Effects of Soil Conditioning by Bromus tectorum on Decomposition Rates of Plant Litter and Soil Properties

Hayley M. Lyon
University of Colorado Boulder, hayley.lyon.9@gmail.com

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Effects of Soil Conditioning by *Bromus tectorum* on Decomposition Rates of Plant Litter and Soil Properties

By

Hayley Lyon

Ecology & Evolutionary Biology, University of Colorado at Boulder

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Thesis Advisor:

Dr. Timothy Seastedt, Ecology & Evolutionary Biology

Defense Committee:

Dr. Timothy Seastedt, Ecology & Evolutionary Biology

Dr. Barbara Demmig-Adams, Ecology & Evolutionary Biology

Dr. Kathryn Plath, Chemistry
Abstract

Cheatgrass (*Bromus tectorum*) is a thoroughly studied invasive species worldwide that possesses multiple characteristics that have allowed it to become a highly competitive invader. Understanding the mechanisms that allow cheatgrass to dominate so many plant communities is an ongoing area of research. One area of current research is analyzing how cheatgrass is able to alter soil characteristics, and how altering those characteristics affects production and decomposition of plant litter by both native and invasive species. My research follows current research inquiries by looking at how decomposition of plant litter is affected by altered soil characteristics. A laboratory study was performed to determine decomposition rates of cheatgrass litter on soils from native grass and cheatgrass sites under constant temperature and moisture conditions. A field study was also performed to determine and compare decomposition rates of cheatgrass litter and a native plains cottonwood (*Populus deltoides monilifera*) on both native grass and cheatgrass soil sites. The results from my study were interpreted in the context of the soil microbial communities using data provided by other studies. My results indicated that litter from native plants is insensitive to the altered cheatgrass environment, while cheatgrass litter decomposes at a significantly slower rate on its own altered soil than on unaltered native soil. These data indicate that cheatgrass experiences a negative home field advantage (HFA) on its own soil. The fact that plains cottonwood was insensitive to the cheatgrass soil but that cheatgrass decayed more slowly on its own soil suggests the soil microbial community generated by the chemical composition of cheatgrass litter is different and not as efficient in processing this substrate.
Introduction

I. Introduction

Factors that allow cheatgrass to be such a successful invader include its ability to exploit soil disturbances and display considerable variability in its morphology and phenology. An invasive species is defined as an organism that has inhabited an area in which it has not been historically present. Cheatgrass is a winter annual, which means it germinates in the fall and develops throughout winter, produces seeds in the following spring/summer, and then dies. Being a winter annual allows cheatgrass to exploit snowmelt and early spring moisture, and soak up available soil moisture before other for plant competitors have a change to germinate and develop (Prevey and Seastedt 2014; Concilio et al. 2017). Few studies have examined the effects of soil conditioning (alteration of soil properties) by cheatgrass on the decay rate of litter and how altering soil properties may support further dominance by the invasive species. It has been previously found that cheatgrass may condition soils in a way that enhances its own production while simultaneously inhibiting the growth of native species (O’Conner et al. 2015).

Understanding the decomposition processes of cheatgrass litter and its effect on soil nutrients and microbial communities is vital information to further understand the ecological processes of this species and ultimately assist with how to manage this invasions by it. My study aims to gain further information on whether the altering of soil characteristics, such as microbial community and soil organic carbon (SOC), by cheatgrass has an effect on the decomposition rates of plant litter.
II. Background

