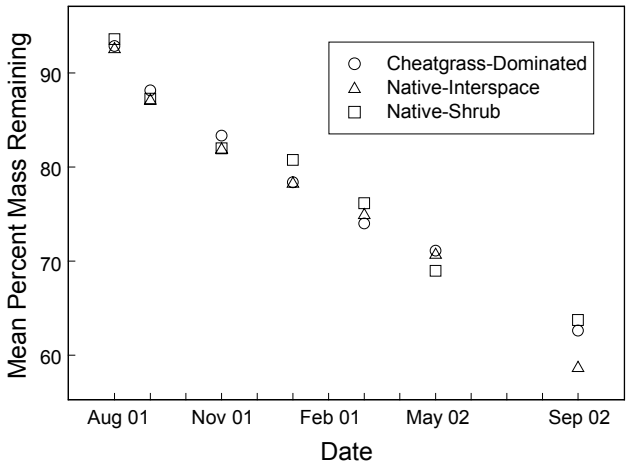

Figure 1. Mean percent mass remaining over time for litter decaying in cheatgrass-dominated communities and native communities (shrub and interspace). Lines represent the linear least squares regression fit to the data.

The grand mean decay rate constant after 14 months of decomposition for all species and communities combined was 0.423 $g \cdot year^{-1}$ (Table 3). Decay rate ranks changed among species and among communities over the course of the experiment (Table 4). Cheatgrass had the slowest decay rate over the rainy season

(November 2001 to May 2002) and the fastest decay over the second summer. Litter decayed fastest underneath shrubs over the first summer and the rainy season, but decayed slowest over the second summer. Litter decayed slowest in the cheatgrass-dominated community over the first summer.

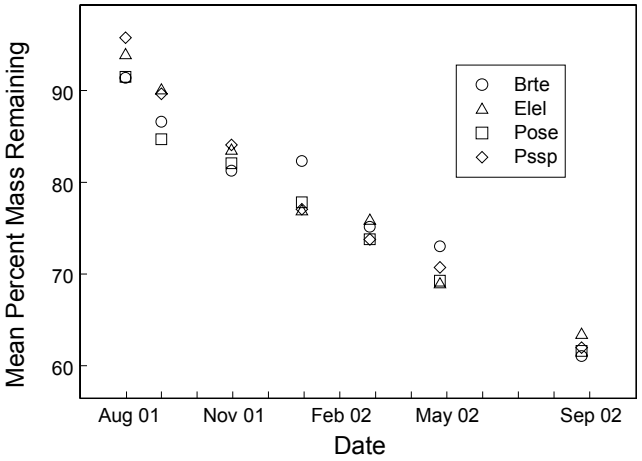

Figure 2. Mean percent mass remaining over time for four litter species: three native (*E. elymoides* (Elel), *P. secunda* (Pose), *P. spicata* (Pssp), and one exotic (*B. tectorum* (Brte)). Lines represent the linear least squares regression fit to the data.

Table 3. Mean (± 1 SE) first-order decay rate constant (k) for grass litter after 14 months (t = 1.151years). Decay rates were calculated using the model: $\ln(X_t) = \ln(X_o) - kt$ (Jenny et al. 1949; Olson 1963) and ranked in order from fastest to slowest mean decay rate.

		Decay rate (k) after t = 1.151 years
Species:		
	B. tectorum	0.438 ± 0.028
	P. secunda	0.427 ± 0.023
	P. spicata	0.419 ± 0.018
	E. elymoides	0.405 ± 0.033
Community:		
	Native – Interspace	0.472 ± 0.034
	Cheatgrass-Dominated	0.413 ± 0.015
	Native – Shrub	0.399 ± 0.036
	Grand mean	0.423 ± 0.013

Table 4. First-order decay rate constants summarized by season. Percent mass remaining from the beginning and end of each time period was used to calculate k from the decay-rate model ($\ln(X_t) = \ln(X_o) - kt$). Time t was the length of time described by each season.

	Decay rate (k)		
	Aug 01 - Nov 01	**Nov 01 - May 02**	**May 02 - Sep 02**
Species:			
***B. tectorum* (Brte)**	0.674	0.217	0.545
***P. secunda* (Pose)**	0.801	0.343	0.356
***E. elymoides* (Elel)**	0.579	0.389	0.252
***P. spicata* (Pssp)**	0.535	0.351	0.401
Slowest to fastest:	Pssp<Elel<Brte<Pose	Brte<Pose<Pssp<Elel	Elel<Pose<Pssp<Brte
Community:			
Cheatgrass-Dominated (C)	0.600	0.322	0.387
Native - Interspace (NI)	0.666	0.297	0.566
Native - Shrub (NS)	0.776	0.350	0.241
Slowest to fastest:	C<NI<NS	NI<C<NS	NS<C<NI

While percent N was smallest for *B. tectorum* and percent lignin and lignin:N ratios were smallest in *E. elymoides* (Table 5), initial percent lignin, N, and lignin:N ratio of *P. spicata* was greatest among the four species. After the first summer, loss of lignin was greatest for litter in cheatgrass-dominated areas, and least for litter under shrubs (Table 6). The one exception to this was cheatgrass, whose loss of lignin was greatest for litter decaying in the interspaces and least for litter decaying under shrubs. After the second summer, a different pattern emerges for each litter species. All litter species except *P. secunda* actually gained a small percentage of lignin (<1%) over the first summer (Appendix A). All species lost lignin over the second summer, with *P. spicata* decaying under shrubs losing the most (1.6 %). Litter species followed the same pattern of lignin loss, regardless of community (Table 6). *P. secunda* lost the most lignin through the first summer and the rainy season, with *P. spicata* losing the least. However, over the second summer, *P. spicata* lost the most lignin among all three communities.

Table 5. Lignin and N concentrations for litter used in the mass loss study (2001 results) and litter collected the following summer (May 2002) while litter (except for Pose) was still green.

	1 June 2001			6 May 2002		
	% Lignin	**% N**	**Lignin:N**	**% Lignin**	**% N**	**Lignin:N**
P. spicata	5.4	0.88	6.08	2.0	2.23	0.90
P. secunda	4.5	0.83	5.45	4.1	0.85	4.82
B. tectorum	2.9	0.70	4.17	1.7	1.43	1.19
E. elymoides	2.1	0.81	2.26	2.2	2.54	0.87

Table 6. Trends in lignin loss by community (C = Cheatgrass - Dominated, NS = Native - Shrub, and NI = Native - Interspace) over seasons, averaged by litter species (Brte = *B. tectorum*, Pssp = *P. spicata*, Pose = *P. secunda*, Elel = *E. elymoides*), and trends in lignin loss by species, averaged by community. Since litter in most communities gained lignin over the first summer, the community that gained the most litter was considered to have lost the least. Trends for July 2001 through April 2002 (i.e. lignin loss from the beginning to the start of the second summer) were determined by the lignin contents of the litter at the start of the second summer. Litter with the lowest % lignin must have lost the most lignin, since all litter of a certain species should have had approximately the same lignin percentage before being placed in the field.

	Loss of lignin, most to least		
	After first summer	**July 01 through April 02**	**After second summer**
Species:			
B. tectorum	NI > C > NS	NI > C > NS	NS > NI >D
P. spicata	C > NI > NS	NI > NS ≥ C	NS >D> NI
E. elymoides	C > NI > NS	NI > C > NS	NI >D> NS
P. secunda	C > NI > NS	NI > C > NS	D> NS > NI
Community:			
Cheatgrass-dominated	Pose>Elel>Brte>Pssp	Pssp>Elel>Brte=Pose	Pssp>Pose>Elel>Brte
Native-Interspace	Pose>Elel>Brte>Pssp	Pssp>Elel>Brte≅ Pose	Pssp>Elel>Brte>Pose
Native-Shrub	Pose>Brte>Elel>Pssp	Pssp>Elel>Pose>Brte	Pssp>Brte>Pose>Elel

Microbial Communities

Bacterial carbon source utilization

Principle components analysis extracted 8 axes that explained significantly more variation than was expected by chance, but only three major axes were interpreted. The cumulative variance explained after 3 axes was approximately 42.2%. Litter bacterial carbon source utilization shifted significantly among sampling dates (Figure 3, Tables 7, 8), though overlapped considerably. However, neither community nor litter species distinguished different bacterial carbon source utilization patterns (Tables 7, 8, Appendix B, C).

All diversity measures were lowest in November 2001 and increased to maximum levels in May 2002 (Table 8). All diversity measures then decreased by the following September 2002 to levels lower then the previous January but higher than the previous November. Despite this similar pattern over time, the various diversity measures had different patterns of significance. For evenness, only May 2002 was significantly different, whereas for Shannon's diversity only November 2001 was significantly different.

The ordination results most closely echoed the results for richness of carbon source utilization, richness was most similar for January 2002 and May 2002, but both November 2001 and

September 2002 were different from January and May 2002 and different from each other. In the PCA ordination, bacterial carbon source utilization patterns for January 2002 and May 2002 were the most similar; both dates were positively associated with Axes 2 and 3, and negatively associated with axis 1. November 2001 was the only date positively associated with axis 1, due to its ability to utilize carbon sources from a wider range of guild types (Table 9). September 2002 was the only date negatively associated with axis 2, also due to its ability to utilize carbon sources from a wider range of guild types (Table 9). Although neither November 2001 nor September 2002 had the highest diversity of carbon source utilization overall, they were both distinguished in the ordination by their ability to utilization certain carbon sources that represented all six carbon source guilds. All dates were positively associated with axis 3, but September 2002 exhibited some negative correlation with axis three.

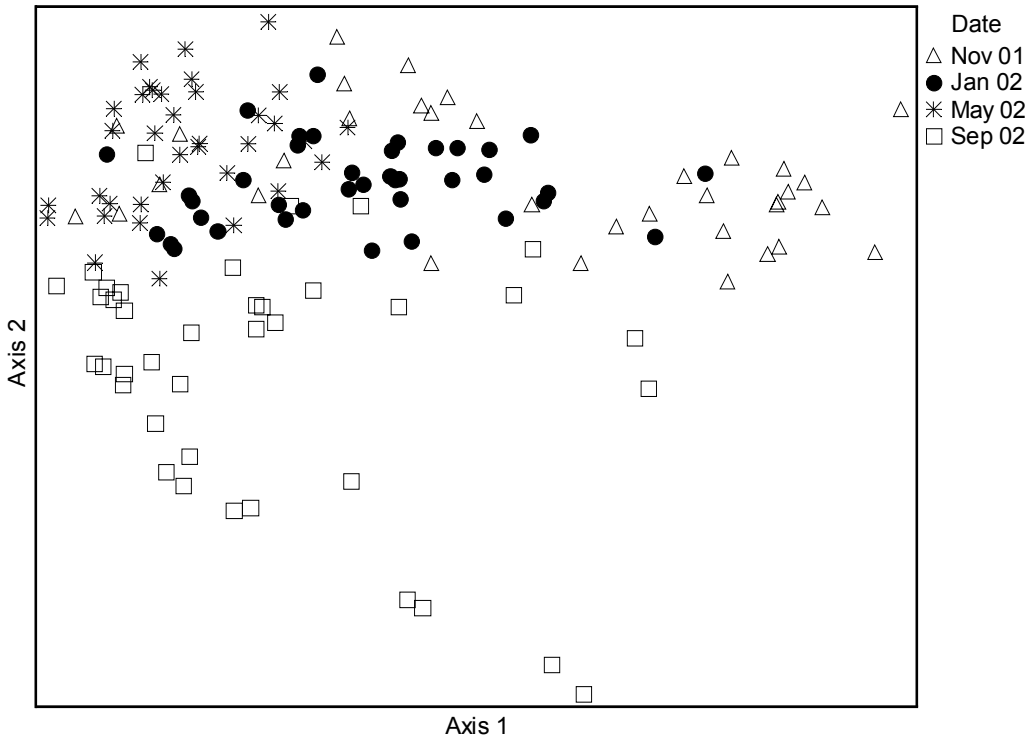

Figure 3. Ordination of sample units in species (95 carbon substrates) space, derived from Principle Components Analysis (PCA) of bacterial carbon source utilization data. Points represent sample units (microplates). Carbon sources correlated with axes 1 and 2 are listed in Table 9.