In many studies around the world, it has been shown in that soils are the largest reservoir of actively cycling carbon (C), even more so than C in the atmosphere and vegetation combined (Averill et al. 2014). Plant-soil-soil biota interactions have been highly studied in the context of a wide array of ecological applications, yet there is a major gap in research that focuses explicitly on SOC cycling. SOC is measurable component of soil organic matter and refers only to the carbon component of organic compounds. Understanding the mechanisms that influence the accumulation and stability of SOC is crucial in predicting the earth’s future climate. Invasive plant species provide model systems for testing our understanding of how plants affect decomposition and SOC storage. Cheatgrass is one of the most studied invasive plant species worldwide (Hulme et al. 2013), and has been the subject of recent studies on plant-soil interactions. Although plants and soil microbes are known as the primary drivers of SOC dynamics, accurately incorporating them into climate models has been a challenge (Porazinska, unpublished results). Climatic factors such as temperature and precipitation are used as the main drivers of SOC dynamics in most climate modeling methods, leading to unreliable predictions of SOC stocks and fluxes because of the way that SOC pools and SOC sensitivity to climate are represented (Giardina et al. 2014, Bradford et al 2016). More complex Earth system models (ESMs) include parameters of soil carbon and as a result generate slightly more accurate SOC projections, however problems still remain as these models still fail to completely capture the mechanisms that primarily control SOC dynamics (Porazinska unpublished results). In current ESMs, one of the main concepts representing plant-soil interactions is the relationship between temperature and decomposition, which predicts faster C loss from soils in higher temperatures due to increased microbial activity (Porazinska unpublished results). However, more recently it
has been indicated that this model may not be accurate due to it being based upon old models of soil organic matter (SOM) composition and microbial responses to warmer temperatures (Porazinska unpublished results). Recent developments have demonstrated that SOM and soil microorganisms exhibit complex and unpredictable responses to changes in temperature, and indicate that other plant-soil factors may be more relevant to incorporate into climate models (Schmidt et al. 2011, Giardina et al. 2014).

Plant-soil-soil biota interactions are some of the least understood factors of SOC dynamics, although for many years they have been recognized as major drivers of SOC dynamics. Many studies have been performed that have attempted to understand ecosystem and SOC responses to disturbances and invasion by foreign invasive species. With the exception of decomposition driven by UVB solar radiation, these ecosystem factors (e.g. plant cover, soil moisture, available nutrients, temperature fluctuations) are influenced by the organic matter content of litter (Swift et al. 1980). Preliminary work performed by Porazinska and Seastedt (Univ. of Colorado unpublished results) indicated that interactions among dominant plant species, soil biota, and global change factors have a strong effect on the balance of SOC.

As native shrub grasslands are invaded by exotic annual grasses (e.g. cheatgrass) litter biomass and chemistry often changes, leading to alterations in SOC and nutrient cycles (Ehrenfeld 2003). Evans et al. (2001) speculated that invasions of exotic annual grasses may increase the amount of immobilized nitrogen (N) in soils in the short-term, and in the long term through shortened fire return intervals may increase the amount of N volatilized, resulting in higher losses of N. In contrast, N availability in cheatgrass soils of non-fire treated sites show increased N availability (O’Conner et al. 2015; Morris et al. 2016). Field studies using additions of labile sources of carbon (e.g. sucrose) to immobilize nutrients in the microbial community
have shown that cheatgrass growth is inhibited when C is added (Concilio et al. 2017). What is unusual with cheatgrass is that it increases inorganic N availability while at the same time increasing organic C storage; usually increasing organic C storage would reduce N availability (Bardgett 2017). Understanding how this pattern occurs is clearly a valid scientific enquiry.

Soil biotic communities beneath native and invasive plant species have been found to be significantly different at my Front Range Colorado research site (Figure 1). In areas that have been invaded by cheatgrass, it has been found that there are significant changes in the diversity and amount of soil biota for bacteria, fungi and protists, and nematodes (Porazinska unpublished results). Similarly, large differences in the composition and abundance of soil microarthropods have been found, and earthworms are four to five times more abundant in native soils than in cheatgrass soils (T. Seastedt Univ. Colo. unpublished results).
Figure 1: Permutational multivariate analysis illustrating compositional differences in communities of bacteria (A), fungi and protists (B), and nematodes (C). Bray-Curtis pairwise dissimilarity matrix and PERMANOVA were used to determine the presence of significance. All results from the same meadow. Figure from D. Porozinska, Univ. Colo. Unpublished results.
At other study sites, cheatgrass has been shown to alter the soil biotic community by reducing the number of nematode and fungi taxa present in the soil soon after invasion (Belnap et al. 2005). These differences in soil biota between invaded and native soils have been found to correlate with the amount of C sequestered in soils. Cheatgrass soils have been found to sequester about 30-40% more C in the top 20 cm of soils compared with native grass soils (Stark and Norton 2014; O’Conner et al. 2015). However, this pattern of increased C storage in cheatgrass soils has not been observed in drier sites (Garmino et al. 2016).

Results presented above from the Front Range Colorado study site suggests that SOC dynamics may be dependent on certain plant-soil interactions involving many trophic levels of the soil biotic community. For example, while earthworms generally enhance soil fertility, they may reduce SOC, suggesting that earthworm density and activity directly affect the amount of SOC sequestered at a site (Porazinska unpublished results). However, moisture availability controls the presence and activities of earthworms, resulting in soil moisture as controlled by plant-soil water dynamics being able to regulate abundance and activity of earthworms (Porazinska unpublished results). Cheatgrass at my site has been found to dry up the soil environment (Porazinska unpublished results), likely affecting earthworm density and activity. Another potential explanation for the difference in the amount of SOC sequestered between the native plants and cheatgrass is the much reduced allocation of C to soil organisms because of the decreased levels of parasites, pathogens, and symbionts under the invasive plant cover (Porazinska unpublished results). Overall, plant-soil biotic interactions are most likely complex and have influence over quantity and quality of SOC (Porazinska unpublished results).

Many plants change the soil microbial community in a way that increases decomposition rates of foliage, known as a home field advantage (HFA). The HFA hypothesis predicts that
plant litter will decompose faster when in the vicinity of the plant that it originated from ('home'), relative to some other location ('away'), due to the presence of specialized decomposers. HFAs occur worldwide, but their role in plant invasion is not very well understood (McTee et al. 2017). Interestingly, in the study performed by Veen et al. (2014) results actually indicated that the most significant drivers of home-field effects were not proximity to the same plant where litter originated from, but instead was the quality of ‘home’ and ‘away’ litters being more dissimilar, such as in their N:P ratio (Veel et al. 2014).

Cheatgrass, as one of the most studied invasive plant species worldwide, provides a great example of a plant species imposing controls on SOC and soil nutrient dynamics. One way that cheatgrass has been found to potentially alter soil properties is through litter quality (Evans et al. 2001). Nutrient availability to microbial communities in soils largely depends on the quality of litter that decomposers have access to (McTee et al. 2017). In general, C:N and lignin:N ratios are used to quantify litter quality (Swift et al. 1980, Liu and Sun 2013). A low C:N ratio generally promotes faster decomposition rates, and vice versa (Liu and Sun 2013). At a site level, quality of senesced leaves depends on the species, the developmental stage of the litter, and environmental conditions (Liu and Sun 2013). Cheatgrass litter possesses significantly greater C:N and lignin:N ratios compared to most native species (Evans et al. 2001). Several recent studies have indicated that decomposition of soil organic matter (SOM) is often limited by N availability to microbes, and have suggested that plants compete directly with decomposers for N via their fungal symbionts (Averill et al. 2014) Plant chemistry controls over SOC and soil N cycling are complicated; generally, plants of higher substrate quality (low C:N) decompose faster, ultimately increasing N cycling that leads to higher plant productivity (Bardgett 2017). It has been previously generalized that N content in litter alone can drive the pattern of high
productivity and rapid decay of litter, however this generalization has been challenged by findings of soil responses to increased atmospheric N-deposition (Neff et al. 2002). These findings have been explained by factors including a change in microbial community composition and function as well as their interactions of their decay products with chemical and physical properties of soil minerals (Zak et al. 2017). While plant chemistry does play a large role in SOC cycling, when the same litter is exposed to a different decomposer community and different soil mineral components, the litter chemistry and sequestration rates are altered (Porazinska, unpublished data). Several studies have indicated that cheatgrass is able to increase N available in soils, contradicting the general pattern of slower decomposition decreasing amount of N present in soils, and can be explained by fine root decay and mineralization of root exudates from cheatgrass (Morris et al. 2016).