Table 7. Multi-Response Permutation Procedure (MRPP) for differences in bacterial carbon source utilization. The test statistic T describes the separations among the grouping variables, while the chance-corrected within-group agreement (A) is a measure of the effect size independent of sample size. Brte = *B. tectorum*, Pose = *P. secunda*, Elel = *E. elymoides,* Pssp = *P. spicata*.

Grouping variable	Test statistic T	Chance-corrected within-group agreement, A	p-value
Site	-0.8685	0.00274	0.175
Community			
Cheatgrass-dominated, Native - Interspace, Native - Shrub	-0.2116	0.00054	0.338
Litter Species			
Brte, Pose, Elel, Pssp	0.3028	-0.00095	0.557
Date	-44.8814	0.14140	0.000

Table 8. Diversity measures for bacterial carbon source utilization. S = richness, the number of wells for each microplate that had non-zero OWCD values. E = evenness and H = Shannon's diversity index. D' = Simpson's diversity index. Different letters indicate a significant ($p \leq 0.05$) difference determined by ANOVA.

	S	E	H	D'
Species:				
B. tectorum	79.5a	0.952a	4.164a	0.9823a
P. secunda	81.1a	0.950a	4.173a	0.9823a
P. spicata	78.3a	0.951a	4.143a	0.9819a
E. elymoides	79.2a	0.954a	4.166a	0.9824a
Community:				
Cheatgrass-Dominated	80.1a	0.951a	4.167a	0.9823a
Native - Shrub	80.3a	0.955a	4.185a	0.9827a
Native - Interspace	78.2a	0.949a	4.135a	0.9817a
Date:				
Nov-01	72.4a	0.946a	4.049a	0.9802a
Jan-02	82.0c	0.949a	4.181b	0.9825b
May-02	84.0c	0.960b	4.253b	0.9841c
Sep-02	79.5b	0.951a	4.160ab	0.9820b

Table 9. Pearson correlations (r) for carbon sources most highly correlated with the first three axes (principle components) for the PCA ordination of bacterial carbon sources utilization. Carbon source names are abbreviated; refer to Table 2 for full names.

Axis 1			Axis 2			Axis 3		
C source	**Guild**	**r**	**C source**	**Guild**	**r**	**C source**	**Guild**	**r**
inosin	miscellaneous	-0.794	Laspar	amino acid	-0.535	ahbuty	carboxylic acid	-0.544
D-arab	carbohydrate	-0.758	a-cycl	polymer	-0.504	succin	amine/amide	-0.490
2ameth	amine/amide	-0.728	succia	carboxylic acid	-0.490	gl6pho	miscellaneous	-0.432
Lserin	amino acid	-0.705	ghbuty	carboxylic acid	-0.447	NaDgal	carbohydrate	-0.426
Dgluam	carboxylic acid	-0.684	NaDglu	carbohydrate	-0.440	mmsucc	carbohydrate	-0.396
Dmanni	carbohydrate	-0.683	aDgluc	carbohydrate	-0.408	gLglut	amino acid	-0.389
uridin	miscellaneous	-0.681	urocan	miscellaneous	-0.408	akbuty	carboxylic acid	-0.384
Lleuci	amino acid	-0.680	Dgluco	carboxylic acid	-0.394	L-fuco	carbohydrate	-0.339
putres	amine/amide	-0.676	L-arab	carbohydrate	-0.377	aDlact	carbohydrate	-0.322
Dgulcu	carboxylic acid	0.742	twee80	polymer	0.382	D-treh	carbohydrate	0.340
twee80	polymer	0.758	bhbuty	carboxylic acid	0.403	Dgluam	carboxylic acid	0.361
Lgluta	amino acid	0.762	gentio	carbohydrate	0.487	Lproli	amino acid	0.369
quinic	carboxylic acid	0.763	NaDgal	carbohydrate	0.505	aDgluc	carbohydrate	0.386
akglut	carboxylic acid	0.785	adonit	carbohydrate	0.534	sucros	carbohydrate	0.389
Dgluco	carboxylic acid	0.800	Lphala	amino acid	0.547	D-fruc	carbohydrate	0.416
Dsacch	carboxylic acid	0.812	Lhisti	amino acid	0.554	uridin	miscellaneous	0.418
Lpyrog	amino acid	0.813	Lthreo	amino acid	0.614	alanin	amine/amide	0.468
Laspaa	amino acid	0.821	glycog	polymer	0.618	glycer	miscellaneous	0.516

Fungal carbon source utilization

PCA extracted 8 axes that explained significantly more of the variation than was expected by chance, but only three axes were interpreted for analysis. The cumulative variance explained after 3 axes was approximately 34.2%. Similar to the results for bacterial communities, neither community nor litter species distinguished different fungal carbon source utilization patterns (Tables 10, 11, Appendix D, E). Four sampling dates are distinguishable (Figure 4); however, they are not as clearly separable as in the bacterial analysis. Only sampling date had a significant within-group agreement (A = 0.0761, p-value = 0.000) based on the MRPP test (Table 10). Although the p-value for site suggests a significant difference (Table 10), its value for A does not achieve the recommended value of A > 0.3 for significance (McCune and Grace 2002).

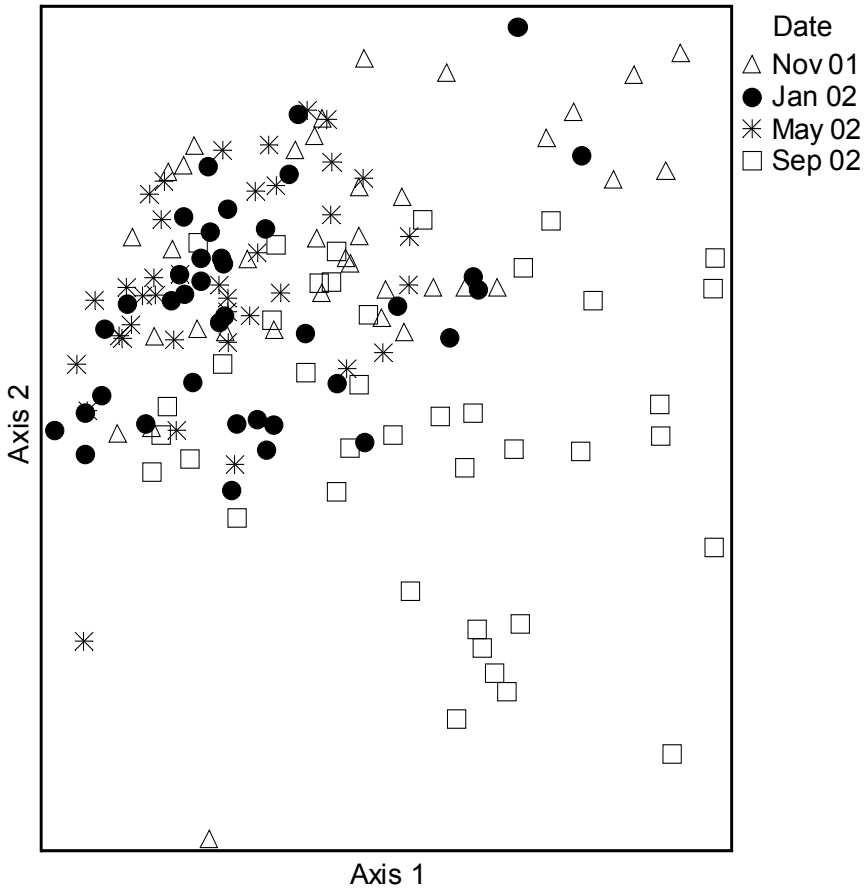

Figure 4. Ordination of sample units in species (95 carbon substrates) space, derived from Principle Components Analysis (PCA) of fungal carbon source utilization data. Points represent sample units (microplates). Carbon sources correlated with axes 1 and 2 are listed in Table 12.

There were no significant differences in the diversity of carbon source utilization by fungi among litter species or among communities, regardless of the diversity measure (Table 11). All measures of diversity increased from November 2001 to the highest levels in January 2002. Diversity then declined by May 2002 and again by the following September, when all measures were similar to the previous November 2001 levels.

Both January and May 2002 were negatively associated with axis 1, while November 2001 and September 2002 were mostly positively associated with axis one. During November 2001 and September 2002 fungi were able to utilize carbohydrates and carboxylic acids, whereas during January and May 2002 they were also able to utilize amino acids (Table 12). Only the September 2002 sampling date was positively associated with axis 2, possibly reflecting its utilization of carbon

sources from only two guilds (Table 12). September 2002 was positively associated with axis 3 and November 2001 was negatively associated with axis 3.

Table 10. Multi-Response Permutation Procedure (MRPP) for fungal carbon source utilization. The test statistic T describes the separations among the grouping variables, while the chance-corrected within-group agreement (A) is a measure of the effect size independent of sample size. Brte = *B. tectorum*, Pose = *P. secunda*, Elel = *E. elymoides,* Pssp = *P. spicata*.

Grouping variable	Test Statistic T	Chance-corrected within-group agreement, A	p-value
Site	-2.0494	0.00512	0.040
Community			
Cheatgrass-dominated, Native - Interspace, Native - Shrub	-0.7633	0.00155	0.192
Litter species			
Brte, Pose, Elel, Pssp	0.3094	-0.00077	0.561
Date	-30.4651	0.07610	0.000

Table 11. Diversity of fungal carbon source utilization. S = richness, the number of wells for each microplate that had non-zero OWCD values. E = evenness and H = Shannon's diversity index. D' = Simpson's diversity index.

	S	E	H	D'
Species:				
B. tectorum	77.0a	0.923a	4.000a	0.9782a
P. secunda	80.12a	0.919a	4.018a	0.9790a
P. spicata	79.3a	0.917a	3.999a	0.9781a
E. elymoides	78.2a	0.917a	3.994a	0.9780a
Community Level:				
Cheatgrass-Dominated	79.9a	0.920a	4.020a	0.9787a
Native - Shrub	77.8a	0.920a	3.995a	0.9781a
Native - Interspace	77.8a	0.917a	3.987a	0.9778a
Date:				
Nov-01	73.3a	0.920a	3.940a	0.9768a
Jan-02	81.7b	0.922a	4.047b	0.9795b
May-02	80.8b	0.918a	4.026b	0.9791b
Sep-02	78.6ab	0.916a	3.995ab	0.9774a

Table 12. Pearson correlations (r) for carbon sources most highly correlated with the first three axes (principle components) for the PCA ordination of fungal carbon sources utilization. Carbon source names are abbreviated; refer to Table 2 for full names.