Figure 2: Carbon model used to summarize cheatgrass-soil interactions; the boxes represent pools of carbon, and the arrows represent the flow of carbon in the system
III. Research Questions and Hypotheses Tested

The overarching focus of this research was to identify whether the physical environment or the microbial food web generated by cheatgrass can affect decay rates of foliage, and understand how invasion of an environment by cheatgrass affects soil carbon dynamics and carbon sequestration. Specifically, the following questions were tested: 1) How fast does cheatgrass litter decay, 2) Is the decay rate of cheatgrass litter affected by the environment created from the invasion and dominance of cheatgrass foliage, and 3) Does the soil altered by cheatgrass contain a microbial community that has an effect (enhances or suppresses) cheatgrass litter decay relative to the microbial community found in soils under native plant dominated communities?

To test if the cheatgrass canopy alters decay rates of foliage, cheatgrass litter decomposition was measured in litterbags placed underneath the cheatgrass canopy or underneath a native grass canopy. A second native reference leaf litter species (plains cottonwood) was also tested in this manner to act as a control. To test if the soil microbial and microfauna community affects decay rates, cheatgrass decomposition was measured in the laboratory in microcosms containing either cheatgrass or native soil.

Applying the HFA hypothesis, cheatgrass litter will decay significantly faster on its own altered soil than on native soil. This faster rate of decomposition would be due to the presence of microbes that have adapted to feed on the cheatgrass litter chemistry. The faster decomposition rate could also be attributed to the more favorable microclimate for litter decay (the soil surface beneath the live and dead plant foliage) at cheatgrass sites than at native sites due to the build-up of undecayed cheatgrass litter foliage found at and above the soil surface. This more favorable microclimate occurs because following fairly large rain events, the soil surface will retain moisture for a longer period of time as surface evaporation is reduced under the denser layer of
cheatgrass litter. Surface temperatures within the cheatgrass microclimate would also likely be somewhat lower, a factor slowing decay rates, but correspondingly less variable underneath the cheatgrass canopy. With this in mind, cheatgrass and cottonwood litterbags placed in the cheatgrass sites should decay faster than litterbags placed in the native grass dominated prairie areas.

As suggested in the literature, C:N ratios of litter also affect decay rates (Melillo et al. 1982). If the C:N ratios in cheatgrass and cottonwood litter are an important factor to decay, it is expected that the cheatgrass litter will decay more slowly than the cottonwood litter in both cheatgrass and native grass environments.

**Materials and Methods**

**I. Site Location and Characterization**

The site used for sample collection and the field portion of this study is a semi-arid shortgrass prairie located approximately 15 km northwest of Boulder, Colorado, USA (40°07’N, 105°18’W). This site has been classified as having a continental climate, with most rainfall in early spring and summer (USDA 2001). Soils at this site have been classified by the USDA as well-drained, colluvial and sandy loams (USDA 2001). The site has been used by a succession of investigators who have presented information on vegetation and soil characteristics (Prevey and Seastedt 2014; O’Conner et al. 2015; Concilio et al. 2017).
II. Study Species

Cheatgrass (*Bromus tectorum*) is a winter annual grass in the Poaceae/Gramineae (grass) family. An annual plant completes its entire life cycle within one growing season, and all parts of the plant die at the end of the growing season, with a dormant seed bridging the gap between generations. Cheatgrass is considered a winter annual because its seeds can germinate in fall and grow rapidly until cold temperatures arrive. Root growth of cheatgrass seedlings continues throughout winter until early spring, when seedlings resume normal growth to ultimately produce seeds and die between mid-July and early August. Roots of cheatgrass plants are fibrous, relatively shallow, and are able to reduce soil moisture levels to the "permanent wilting point" (the minimal amount of water in the soil that the plant requires not to wilt, about 4-8% soil moisture) up to 70 cm deep (Zouhar 2003). Cheatgrass grows rapidly often in pure stands, and is capable of growing at a rate of 2.9 g/mm²/day (Zouhar 2003).
The second species used in this study was Plains Cottonwood (*Populus deltoides monilifera*). The plains cottonwood is a native species to Colorado, and is the largest broadleaf tree of Colorado, New Mexico, and Wyoming (Wier 2019). The plains cottonwood is a relatively short-lived tree, with few living much past 100 years. The leaves are glossy and are 7.5 to 15 cm long and wide in a broad triangle or heart shape (Wier 2019). Rates of decomposition and N content of foliage of this species from Colorado have been previously reported by Simons and Seastedt (1999).

**II. Soil and Litter Collection**

Senescing cheatgrass litter was cut and collected from the study site and brought back to the laboratory. Senesced plains cottonwood leaves were collected in fall of 2017 and stored in the laboratory until used in this study. Soil from cheatgrass-dominated and native-grass dominated sites was collected from the study site in fall of 2018 for use in the laboratory experiment. Native-grass-dominated soil was collected from areas dominated by native grass species such as western wheatgrass (*Agropyron smithii*), but that also contained a variety of native and non-native forbs. Cheatgrass-dominated soil was collected from areas that were more than 90% covered by cheatgrass.

**III. Litter Bag Creation**

Litterbags were constructed from 1 mm mesh fiberglass window screen by melting the mesh on three sides to form the pocket, and securing the top with a flap sealed by a wire tag. Empty litterbags were given a tag number and pre-weighed. Bags for cheatgrass litter measured a 10 cm X 10 cm square, and approximately one to two grams of moistened senesced cheatgrass
litter collected from the study site was added to each bag. Bags for the plains cottonwood leaf material were somewhat smaller with interior dimensions of 5 cm X 5 cm. Approximately one gram of dry senesced cottonwood leaf material was added to each bag, dried at 70°C, and weighed to the nearest 0.01 g. Bags were dried at room temperature for two days and were then weighed to the nearest .01 g. Ten cheatgrass litterbags were separated and oven dried at 70°C and then weighed again. The difference in weights of the litter in the separated bags prior to and post drying was used to calculate a correction factor for the moisture weight in the rest of the cheatgrass litter bags.

![Figure 4: The completed litterbags prior to being assigned to treatments](image)

**IV. Field Study**

On 20 October, 2018, 68 cheatgrass litterbags were placed at the study site for the field experiment. A transect was drawn using a 100-m measuring tape across an area that included both native-grass-dominated and cheatgrass-dominated sites. Bags were placed in numerical order along the transect. Thirty four bags were placed on native-grass-dominated soil sites, and 34 on cheatgrass dominated soil sites. Soil locations had similar slope, elevation, and aspect in
order to minimize spatial heterogeneity. Cheatgrass-dominated soil sites were areas covered almost entirely of cheatgrass, while native grass sites were dominated by native grasses and forbs with little or no cheatgrass present.

Thirty litterbags containing plains cottonwood leaves were also placed at the field study site, 15 at cheatgrass-dominated sites and 15 at native-grass-dominated sites. On 24 May, 2019, the litterbags were collected from the field site. Bags clearly chewed and ripped open by unknown animals were discarded. Bags in the cheatgrass soil sites were notably more damaged than the bags in native sites. The cheatgrass litterbags spent 210 days in the field (214 days for cottonwood litterbags) and were exposed to about 26 cm of precipitation, mostly during late winter and spring. The bags were brought back to the laboratory and gently cleaned off of excess dirt and debris, and were placed in an oven to dry for a full day at 70°C. After drying, the litter was re-weighed and percent mass lost was calculated.

V. Laboratory Study

On 31 October 2018, 72 cheatgrass bags were used for a laboratory study of the effect of native grass dominated soil and cheatgrass-dominated soil on decomposition rate of cheatgrass litter. A total of 8 large aluminum pans were used to contain the soils, 4 designated to native soil and 4 designated to cheatgrass soil. Each pan was lined with paper towels and about 1 cm of soil was placed into the corresponding tins. 8 litter bags were placed into each pan such that the bags did not overlap. A small amount of soil was then sprinkled over the top of the bags, and they were misted until very moist. The tins containing the moistened soils and litterbags were placed on a table and covered with paper bags and a cotton sheet in order to help retain moisture while still allowing the passage of air for aerobic decomposition. To act as a control group, 8 litter bags
were placed on paper towels on in a separate metal tin without any soil. Over the course of the next few months, the tins were misted daily in order to keep the soil moist and attempt to maximize decomposition. Water additions were terminated on February 6, 2019, and the bags were allowed to air dry for 2 days at room temperature. The bags were then gently cleaned of excess dirt and debris. Once clean, the litter was oven dried in a forced-air oven for a full day at 70°C, weighed, and percent mass loss was calculated.