Axis 1			Axis 2			Axis 3		
C source	**Guild**	**r**	**C source**	**Guild**	**r**	**C source**	**Guild**	**r**
Lserin	amino acid	-0.779	D-psic	carbohydrate	-0.749	gentio	carbohydrate	-0.487
L-fuco	carbohydrate	-0.748	gambut	amino acid	-0.653	uridin	miscellaneous	-0.393
Lornit	amino acid	-0.711	23buta	miscellaneous	-0.63	Dlagly	miscellaneous	-0.373
Lpyrog	amino acid	-0.656	formic	carboxylic acid	-0.619	Dgulcu	carboxylic acid	-0.372
Dgluam	carboxylic acid	-0.572	acetic	carboxylic acid	-0.586	23buta	miscellaneous	-0.371
adonit	carbohydrate	-0.567	akbuty	carboxylic acid	-0.577	maloni	carboxylic acid	-0.362
Lalani	amino acid	-0.562	gLglut	amino acid	-0.564	Dserin	amino acid	-0.355
Dmanni	carbohydrate	-0.52	glucur	amine/amide	-0.558	gambut	amino acid	-0.349
Laglyc	amino acid	-0.502	propio	carboxylic acid	-0.537	gl1pho	miscellaneous	-0.34
Dsacch	carboxylic acid	0.602	Dgluam	carboxylic acid	0.422	L-arab	carbohydrate	0.284
Dgulcu	carboxylic acid	0.681	c-acon	carboxylic acid	0.433	glycer	miscellaneous	0.29
Dmanno	carbohydrate	0.682	gentio	carbohydrate	0.435	bromos	miscellaneous	0.291
sucros	carbohydrate	0.707	D-gala	carbohydrate	0.444	dextri	polymer	0.293
bmDglu	carbohydrate	0.716	D-meli	carbohydrate	0.455	succin	amine/amide	0.323
L-arab	carbohydrate	0.735	Dgluco	carboxylic acid	0.5	sebaci	carboxylic acid	0.336
cellob	carbohydrate	0.736	adonit	carbohydrate	0.572	twee40	polymer	0.381
Dgaltu	carboxylic acid	0.761	NaDglu	carbohydrate	0.598	akglut	carboxylic acid	0.438
maltos	carbohydrate	0.802	aDlact	carbohydrate	0.648	i-eryt	carbohydrate	0.523

Bacterial and fungal biomass

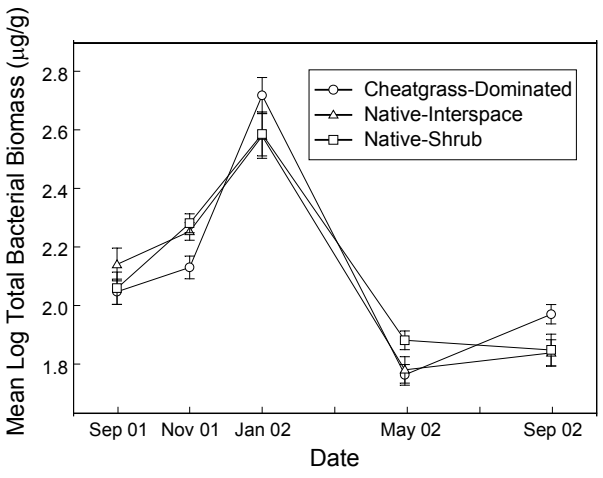

Figure 5. Mean log total bacterial biomass over time for litter decaying in cheatgrass-dominated and native (shrub and interspace) communities. Error bars represent ± one standard error from the mean.

Total bacterial biomass was not significantly different among communities (Figure 5), after accounting for litter species and time ($F_{2,204} = 0.062$ $p = 0.939$). Total bacterial biomass differed with time ($F_{1,204} = 65.897$ $p = 0.000$). Estimated median effects changed slightly with outlier removal, but did not change the significance of the results (Table 13).

There was slight evidence overall that total bacterial biomass differed among litter species after

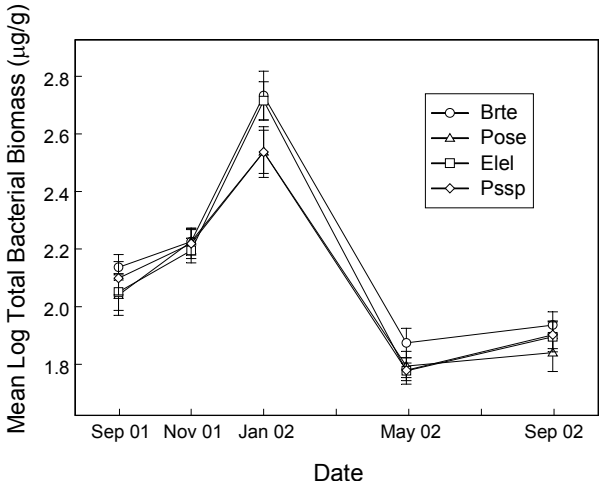

Figure 6. Mean log total bacterial biomass over time for four species of decaying litter: three native (*E. elymoides* (Elel), *P. secunda* (Pose), *P. spicata* (Pssp), and one exotic (*B. tectorum* (Brte)). Error bars represent ± one standard error from the mean.

accounting for community and time ($F_{3,204} = 2.308$ p = 0.078, Table 13, Figure 6). The estimated median total bacterial biomass for *P. secunda, E. elymoides* and *P. spicata* were all significantly less than that for *B. tectorum* (Table 13) within the same community and sampling date, but none of these perennial grasses were significantly different from each other. Removing outliers eliminated the significance of the estimated difference between each of the perennial grasses and cheatgrass (Table 13).

Analysis of randomly selected litter samples yielded no difference in total bacterial biomass among communities ($F_{2,47} = 0.425$, p = 0.657, Figure 7). The difference among sampling dates was significant ($F_{1,47} = 6.336$, p = 0.001).

Table 13. Multiplicative effect sizes and significance values for parameters in the LME model for total bacterial biomass, with and without outliers. An * indicates a significant ($p \leq 0.05$) difference.

Parameter	Reference Level	Estimated Median Multiplicative Effect		p-value	
		all data	no outliers	all data	no outliers
P. secunda	*B. tectorum*	0.888 (0.806 to 0.979)	0.958 (0.914 to 1.004)	0.017*	0.075
E. elymoides	*B. tectorum*	0.910 (0.828 to 0.999)	0.968 (0.926 to 1.013)	0.048*	0.167
P. spicata	*B. tectorum*	0.902 (0.820 to 0.991)	0.965 (0.923 to 1.010)	0.032*	0.129
E. elymoides	*P. secunda*	1.024 (0.930 to 1.128)	1.011 (0.965 to 1.058)	0.626	0.643
P. spicata	*P. secunda*	1.015 (0.922 to 1.118)	1.007 (0.962 to 1.055)	0.757	0.751
P. spicata	*E. elymoides*	0.991 (0.903 to 1.088)	0.997 (0.953 to 1.042)	0.854	0.881
Interspace	Cheatgrass-Dominated	1.011 (0.931 to 1.098)	0.998 (0.960 to 1.038)	0.793	0.937
Shrub	Cheatgrass-Dominated	1.015 (0.936 to 1.101)	1.003 (0.964 to 1.042)	0.708	0.896
Interspace	Shrub	0.996 (0.915 to 1.083)	0.996 (0.956 to 1.037)	0.918	0.840

The overall trends in the data (Figures 5, 6) show that bacterial biomass increased as decomposition proceeded up to a maximum around January 2002. Biomass then declined sometime between January and May 2002, and increased slightly over the second summer of decay. As there

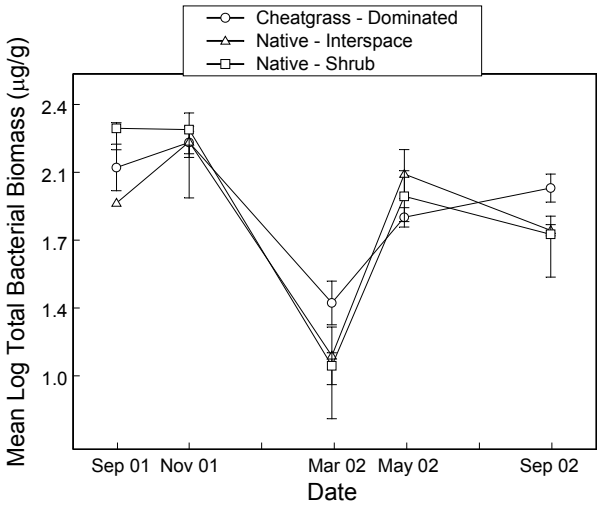

Figure 7. Mean log total bacterial biomass over time for randomly sampled litter decaying in native (shrub and interspace) communities and cheatgrass-dominated communities. Error bars represent ± one standard error from the mean.

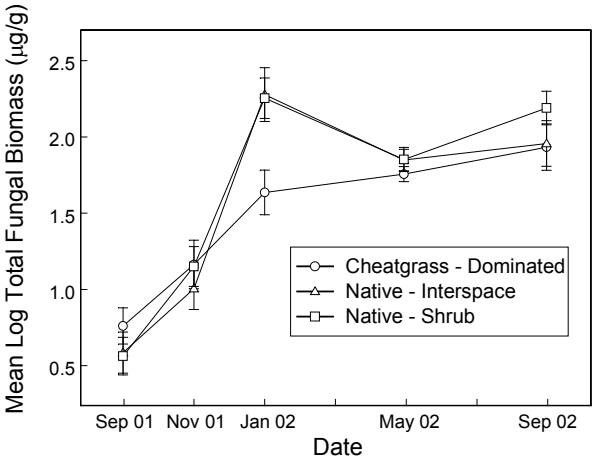

Figure 8. Mean log total fungal biomass over time for litter decaying in cheatgrass-dominated and native (shrub and interspace) communities. Error bars represent ± one standard error from the mean.

was no way to tell the exact age of the litter collected for the random samples, these results (Figure 7) cannot be directly compared to the results for the non-random samples. However, values for the log bacterial biomass were similar for the random and non-random samples on the same dates. This suggests that there was no significant litter bag effect. The data from the random litter also indicates that the large decline in bacterial biomass may have reached its lowest point sometime in March 2002.

There was no evidence of a significant difference in total fungal biomass among communities (Figure 8), after accounting for litter species and time ($F_{2,204} = 2.174$ $p = 0.116$). However, the estimated median total fungal biomass for litter underneath shrubs was significantly greater than it was for litter in cheatgrass-dominated areas given the same litter species and sampling date (Table 14). After removing outliers, this significance was eliminated. Total fungal biomass did not differ among litter species (accounting for communities, time: $F_{3,204} = 1.986$, $p = 0.173$, Figure 9). However, the estimated median total fungal biomass for *P. spicata* was significantly greater than that for *P. secunda* (Table 14). This multiplicative effect was significantly different from one ($p = 0.041$) with all data included, but weakened the significance ($p = 0.071$) after outliers were removed.