![Image showing the laboratory soil treatments for cheatgrass litter bags. Bags and soils were kept moist to stimulate decomposition](image)

**VI. Statistical Analyses**

The data obtained from both the field and laboratory study were statistically analyzed using R Studio version 1.1.383. A correction factor for moisture present in the initial cheatgrass litter samples was calculated prior to data collection (see appendix A). Welch’s 2-sample t-tests were used to compare the means of each of the treatments for most experiments. A two-way factorial ANOVA was conducted using SAS (Statistical Analysis System) software to measure effects of litter type (cheatgrass vs cottonwood) and litter placement (on cheatgrass soils versus
native plant soils) at the Left Hand research site. I used the SAS GLM (general linear model) procedure. Graphs visually representing the results were created using both R Studio version 1.1.383 and Microsoft Excel version 16.25.

**Results**

**I. Laboratory Study**

In the laboratory study, litter was kept moist and at about 22°C constant temperature in order to mimic one full year of degree days for litter decay. In the cheatgrass soil treatment, the cheatgrass litter averaged 25.6% mass lost. In the native soil treatment, the cheatgrass litter averaged 30.7% mass lost. In the control water treatment with no soil, the cheatgrass litter averaged 27.6% mass lost. A Welch’s two sample t-test between the amount of decomposition of litter on the cheatgrass soil treatment and the control water treatment indicated an insignificant difference between the amount of decomposition (p-value = 0.265). A Welch’s two sample t-test between the amount of decomposition of litter on native soil treatment and the control water treatment also indicated an insignificant difference between the amount of decomposition (p-value = 0.123). However, a Welch’s two sample t-test between the amount of decomposition of litter in the native soil versus that of the cheatgrass soil treatment indicated a significant difference between the amount of decomposition (p-value = 0.018).
II. Field Study

In the field experiment, there was an average of 13.7% mass lost from cheatgrass litter on cheatgrass soil sites, as compared to an average of 11.3% mass lost from cheatgrass litter on native soil sites. A Welch’s two sample t-test of the percent mass lost from cheatgrass litter indicated a significant difference between the amount of decomposition that occurred on the two soil treatments (See figure 7; p-value = 0.027).

For plains cottonwood litter, there was an average of 29.1% mass lost from cottonwood litter on cheatgrass soil sites, whereas there was an average of 28% mass lost from cottonwood litter on native soil sites. A Welch’s Two Sample t-test of the cottonwood litter field treatments indicated an insignificant difference between the amount of decomposition between the two soil treatments (See figure 8; p-value = 0.703).
Figure 7: Comparison of percent mass lost from cheatgrass on cheatgrass soil and native soil treatments in the field (p-value = 0.027)

Figure 8: Comparison of the percent mass lost from plains cottonwood litter on cheatgrass soil and native soil treatments in the field (p-value = 0.703)
The plains cottonwood mass loss was then compared to the mass lost in the cheatgrass litter on each respective soil treatment (See figure 9). In the cheatgrass soil sites, there was a highly significant difference between the amount of mass lost between the cottonwood litter and the cheatgrass litter, with cheatgrass litter losing significantly less mass than cottonwood litter (p-value = < 0.0001). In the native soil sites there was also a significant difference between the amount of mass lost between the two litter types, with cheatgrass litter having lost significantly more mass than the plains cottonwood litter (p-value = < 0.0001).