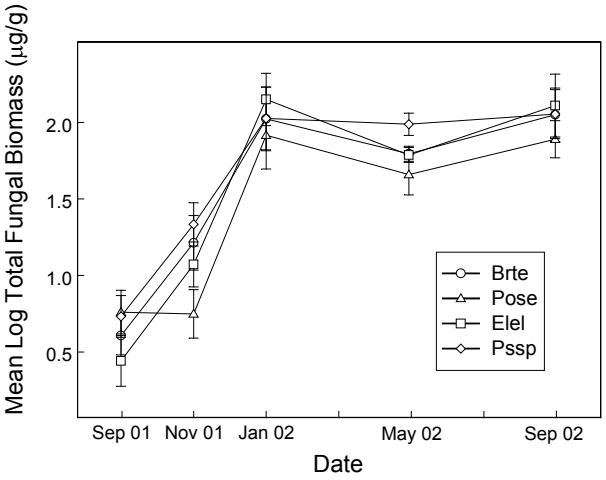

Figure 9. Mean log total fungal biomass over time for four species of decaying litter: three native (*E. elymoides* (Elel), *P. secunda* (Pose), *P. spicata* (Pssp), and one exotic (*B. tectorum* (Brte)). Error bars represent ± one standard error from the mean.

Total fungal biomass differed among sampling dates ($F_{1,204} = 130.25$, $p = 0.000$, Figures 8, 9). Litter in cheatgrass-dominated communities had greater total biomass of fungi over the first summer, but fungal growth on litter from native communities surpassed cheatgrass-dominated communities as soon as the rainy season began. Biomass increased as decomposition proceeded to a maximum sometime between January and March 2002 (as suggested by the random litter samples data). In contrast, litter from cheatgrass-dominated communities gained fungal biomass between November 2001 and January 2002 at the same rate as between September 2001 and November 2001. Fungal biomass for litter in native communities fell again between January 2002 and May 2002, but biomass for litter in the cheatgrass-dominated communities continued to rise steadily from January 2002 to May 2002 to a maximum the following September 2002.

Table 14. Estimated effect sizes and significance values for parameters of the LME model for total fungal biomass, with and without outliers. An * indicates a significant ($p \leq 0.05$) difference.

Parameter	**Reference Level**	**Estimated Median Multiplicative Effect**		**p-value**	
		all data	**no outliers**	**all data**	**no outliers**
P. secunda	*B. tectorum*	0.950 (0.855 to 1.056)	0.950 (0.858 to 1.052)	0.341	0.320
E. elymoides	*B. tectorum*	1.001 (0.904 to 1.108)	0.984 (0.892 to 1.084)	0.987	0.741
P. spicata	*B. tectorum*	1.060 (0.956 to 1.174)	1.042 (0.944 to 1.149)	0.265	0.409
E. elymoides	*P. secunda*	1.053 (0.948 to 1.170)	1.036 (0.937 to 1.147)	0.327	0.490
P. spicata	*P. secunda*	1.115 (1.004 to 1.239)	1.096 (0.992 to 1.212)	0.041*	0.071
P. spicata	*E. elymoides*	1.059 (0.957 to 1.171)	1.059 (0.962 to 1.165)	0.265	0.240
Interspace	Cheatgrass-Dominated	1.064 (0.973 to 1.164)	1.042 (0.957 to 1.135)	0.168	0.340
Shrub	Cheatgrass-Dominated	1.104 (1.011 to 1.206)	1.079 (0.992 to 1.174)	0.027*	0.076
Interspace	Shrub	0.964 (0.880 to 1.056)	0.966 (0.885 to 1.054)	0.430	0.433

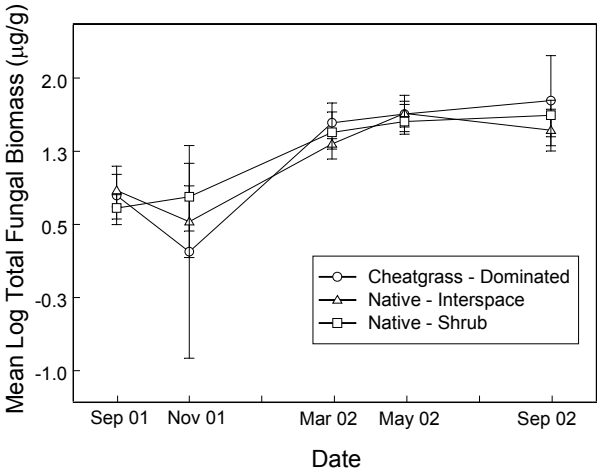

Figure 10. Mean log total fungal biomass over time for randomly sampled litter decaying in native (shrub and interspace) communities and cheatgrass-dominated communities. Error bars represent ± one standard error from the mean.

Randomly selected litter samples showed no evidence of a significant difference among communities after accounting for time ($F_{2,46} = 1.029$ p = 0.365, Figure 10). There was a significant difference among sampling dates, after accounting for community ($F_{1,46} = 34.407$ p = 0.000).

There was no significant difference in the ratio of total fungal to total bacterial biomass (hereafter: ratio) among communities (Figure 11), after accounting for litter species and time ($F_{2,204} = 2.416$ p = 0.092). However, the estimated median ratio for litter underneath shrubs was significantly greater (Table 15) than litter in cheatgrass-dominated areas (p = 0.021), but this significance was weakened after outliers were removed (p = 0.081). There was suggestive evidence of a difference in ratio among litter species (Figure 12), after accounting for community and time ($F_{3,204} = 2.720$, p = 0.046). The estimated median ratio for *P. spicata* was 1.133 times greater than that for cheatgrass, and this difference remained after removing the outliers (Table 15). The estimated median ratio for *P. spicata* was also significantly greater than that for *P. secunda*, but removing two outliers resulted in a weakened significance between litter species.

Table 15. Estimated effect sizes and significance values for parameters of an LME model for the log ratio of total fungal to total bacterial biomass, with and without outliers. An * indicates a significant ($p \leq 0.05$) difference.

Parameter	Reference Level	Estimated Median Multiplicative Effect		p-value	
		all data	no outliers	all data	no outliers
P. secunda	*B. tectorum*	1.006 (0.900 to 1.125)	1.005 (0.910 to 1.111)	0.912	0.914
E. elymoides	*B. tectorum*	1.066 (0.953 to 1.180)	1.033 (0.938 to 1.136)	0.282	0.509
P. spicata	*B. tectorum*	1.133 (1.018 to 1.262)	1.103 (1.001 to 1.214)	0.023*	0.047*
E. elymoides	*P. secunda*	1.054 (0.944 to 1.176)	1.027 (0.931 to 1.133)	0.350	0.594
P. spicata	*P. secunda*	1.126 (1.008 to 1.258)	1.097 (0.993 to 1.211)	0.035*	0.067
P. spicata	*E. elymoides*	1.068 (0.961 to 1.188)	1.068 (0.971 to 1.174)	0.217	0.172
Interspace	Cheatgrass-Dominated	1.078 (0.982 to 1.185)	1.044 (0.960 to 1.136)	0.115	0.310
Shrub	Cheatgrass-Dominated	1.115 (1.016 to 1.223)	1.077 (0.991 to 1.170)	0.021*	0.081
Interspace	Shrub	0.967 (0.879 to 1.065)	0.970 (0.890 to 1.006)	0.499	0.488

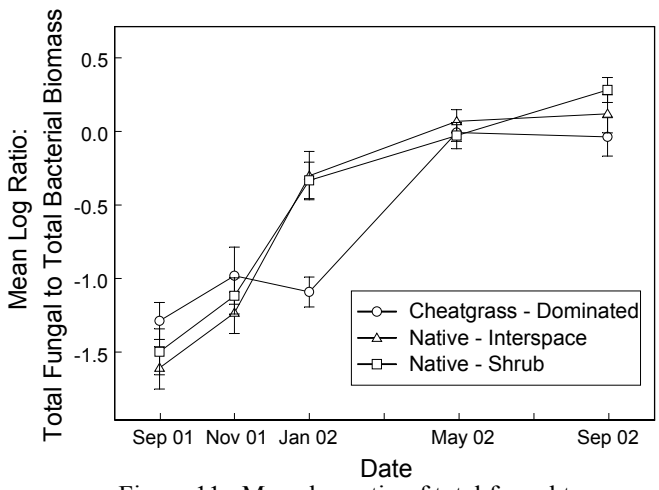

Figure 11. Mean log ratio of total fungal to total bacterial biomass over time for litter decaying in cheatgrass-dominated and native (shrub and interspace) communities. Error bars represent ± one standard error from the mean.

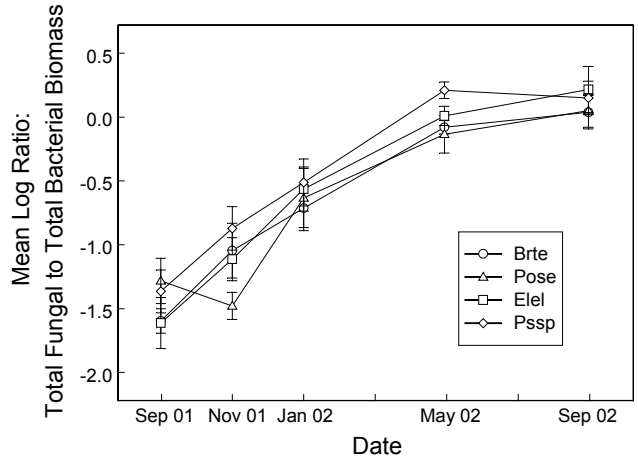

Figure 12. Mean log ratio of total fungal to total bacterial biomass over time for four species of decaying litter: three native (*E. elymoides* (Elel), *P. secunda* (Pose), *P. spicata* (Pssp)), and one exotic (*B. tectorum* (Brte)). Error bars represent ± one standard error from the mean.

The log ratio increased over time up until May 2002, after which it remained essentially stable (Figures 11, 12). By January 2002, the log ratio approached zero for litter in native communities, indicating the point of shift in the decomposition process from bacterial dominance to fungal dominance (in terms of biomass). Among the random samples, the highest ratio was achieved during March 2002 (Figure 13), and the ratio then fell back to zero by May 2002. Removing the March data, we create a plot similar to the one for total fungal biomass from the litter bag data.

There were no significant differences in ratio among communities for randomly selected litter samples, after accounting for time ($F_{2,45} = 0.043$ $p = 0.958$). There was a significant difference among sampling dates ($F_{1,45} = 25.79$ $p = 0.000$, Figure 14).

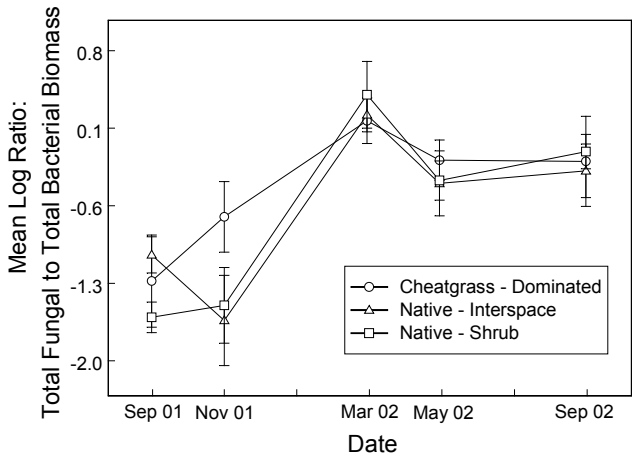

Figure 13. Mean log ratio of total fungal to total bacterial biomass over time for randomly sampled litter decaying in native (shrub and interspace) communities and cheatgrass-dominated communities. Error bars represent ± one standard error from the mean.

Climate

Most of the precipitation came in November 2001 through April 2002 (Table 16), and much of that in December and January fell in the form of snow. Total precipitation for July 2001 through Aug 2002 was about 62% of average. While precipitation from September 2001 through December 2001 was slightly above average, precipitation for January 2002 through September 2002 was below average. February and May 2002 were much drier than normal (16% and 1% of average, respectively). Total yearly precipitation for this climate station is typically 300mm.

Table 16. Climate data for time period of study, plus 30-year averages. NA= Not available. Monthly averages obtained from the University of Idaho climate data website (inside.uidaho.edu/asp/liststations.asp). Thirty-year averages obtained form the Western Regional Climate Data website (www.wrcc.dri.edu/climatedata.html.

Boise WSFO	**Elev: 284 ft (86.6 m)**				**Lat: 43°43"**		**Long: 116°13**							
	Jul-01	**Aug-01**	**Sep-01**	**Oct-01**	**Nov-01**	**Dec-01**	**Jan-02**	**Feb-02**	**Mar-02**	**Apr-02**	**May-02**	**Jun-02**	**Jul-02**	**Aug-02**
ave temp (F)	74.3	78.7	68.4	53.5	44	NA	31.6	34	40.9	50.7	59.4	69.8	79.8	71.2
30 year ave temp (F)	74.1	72.6	63.1	52	39.4	31	29.3	35.8	42.2	49.4	57.6	65.5	74.1	72.6
total precip (in)	0.15	0	0.44	0.86	1.52	NA	0.94	0.19	1.06	0.83	0.01	0.19	0.09	0.05
30 year ave total precip (in)	0.27	0.30	0.60	0.79	1.35	1.36	1.44	1.16	1.23	1.21	1.28	0.89	0.27	0.30
% of average	55.6	0.0	73.3	108.9	112.6	NA	65.3	16.4	86.2	68.6	0.8	21.3	33.3	16.7
# days w/ snowdepth	0	0	0	0	1	NA	9	0	2	0	0	0	0	0
ave snow depth	0	0	0	0	0.07	NA	0.45	0	1	0	0	0	0	0
Boise Lucky Peak	**Elev: 284 ft (86.6 m)**				**Lat: 43°32"**		**Long: 116°04**							
	Jul-01	**Aug-01**	**Sep-01**	**Oct-01**	**Nov-01**	**Dec-01**	**Jan-02**	**Feb-02**	**Mar-02**	**Apr-02**	**May-02**	**Jun-02**	**Jul-02**	**Aug-02**
ave temp (F)	74.6	77.9	69.9	NA	NA	NA	NA	33.1	40.7	50.4	58.4	69.5	80.4	70.8
30 year ave temp (F)	74.4	73.5	64.3	53.7	40.6	31.4	28.8	36.1	42.3	49.6	58.1	66.2	74.4	73.5
total precip (in)	0.35	0	0.95	0.35	1.82	1.41	1.62	0.24	3.18	1.13	0.08	0.2	0.12	0.01
30 year ave total precip (in)	0.31	0.41	0.69	0.79	1.73	1.54	1.75	1.22	1.44	1.42	1.4	1.04	0.31	0.41
% of average	112.9	0.0	137.7	44.3	105.2	91.6	92.6	19.7	220.8	79.6	5.7	19.2	38.7	2.4
# days w/ snowdepth	0	0	0	0	0	0	NA	0	0	0	0	0	0	0
ave snow depth	0	0	0	0	0	0	NA	0	0	0	0	0	0	0
Boise 7N	**Elev: 389 ft (118.6 m)**				**Lat: 43°43"**		**Long: 116°12**							
	Jul-01	**Aug-01**	**Sep-01**	**Oct-01**	**Nov-01**	**Dec-01**	**Jan-02**	**Feb-02**	**Mar-02**	**Apr-02**	**May-02**	**Jun-02**	**Jul-02**	**Aug-02**
ave temp (F)	71.3	76	66.5	52.3	42.5	28.7	29.9	31.9	38.2	47.5	54.7	64.7	76.1	68
30 year ave temp (F)	71.8	71.5	62.4	50.8	37.6	29.4	29.1	34.1	40.9	47.4	54.7	63.4	71.8	71.5
total precip (in)	0.45	0.01	0.55	0.54	2.61	1.92	1.79	0.46	2.02	2.04	0.1	0.17	0.15	0.17
30 year ave total precip (in)	0.52	0.47	1.07	1.27	2.22	2.21	2.15	2.02	2.27	2.01	2.06	1.12	0.52	0.47
% of average	86.5	2.1	51.4	42.5	117.6	86.9	83.3	22.8	89.0	101.5	4.9	15.2	28.8	36.2
# days w/ snowdepth	0	0	0	0	6	31	11	6	6	0	0	0	0	0
ave snow depth	0	0	0	0	1	5.3	NA	NA	0.35	0	0	0	0	0

Nitrogen

The log RAQ for NH_4 differed among sites, after accounting for community and time ($F_{3,228}$ = 3.196 p = 0.024). Because site was significant, it was retained in the inferential model to answer the questions of interest. There was no evidence that the log RAQ for NH_4 differed among communities (Table 17, Figure 14), after accounting for site and time ($F_{2,228}$ = 0.410, p = 0.960). There was strong evidence that the log RAQ for NO_3 differed among communities (Table 17, Figure 15), after accounting for time ($F_{2,233}$ = 6.127, p = 0.002). The estimated median NO_3 RAQ for soils under shrubs was about 10% less than that for cheatgrass-dominated or interspace soils (Table 17).

Table 17. The estimated median multiplicative effect for the Resin Adsorption Quantity (RAQ) for NO_3 and NH_4 and associated significance ($p \leq 0.05$).

Parameter	Reference level	Estimated median multiplicative effect			
		NO_3		NH_4	
		estimate	p-value	estimate	p-value
Shrub	Cheatgrass-Dominated	0.909 (0.855 to 0.966)	0.002*	1.001 (0.968 to 1.036)	0.938
Interspace	Cheatgrass-Dominated	0.987 (0.929 to 1.048)	0.660	1.003 (0.964 to 1.038)	0.867
Interspace	Shrub	1.085 (1.027 to 1.147)	0.004*	1.001 (0.972 to 1.032)	0.921

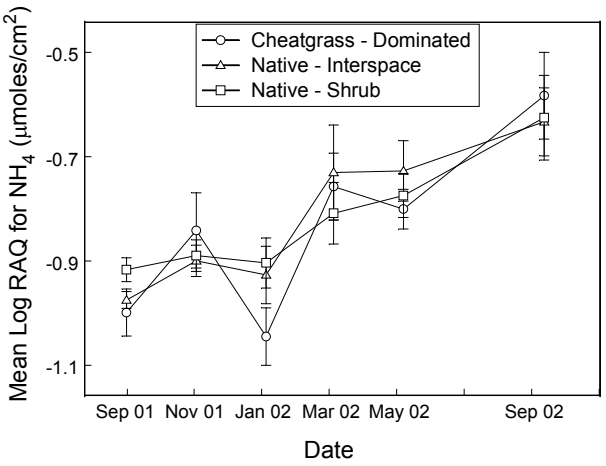

Figure 14. Mean log Resin Absorption Quantity (RAQ) for NH_4 over time for soils under native (shrub and interspace) and cheatgrass – dominated communities. Error bars represent ± one standard error from the mean.

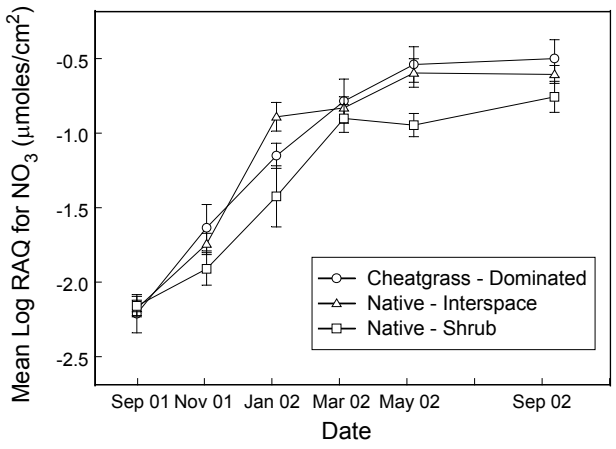

Figure 15. Mean log Resin Absorption Quantity (RAQ) for NO_3 over time for soils under native (shrub and interspace) and cheatgrass – dominated communities. Error bars represent ± one standard error from the mean.

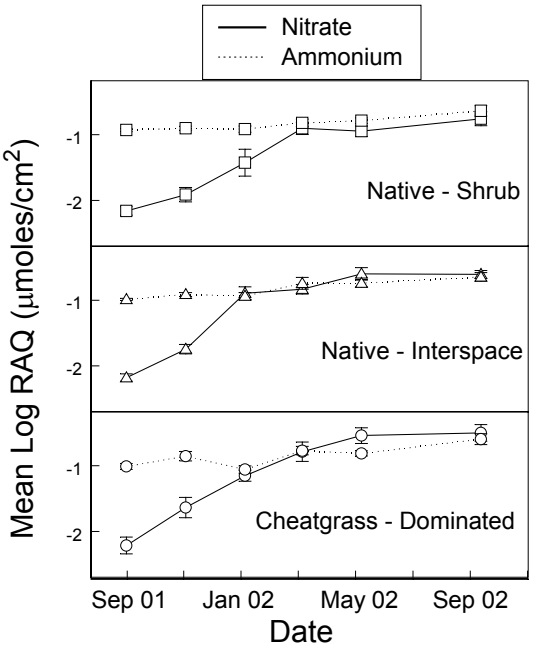

Figure 16. Mean log Resin Absorption Quantity (RAQ) for NO_3 and NH_4 over time for soils under native (shrub and interspace) and cheatgrass – dominated communities. Error bars represent ± one standard error from the mean.