![Graph](image)

**Figure 9:** Comparison of the percent mass lost from plains cottonwood litter and cheatgrass litter either native soil or cheatgrass soil in the field. Values are means and standard errors of cottonwood and cheatgrass in cheatgrass litter (n = 11 and 21, respectively), and cottonwood and cheatgrass in native soils (n = 16 and 33, respectively).
The results of the ANOVA were as follows:

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**Discussion**

**I. Discussion of Results**

My research identified one new finding and produced several findings that add support to previous research. I demonstrated that cheatgrass soils microbial community clearly did not increase and may actually have decreased decomposition rates of cheatgrass litter under laboratory conditions. Based on the low lignin:N ratios found in cheatgrass litter, the litter is expected to have a relatively fast decomposition rate (Harrison et al. 2003). The HFA hypothesis also predicts cheatgrass litter decay to be faster on its own soil, however my findings were the opposite of what both the lignin:N ratio and the HFA hypothesis would predict. My findings from the laboratory experiment found that cheatgrass litter decayed more slowly on its own altered soil than it does on native, unaltered soil. This lack or suppression of decomposition can
be interpreted based upon the microbial diversity and abundance data from this site provided by Porazinska (unpublished results). Porazinska’s data reported an overall reduction in species diversity and a switch towards bacterial as opposed to fungal dominance from native to invasive soil sites. Bacteria tend to be less active in the decomposition of high C:N materials such as cheatgrass litter, ultimately reducing the decay rate of cheatgrass litter. Additionally, reduced microbial diversity may have contributed to the reduced decay rates. The soil used to prime the cheatgrass litter appeared to have few if any visible invertebrates, and whatever nematodes were added, like the microbes, were largely bacterivores and also low in diversity (Porazinska, unpublished data). Irrespective of the underlying mechanism, the rate of decay clearly was not enhanced by placing cheatgrass litter in cheatgrass soils.

The fact that the laboratory experiment lacked either the large numbers of macroarthropods found within cheatgrass soils and the presence of the relatively few earthworms in the soils limits the conclusions that can be drawn from the laboratory findings. Field results show a stimulation of decay beneath the cheatgrass canopy, and while that effect might have been induced by microclimatic factors, alone, the absence of microarthropods in the laboratory experiment would likely reduce laboratory decay rates and contribute to the lack of a significant response. Earthworms found at the site have not been found to consume litter, but instead process soil organic matter (organic matter component of soil consisting of plant and animal detritus at various stages of decomposition, cells and tissues of soil microbes, and substances that soil microbes synthesize), so their absence in the laboratory was likely insignificant unless castings from earthworms can ‘prime’ (add microbes and stimulate litter decay) the litter.

The results of the field study show that the rate of cheatgrass litter decay is slower than the native reference species used (plains cottonwood). Plains cottonwood itself is already a relatively
recalcitrant (resistant to decomposition) litter and decays at a slower rate than many other litter types (Simons and Seastedt 1999). Plains cottonwood was insensitive to the cheatgrass environment as there was no significant difference between decomposition rates of cottonwood litter on the two soil treatments. The significant difference found for the cheatgrass decomposition in litter bags compared to the plains cottonwood decomposition in litter bags on both the native and cheatgrass soil sites indicates that cheatgrass affects the physical conditions of the soil site that are important to decomposition.

My study showed that cheatgrass litter decayed faster beneath a cheatgrass canopy while cottonwood did not decay significantly faster beneath the cheatgrass canopy. The HFA hypothesis predicts a positive effect where litter decomposes faster in its local environment close to the plant where litter originated from, however HFA effects are not always positive, suggesting that the response is context-dependent (McTee et al. 2017). My finding could support that there is a modest positive HFA for soil surface litter decay of cheatgrass in cheatgrass environments. That said, the trend for cottonwood decay being the same as cheatgrass litter, cottonwood decomposition being faster than cheatgrass, and the large build-up of cheatgrass litter that produced the microclimate (c.f. Prevey and Seastedt 2014) do not support a positive HFA for cheatgrass decay in a cheatgrass environment, and instead indicate that cheatgrass may create a negative HFA for itself. McTee et al. (2017) also did not find a significant HFA in their study that tested cheatgrass litter. Freschet et al. (2012) proposed HFA is just one aspect of a more comprehensive hypothesis known as the substrate quality-matrix quality interaction (SMI), where HFA effects are greatest when litter quality is highly dissimilar from the native litter matrix associated with a particular site. McTee et al. (2017) and Veen et al. (2014) in a meta-analysis of their results indicated that HFA effects in grasslands may be minimal due to the
minimal difference between litter composition of different grass species, which aligns with the SMI hypothesis. The ANOVA model accounted for 68% of the variance and was driven by a very strong litter type effect on decomposition rates. Site placement had no effect on decay rates and there was no interaction effect between litter type and site on decomposition rates. Site placement having no significant effect as indicated by this ANOVA analysis also supports the SMI hypothesis over the HFA hypothesis.

The additional findings of this study are consistent with the known effects of microclimate, and known effects of litter chemistry. Decay of the relatively high C:N cheatgrass litter was slower than the relatively lower C:N litter of cottonwood. Similarly, the soil surface beneath cheatgrass was shown to be more conducive to decomposition than the soil surface beneath native vegetation, likely due to the build-up and matting of cheatgrass litter on these soil sites, creating a moister microclimate for decay and providing a more rapid rate of litter decay. These findings are consistent with well-developed literature (Swift et al. 1980). At the same time, however, the more benign cheatgrass soil environment was unable to reverse the trend of reduced decay of cheatgrass litter, or enhance total carbon decomposition, as indicated by the higher SOM beneath cheatgrass soils reported at my site by O’Conner et al. (2015).

The type of vegetation found at the field litterbag sites was important for cheatgrass decomposition, however was not important for cottonwood decomposition, suggesting that a plant chemistry-site interaction occurs that affects the decay rate of cheatgrass litter. Based on the above results, evidence is presented that it is the plant chemistry of cheatgrass litter rather than the microclimate created by cheatgrass that produces such a large build-up of cheatgrass litter. This plant chemistry may also contribute to the accumulation of SOC at the cheatgrass sites.
The results of both the laboratory and field study suggest that the microbial community found within altered cheatgrass soils does not stimulate decomposition but instead may actually suppress decomposition of cheatgrass litter, negating my original hypothesis.

II. Limitations of the Study and Future Research

Two important abiotic factors that influence decomposition are soil moisture and temperature. Differences in these conditions were kept minimal between plant communities as sites were chosen along a transect of 100 m that shared similar aspect, slope, and elevation. However, differing plant density can cause shading of soils, in turn affecting soil temperature and moisture, both of which influence decomposition rates, causing a confounding effect on interpretation of plant chemistry effects.

Further studies of this subject should attempt to explain the unusual pattern of cheatgrass increasing inorganic N availability while at the same time increasing organic carbon storage, a phenomenon opposite to the usual pattern of increasing organic carbon storage with reduced N availability. Another topic future studies could pursue is the analysis of the consequences of shifts in soil detritivores relative to carbon sequestration. Decadal time scales are required to measure cumulative effects of plant characteristics on SOM and future studies must accommodate this reality.
Conclusions

In conclusion, the laboratory study showed no positive HFA and actually indicated a negative HFA effect. The field study suggested modest benefits to decomposers under cheatgrass, although the rate of cheatgrass litter decay was still significantly slower than that of the plains cottonwood litter. While these are conflicting findings, the lack of decay of cheatgrass litter as well as the lack of any benefit from soil microbes to cheatgrass decomposition can both explain the build-up of SOC. However, this finding suggests that the increased N in cheatgrass soils is produced by some factors that do not immobilize N with the increased SOC. This remains outside the scope of my study but suggests that sources of N such as root exudates and rapid decay of fine roots may be involved.

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Appendix A

I. Additional Photos

Figure A: An example of the litter bags and tags that contained the litter throughout the study

Figure B: The litter bags used in the laboratory experiment in their respective soil treatments
Figure C: One portion of the transect that was drawn where litter bags were placed in the field. The yellow flags in this image represent native grass field sites.
Figures C and D: Examples of litter bags that were so significantly damaged by unknown animals that they were thrown out of the data set. Interestingly, litter bags in cheatgrass soil sites were significantly more damaged than litter bags in native soil sites.

Figure F: Example of litter being oven-dried after collection from the field. Once cleaned, litter was oven-dried at 70 °C for a day and then re-weighed to obtain final mass.
II. Moisture Correction Linear Regression

Figure D: The calculated moisture correction factor for the cheatgrass litter bags, used to calculate total percent mass loss of the cheatgrass litter