DISCUSSION

Decomposition Processes

Meentemeyer (1978) found that actual evapotranspiration (AET) was the best predictor of decay rates on a global scale, whereas lignin:N ratios were the best predictor of decay rates within a particular region. The relationship of AET, lignin, and litter decay is a triangular one, in which climate can have both direct and indirect effects on decay rates via litter quality (Aerts 1997). Given the average annual AET of 800mm for our study region, and initial litter lignin concentrations of about 2-5% (Table 5), Aert's (1997) rework of the model would predict a decay rate constant of 0.6 for our study area, which is somewhat higher than our findings (0.423, Table 3), but similar to the findings of Mack (1977) for decomposition of *Artemisia tridentata* (50% mass loss/year, k = 0.693). Our 1.5 mm mesh most likely excluded some macrofauna, thereby underestimating actual decay rates slightly, though not enough to explain this difference.

Meentemeyer (1978) suggested that decay rates in deserts might be much higher than predicted by his model. One study found 35-70% decomposition in one year (depending on litter species: various desert shrubs and annual forbs) in the Chihuahuan desert (Schaefer et al. 1985). These values are as high or higher than more mesic environments. Decay rates as high as 0.35 are typical of temperate and Mediterranean regions (Aerts 1997).

How can decomposition rates be so high in an arid environment? Moisture is essential for microbial action in decomposition, yet moisture is limiting in these ecosystems. Our study found that decay rates were fastest over the first summer of decay (Table 4), even though the area only received 1.5 inches of rain over those 3 months (Table 16). Decay rates over the second summer were slightly faster than rates over the rainy season, even though the area received less than a 0.5 inches of rain from May to September 2002. Thus we can conclude that above-ground decay rates are independent of moisture availability. In support of this, watering treatments in the Chihuahuan desert had no effect on decay rates (Whitford et al. 1986). This still does not adequately explain the high decomposition rates, however, leading several authors to suggest that abiotic factors may have a dominant influence on above-ground decay rates in arid environments (Montaña et al. 1988, Pauli 1964, Schaefer et al. 1985).

Our study provided marginal statistical evidence of differences in percent mass remaining for different grass litter species or life forms (annual vs. perennial), even though the species had different lignin:N ratios. Assuming that Meentemeyer's (1978) model holds true for our study area, then decomposition rates for our litter species should be negatively correlated with lignin:N ratios (slowest to fastest: *P. spicata* < *P. secunda* < *B. tectorum* < *E. elymoides*). Decomposition never

followed this pattern consistently (Tables 3,4). Interestingly, Meentemeyer (1978) predicts that litter with highly different lignin concentrations may decay at the same rate when AET is low. Conversely, differences in decay rates may relate to lignin concentrations of the litter species when AET is high. In the Great Basin, low AET occurs during winter when soil moisture recharge occurs. The January 2002 decay rates of our different litter species were similar (Figure 2), thus fitting this pattern. By May 2002, cheatgrass had the most mass remaining and the slowest rate of decomposition, whereas *E. elymoides* had the fastest rate and the least remaining. The trend over the second summer seems to indicate that the decomposition rates of the four species may indeed be separating with time (Figure 2). The overall 14 month trend, from slowest to fastest, was: *E. elymoides* < *P. spicata* < *P. secunda* < *B. tectorum*, providing evidence that the shift to cheatgrass dominance my accelerate litter turnover (Table 3).

The failure of initial lignin content to predict decay rates has also been found in other decomposition studies in North American deserts (Schaefer et al. 1985, Mack 1977, Murray 1975, Whitford et al. 1986). There have been various attempts to explain this occasional failure. Similar to our study, Berg et al. (1996) found that the relationship between litter chemistry and decay rates differed among phases of the decomposition process because the lignin concentration of litter typically increases as decomposition proceeds and continues until lignin breakdown begins. There are two causes for this increase. First, more easily decomposable substrates (e.g. sugars, amino acids) are broken down initially, causing the percentage of lignin in the remaining litter to rise. Second, lignin is also formed through condensation reactions as decay proceeds (Horner et al. 1988). Not only did our lignin concentrations rise over the first summer for all species except *P. secunda* (Appendix A), but the actual grams of lignin increased, suggesting lignin formation. These mechanisms obviously make lignin control over decay rates somewhat more complex in the short term.

The lack of a highly significant difference in percent mass remaining for litter species may be due to: 1) inadequate length of decay (i.e. during the second year of decomposition differences among litter species may have been more pronounced), 2) initial lignin:N ratios were not different enough to create different decay rates, and/or 3) differences among litter species were masked by the differences among communities. In support of conclusion 3, litter in a shortgrass steppe ecosystem decayed at different rates based on the site in which the litter was placed (communities of different seral stages), and not the litter species type (Pashcke et al. 2000). However, our results do not support conclusion 3, since there were no significant differences among communities. The difficulty with conclusion 2 is defining the minimum difference in lignin: N ratios needed to produce significantly different decay rates.

We predicted differences in decomposition rates among communities owing to subtle differences in litter-layer microclimate (UVB exposure, temperature and moisture fluctuations) and

possibly different litter microbial community structure. Shrub areas are obviously shaded from UVB light, and this shading also creates temperature and moisture differences (Blackburn 1975, Doescher et al. 1984, Eckert et al. 1986). The three communities seemed to have increasingly dissimilar decay rates with time (Figure 1). Litter decaying under shrub cover had significantly higher total fungal biomass than litter in cheatgrass-dominated communities. Despite this, the slowest decomposition was underneath shrubs (followed by cheatgrass-dominated and then interspace) by the end of the second summer. However, lignin loss through the rainy season, least to most, also followed the pattern shrub < cheatgrass-dominated < interspace (Table 6). This trend is also one of decreasing shade, in terms of plant cover, suggesting lignin photodegradation. The trend in lignin loss over the second summer was less clear, although the overall pattern was interspace < cheatgrass-dominated < shrub (least to most). Curiously, litter under shrubs had the lowest decay rate over the second summer, despite its higher total fungal biomass and greater lignin loss. The trend in decay rates over the second summer indicated faster decay rates with decreasing shade. Further study is needed to determine whether UVB radiation is directly responsible for lignin degradation in this ecosystem and if so, how this compares to decay by fungi.

Putting these many pictures together, it seems that although decay rates for the different litter communities were quite similar throughout the first year of decomposition, the processes by which these communities obtained these similar results may indeed be different. Cheatgrass-dominated communities had slightly greater total bacterial biomass than native communities (Figure 5) in January and May 2002, and the January 2002 spike in fungal biomass was not as dramatic as in the native litter communities (Figure 8). The fungal biomass for cheatgrass did not exhibit any different patterns in biomass over time than the perennial species (Figure 9). This suggests that the different fungal biomass pattern in cheatgrass-dominated communities (Figure 8) was not due to the litter quality of cheatgrass, but instead were due to some characteristic of its litter layer.

The decrease in biomass for both bacteria and fungi occurring between January 2002 and May 2002 (Figures 5, 6, 8, 9) may have been caused by freezing temperatures in January 2002 or by the unusually dry February that followed (Table 16). Dry-wet cycles can significantly reduce microbial biomass (Schimel et al. 1999). The stress event causing the reduction in biomass had little effect on the functional diversity for both bacteria and fungi (Tables 8, 11). If the winter decline in fungal biomass was caused by dry conditions in February, we could predict that in a typical year this winter decline in the native communities may not occur. This could cause native communities to have faster decay rates due to greater fungal biomass than cheatgrass-dominated communities. Similarly, if the cause was freezing temperatures, this decline may not occur in a mild year. Despite the freezing temperatures and dry conditions, fungal biomass in cheatgrass-dominated communities continued to increase through the winter. This suggests that the fungi dominating the

cheatgrass communities over the winter months (Table 16) may have been more stress-tolerant (and possibly drought-tolerant) than the fungal communities in native areas.

The ratio of total fungal to total bacterial biomass can be a useful indicator of the degree of disturbance for an ecosystem. Typically, a high fungal to bacterial biomass ratio indicates a stable, undisturbed ecosystem. For example, Grayston et al. (2001) found that a high-fertility, highly managed grassland dominated by *Lolium perenne* supported more bacteria relative to fungi. The readily available carbon sources in this managed community were easily utilized by zymogenous bacteria, as evidenced by high respiration rates. In unmanaged grasslands, native grasses contributed more recalcitrant forms of carbon to the soil organic matter. The proportion of the number of fungi to bacteria was higher in these communities, reflecting fungal ability to breakdown more recalcitrant forms of carbon such as lignin and phenolic compounds.

In our study, fungi began to dominate the microbial biomass during the second summer of decomposition, for all communities (Figure 11). This is curious, given that bacteria may not be able to find the moisture and stability they need to exist above the soil in this arid ecosystem, whereas fungi have a greater ability to break down celluloses and to grow without significant moisture. Our results contrast those of Dilly et al. (2001) who also looked at microbial communities inhabiting tree leaf litter as decomposition proceeded. They found that fungal biomass dominated early in the decay process, with bacteria dominating later. They suggest that fungi were needed for initial breakdown of the litter before bacteria are able to mineralize it. In our study, fungi were less able to establish themselves on fresh litter that was created at the start of the dry summer season. As the rainy season began, fungi grew steadily and became dominant in terms of biomass by the start of the second summer.

The pattern of the ratio of total fungal to total bacterial biomass was similar for all litter species as decomposition proceeded through the seasons (Figure 12). However, native and cheatgrass-dominated litter layers had different microbial dominance dynamics (Figure 11). Within native communities, the fungal to bacterial biomass ratio increased over time and leveled-off over the second summer. In cheatgrass-dominated communities, the ratio declined between November 2001 and January 2002, creating a large difference in the ratios among communities for the January 2002 sampling date. This decline was due to the fact that cheatgrass-dominated communities had a sharp rise in bacterial biomass and only a slight increase in fungal biomass, whereas the native communities had a very large rise in fungal biomass and a slightly smaller rise in bacterial biomass than the cheatgrass-dominated communities. Overall, the shrub community had a significantly greater ratio than the cheatgrass-dominated community, and this was mainly due to their differences in fungal biomass.

Soil Nitrogen Availability

There were no significant differences found in NH_4 availability among soils of different communities. This is contrary to expectations of higher NH_4 levels in shrub soils due to typically larger soil C and N pools and higher N mineralization than interspace soils. There was a pulse of mineralization between January and March 2002 (Figure 14) as predicted. Curiously, increases in NH_4 seemed equally high over the second summer, even though soils had dried. One explanation for this may be that there was no sampling between May and September 2002; thus the increase in NH_4 may have occurred only in May. Since resin capsules accumulate ions irreversibly, NH_4 availability should never decrease over time. However, it seems that available NH_4 did decrease between November 2001 and January 2002, especially in cheatgrass-dominated soils (Figure 14). Since samples from each date were completely independent of one another, this apparent decrease may simply be random variation. Additionally, frozen soils in January prevented complete recovery of all of the resin capsules; thus capsules were only recovered from two sites in January. Since site was a significant factor in the regression analysis, this apparent decrease from November 2001 to January 2002 should not be interpreted as a real decrease in field NH_4 availability.

As we hypothesized, shrub soils had significantly less NO_3 availability than both interspace soils and cheatgrass-dominated soils at every sampling date, except initially when there was no difference. The lack of any initial difference in NO_3 availability may be due to the fact that there was little moisture between July 2001 and the first sampling date in September 2001. Cheatgrass-dominated soils had the highest amount of available NO_3 at every date except January 2002, when interspace soils were highest (Figure 15). This lends support to our prediction that native soils indeed have a tighter N cycle, in that plants and microbes quickly immobilize NH_4 before significant NO_3 can be produced. Our results suggest that this is mostly due to shrub soil dynamics, which typically have higher microbial biomass and mineralization.

The second largest difference in NO_3 availability between shrub soils and cheatgrass-dominated soils occurred in the May 2002 sampling. By May, cheatgrass has typically set seed and senesced. Mineralization may still be occurring the soil, although little N is being used. Thus cheatgrass-dominated soils may be effectively storing N during this late-spring period. This is evident by the May 2002 sampling date, where NO_3 availability surpassed NH_4 availability in cheatgrass-dominated soils (Figure 16). Ammonium availability was always higher than NO_3 availability in the shrub soils (Figure 16), once again suggesting that shrub soils have a tighter N cycle. The dynamics of N availability were much different for the three communities, and these differences were mostly attributable to NO_3 availability (Figure 16). It is also evident that interspace soils were more similar to cheatgrass-dominated soils in terms of their N availability. Since all of

the interspace soils in this study contained some percentage of cheatgrass, however small, we do not know whether this similarity is a cause or effect of cheatgrass invasion.

Even though we see a tighter N cycle in the native communities, nitrification may account for > 90% of net N mineralization rates (Burke 1989) in semi-arid regions. If this is true for our native areas, then NO_3 losses by denitrification or leaching must be high. Thus an alternative explanation for greater NO_3 availability in cheatgrass-dominated soils is that denitrification may somehow be inhibited or depressed. There is little knowledge of denitrification in arid ecosystems. Initial work in a southwest desert indicates that > 77% of N inputs are lost to the atmosphere (Peterjohn and Schlesinger 1990). This relatively high amount of denitrification is due to the ability of denitrifying enzymes to endure desiccation and respond rapidly to rewetting (Peterjohn 1991). Further study should be conducted regarding the effect that the cheatgrass litter layer has on denitrification via soil temperatures and water-holding capacity.

Evans et al. (2001) found that native sites newly invaded by cheatgrass had lower denitrification than native, non-invaded sagebrush sites. They attributed this to the fact that cheatgrass-invaded sites had lower inorganic N availability. Despite this apparent conservation of N, the authors predicted long-term decreases in N availability with cheatgrass dominance due to: 1) poor soil crust recovery, thereby decreasing N fixation, 2) N immobilization due to the high C:N and lignin:N ratio of cheatgrass, and 3) N volatilization by fire. While 1) and 3) are certainly vectors of N loss for our sites, after approximately 20 years of cheatgrass dominance our sites had greater levels of available inorganic N, due to higher levels of NO_3 than native soils. However, our results call into question the high lignin:N ratios found by Evans et al. (2001). Our lignin:N ratios for cheatgrass were not significantly different from the other perennial grasses; therefore cheatgrass may not stimulate immobilization. Additionally, our results indicate that lignin:N ratios can vary considerably based on the time of year the litter was collected and its stage of decay (Table 5).

Within cheatgrass-dominated communities, out-of phase mineralization in late spring allows nitrification to occur and significant NO_3 to accumulate in the soil. The cheatgrass environment then must exert some type of NO_3 conservation mechanism. Possibilities for this NO_3 conservation mechanism include decreased denitrification, decreased erosion, or decreased leaching. In a study by Young et al. (1999), N-enrichment treatment of NH_4SO_3 increased cheatgrass abundance, yet application of NH_4SO_3 plus nitrapyrin (a nitrification inhibitor) caused complete disappearance of cheatgrass, with 100% recovery of native Indian rice grass. The results of this study and ours suggest the need to investigate the NO_3 conservation mechanisms of cheatgrass – dominated ecosystems and the possible dependence of cheatgrass on NO_3. Although cheatgrass cannot sequester N within its tissues as a perennial can, our results suggest that it may have an indirect method of conserving N within its environment.

Our results are more similar to the findings of Svejcar and Sheeley (2001), who found no significant differences in N mineralization, extractable soil N, total soil C and N, and C/N ratios of above-ground tissues between native and cheatgrass-dominated (> 40 years without fire) sites. Although these authors agree that total soil N in cheatgrass-dominated soils should be lost over time, they suggest that available N can remain high even though total soil fertility declines. Although our results show higher levels of NO_3 in cheatgrass-dominated soils, further study is needed as to the role of this phenomenon in cheatgrass persistence. Conclusive evidence of this long-term depletion of total soil N in cheatgrass-dominated systems is also needed.

CONCLUSION

Cheatgrass currently covers 40 million hectares of land in the Intermountain West (DiTomaso 2000). As perennial grasslands are converted to annual grasslands by cheatgrass, it is important to understand the effect that cheatgrass has on major environmental processes such as decomposition, nutrient, and water cycles and primary production if we are to restore these ecosystems to a previous state. Alterations in decay rates can point to differences in microbial communities, nutrient cycling, and microclimate. Thus they can provide an assessment of the overall effect that disturbance has had on an ecosystem.

It is not far-fetched to believe that the widespread domination of cheatgrass may be altering the C and N balance of these ecosystems, especially since some studies have found that cheatgrass has a much higher C:N ratio than native grasses (Evans et al. 2001). However, our results indicate little difference in decomposition rates for above-ground litter between native and cheatgrass-dominated communities. This seems to indicate that disturbance has not had a drastic effect on this ecosystem process. However, the amount of above-ground litter that is actually incorporated into the soil in these communities may be minimal. Above-ground litter decay may be a mostly abiotic process, with most of the litter breakdown occurring before entering the soil. Thus disturbance-induced changes in soil microbial communities may still have dramatic effects on the ecosystem, even though above-ground decay rates indicate little effect of disturbance.

Although decay rates among our communities were not significantly different, our data indicate that the dynamics of microbial action in decomposition in cheatgrass-dominated ecosystems may be different from native sagebrush ecosystems. The patterns in bacterial biomass cheatgrass-dominated communities were due to the litter quality of cheatgrass, whereas patterns of fungal biomass were due to microclimate effects of the litter layer in cheatgrass-dominated communities. Litter microbial dynamics have been altered by cheatgrass invasion, and at least some of this alteration may be due to the litter quality of cheatgrass itself, and not just the microclimate it creates with its substantial litter layer. Belnap and Phillips (2001) found alterations in most soil food web

components upon addition of cheatgrass to an arid community, and speculated that these changes may alter decomposition and nutrient cycling. However, we did not find significantly altered litter decomposition rates over the first 14 months. There are also indications that cheatgrass significantly alters soil bacterial communities (Kuske et al 2002). We found that cheatgrass litter may support a larger bacterial biomass than perennial grasses, no matter in which community the litter is decaying.

In many ecosystems, bacteria dominate the microbial biomass with increased levels of disturbance, whereas native ecosystems tend to be dominated by fungi. Our results showed a large difference in total fungal biomass between native and cheatgrass-dominated areas at our January 2002 sampling date. Native communities were more highly influenced by fungi much earlier than the disturbed community. However, neither community was dominated by fungi (in terms of biomass) until May 2002. Trends over the second summer indicate that native communities may indeed have greater fungal dominance than cheatgrass-dominated communities. Bolton et al. (1993) found higher fungal biomass, microbial biomass C and N, and soil respiration in soils underneath cheatgrass than soils underneath sagebrush and *P. spicata*. However, landscape estimates of the same variables showed no differences between native and cheatgrass-dominated ecosystems, suggesting that the major difference in the communities was the distribution of microbial biomass and activity, and not the amount.

The lack of significant differences in decay rates among communities did not translate to soil N availability. Soil NO_3 availability was greater in cheatgrass-dominated soils than in native soils, but soil NH_4 availability was similar, suggesting that cheatgrass soils may accumulate NO_3 formed during out of phase mineralization in late spring. Further testing is needed in order to confirm this hypothesis. Lower overall levels of soil NO_3 availability in the native communities support the idea that the native communities have a tighter N cycle.

The overall results of our study indicate that the years of cheatgrass dominance have had little effect on above-ground decay rates, although the microbial dynamics of the litter may have indeed changed. As there were no consistent correlations between litter microbial community dynamics, litter lignin concentrations, or moisture with decay rates, our findings support the theory that abiotic factors may have greater control over above-ground decay rates than biotic factors. Further study is needed on the relative importance of UVB radiation versus fungi in lignin degradation and decay processes in arid ecosystems. Availability of NH_4 in the soil has not changed with cheatgrass dominance, but NO_3 availability has increased. Soil amendments have been used to successfully alter soil N availability (McClendon and Redente 1992); however, continued research into the effect of particular soil amendments on perennial grass establishment and cheatgrass elimination will help land managers create successful restoration plans. Further study into below-ground decay and ecosystem processes is recommended in order to provide a complete picture of how cheatgrass has (or has not) altered its ecosystem.

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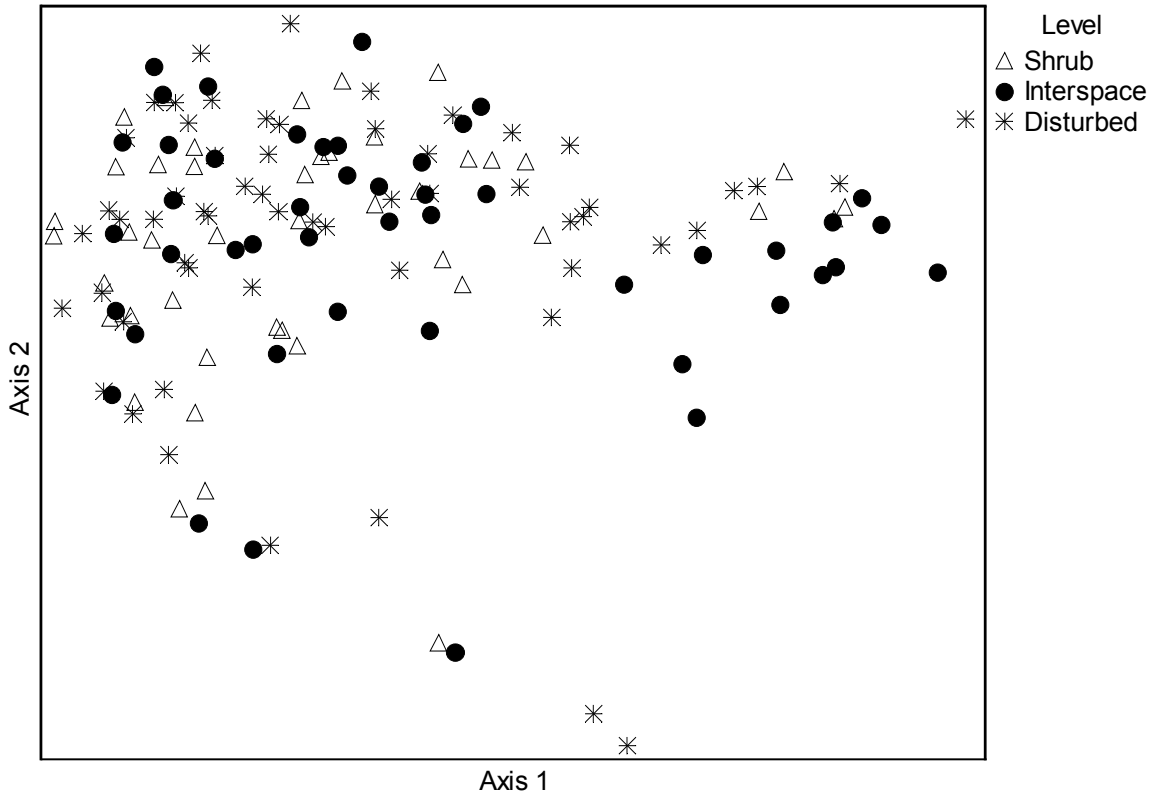
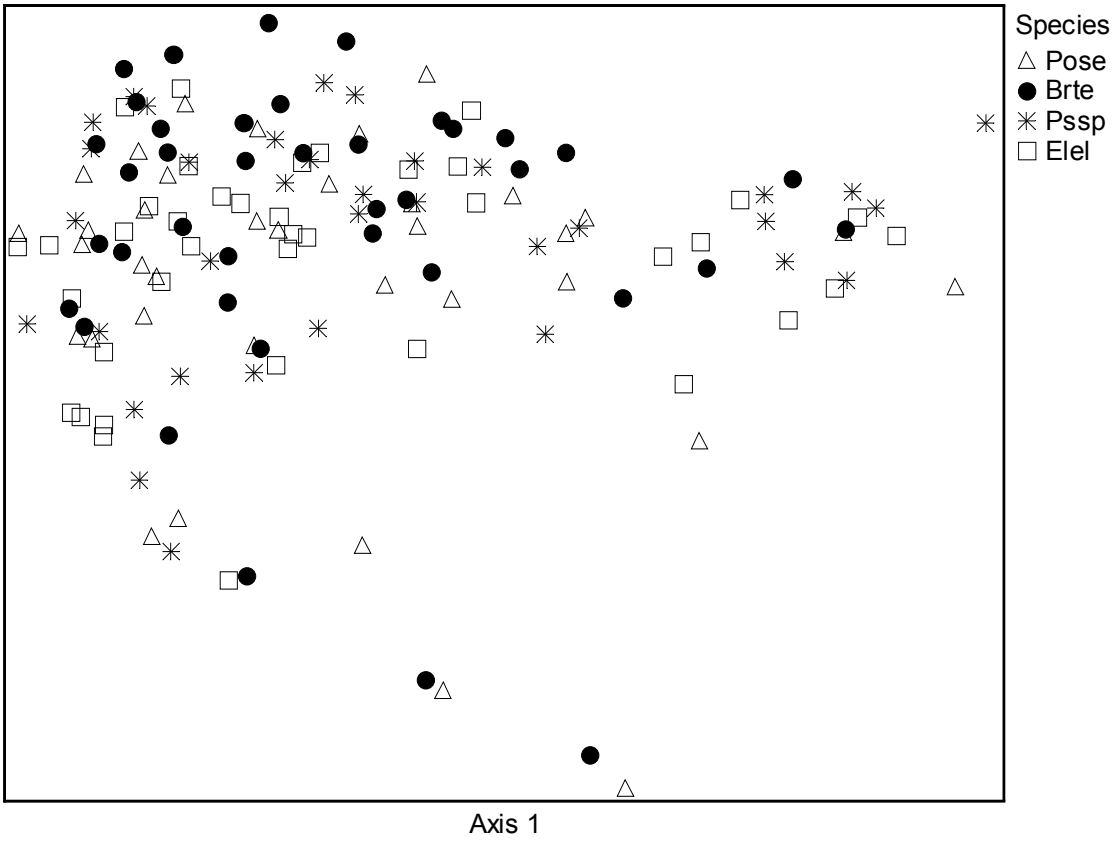
APPENDICES

Appendix A. Change in lignin over the first summer and second summer. Data from the first summer came from a different set of litter bags than data from the second summer. Thus numbers are not directly comparable between summers. Numbers in front of parentheses indicate grams, numbers in parentheses indicate percent. Values in grams were calculated from percentages, using knowledge of initial mass and average mass loss over each summer. C = Cheatgrass-Dominated, NS = Native-Shrub, and NI = Native – Interspace. Brte = *B. tectorum*, Pssp = *P. spicata*, Pose = *P. secunda*, Elel = *E. elymoides*.

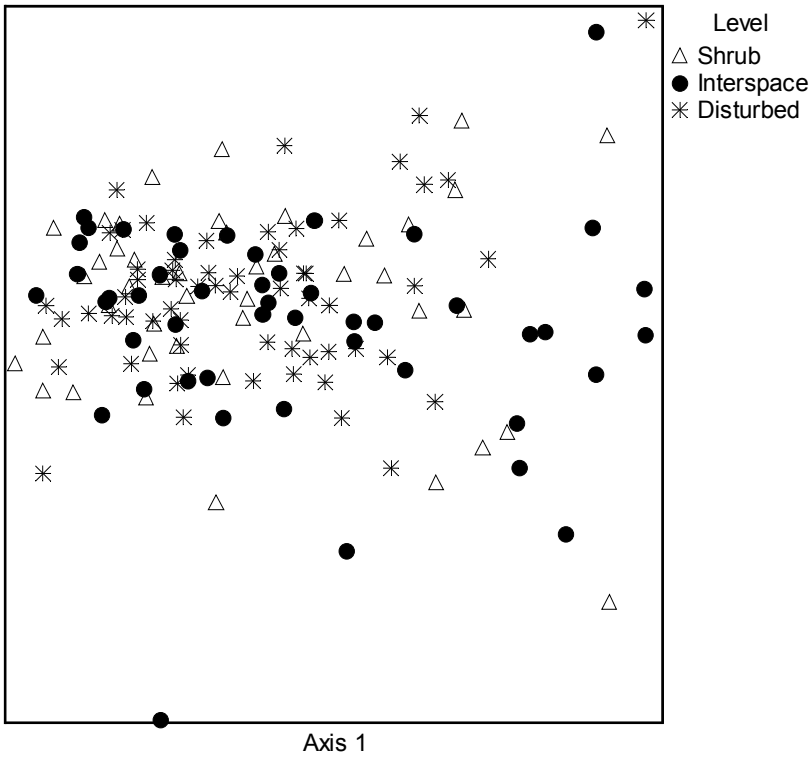
		First summer				**Second summer**			
		Brte	**Pose**	**Pssp**	**Elel**	**Brte**	**Pose**	**Pssp**	**Elel**
Δ lignin	**C**	+0.012 (1.0)	-0.033 (1.2	+0.022 (1.5)	+0.004 (0.6)	-0.011 (0.3	-0.024 (1.3	-0.031(1.5)	-0.015 (0.6)
	NS	+0.025 (1.7)	-0.012 (0.0	+0.035 (2.3)	+0.015 (1.2)	-0.023 (1.3	-0.018 (0.8	-0.032 (1.6	-0.011 (0.2)
	NI	+0.008 (0.7)	-0.028 (1.0	+0.026 (1.8)	+0.012 (1.0)	-0.016 (0.8	-0.005 (0.0	-0.022 (1.0	-0.019 (1.0)



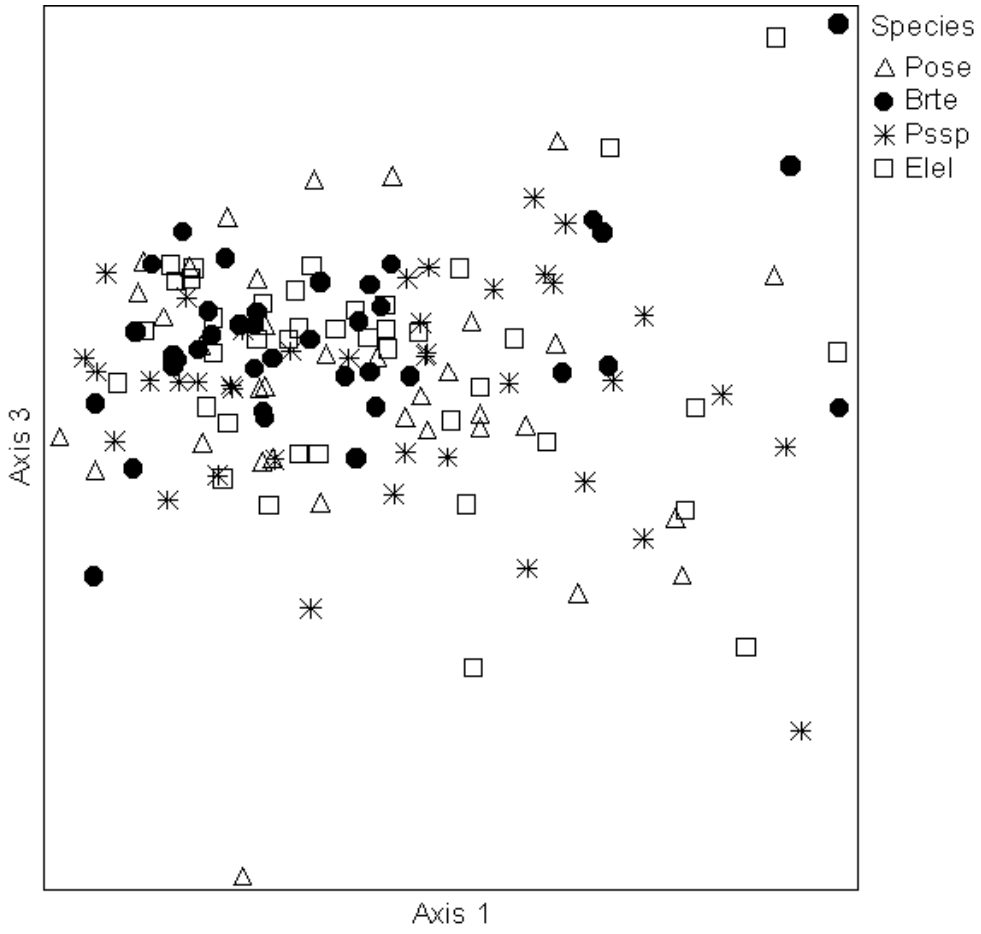
Appendix B. Ordination of sample units in species (95 carbon substrates) space, derived from Principle Components Analysis (PCA) of bacterial carbon source utilization data. Points represent sample units. Overlay is community.



Appendix C. Ordination of sample units in species (95 carbon substrates) space, derived from Principle Components Analysis (PCA) of bacterial carbon source utilization data. Points represent sample units. Overlay is litter species: Pose = *P. secunda*, Brte = *B. tectorum*, Pssp = *P. spicata*, Elel = *E. elymoides*.



Appendix D. Ordination of sample units in species (95 carbon substrates) space, derived from Principle Components Analysis (PCA) of fungal carbon source utilization data. Points represent sample units. Overlay is community.



Appendix E. Ordination of sample units in species (95 carbon substrates) space, derived from Principle Components Analysis (PCA) of fungal carbon source utilization data. Points represent sample units. Overlay is litter species: Pose = *P. secunda*, Brte = *B. tectorum*, Pssp = *P. spicata*, Elel = *E. elymoides*.