LITTER DECOMPOSITION IN OREGON PRAIRIES DEPENDS ON FIRE

by

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A THESIS

Presented to the Department of Environmental Science
and the Robert D. Clark Honors College
in partial fulfillment of the requirements for the degree of
Bachelor of Science

May 2024

An Abstract of the Thesis of

Ellen Ralston for the degree of Bachelor of Science
in the Department of Environmental Science to be taken June 2024

Title: Decomposition in Oregon Prairies Depends on Fire

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Primary Thesis Advisor

Prairies in the PNW were historically maintained by Indigenous burning practices, which favored some of their food plants and kept the prairies from becoming forested. Current prairie restoration practices are returning to the use of fire, but the consequences of fire for decomposition are unknown in these prairies. To examine decomposition, litter from both burned and unburned prairies was put in decomposition bags, and the bags were removed and weighed at three, six, and nine months. Half of all litter samples were also sterilized to remove their native fungal endophytes to determine whether that reduced decomposition. In general, litter from burned prairies had greater decomposition than litter from unburned prairies. Sterilized litter also had greater decomposition than unsterilized. This information can aid prairie managers as they continue to use fire to manage Oregon prairies.

Acknowledgements

I would like to thank all members of the Roy lab for their help with this thesis. This includes, but is not limited to; Heather Dawson, Addie Kelly, Hilary Dawson, and Carolyn Delevich. I would also like to thank Haley Burrill and Bitty Roy for all of their help in the construction, analysis, and write-up of this work. Many of my instructors in the Clark Honors College, such as Yalda Asmatey, Corinne Bayerl, and Casey Shoop were also integral in the creation of this project. Thank you to the site managers for permission to do this study (Wes Messinger for the Fern Ridge Corps of Engineers sites, and Ed Alverson and Jason Blazar for Buford Park (Pisgah)), and for many of the supplemental pictures used here. Also, to Caitlin Winterbottom of the Army Corps of Engineers for her assistance in removing Fern Ridge samples when the sites needed to be mowed. To Marsha McCloskey for all of her help in the construction and sewing of the litter bags used. Finally, I would like to thank Meredith Jacobsen for first introducing me to the idea of Indigenous fire practices and for teaching me that fire can have many benefits.

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Introduction

Landscape surveys done in Oregon in the 1800s, before large-scale colonial settlement, describe the Willamette valley as being dominated by prairie ecosystems (Christy & Alverson 2011). As settlers arrived in the valley in the mid-1800s, the prairie ecosystems began to degrade as settlers ended historic Indigenous practices of prescribed burning (Hamman et al. 2011). The exclusion of fire as a result of ongoing colonization practices allowed for the invasion of trees and shrubs, higher litter accumulation, and growth of moss leading to near extirpation of the PNW prairie ecosystems (Noss et al 1995; Hamman et al. 2011). Fire is currently being used as a tool for restoration as it is more sustainable than herbicides and some of our plants have coevolved with its use, but fire can favor invasives in some circumstances (Brambila et al. 2023) and its effects on other organisms, such as fungi and ecosystem services are only just beginning to be understood. My thesis will focus on how fire affects decomposition.

Fire affects the communities of fungi present in the soil (Semenova-Nelsen 2019; Holden 2019; Roy 2023) and when fungi available for decomposition at a particular place differ then so will decomposition (Semenova-Nelson et al. 2019). We know that fire affects the fungi in soil and litter at least one of our sites, Pisgah. Delevich et al. (2022 and unpublished data) found wildly different fungi depending on whether the prairie had been burned or not (Figure 1).

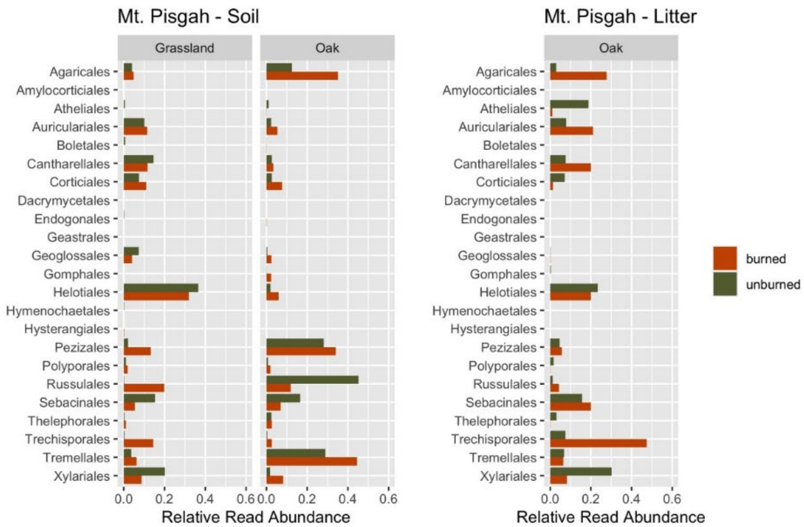


Figure 1: Initial macrofungal abundances taken from Pisgah site, from Spring and Fall of 2022. Graph by Carolyn Delevich, UO

Fungi are an important part of the decomposition process; for example, they are the main decomposers of wood and litter (Lustenhower 2020**)**, and they are often implicated in early successional stages of decomposition (Lustenhower 2020). The early fungal "bump" in decomposition may be a result of the endophytic fungi that live within living plants (Hobara 2013). Endophytes are microscopic fungi that are housed between plant cells, but the leaves show no signs of infection and the fungi do not reproduce (Stone & White 2004). Since these internal fungi are not acting as plant pathogens, what are they doing inside the plants? One idea is that some of these fungi play a role in decomposition once the plant material they are within has died. If the fungi can get into the leaf before the plant dies, they have a "head start" in the competition for resources after death. Evidence that decomposition was faster with the addition of litter compared to the exclusion of litter suggests that the endophytes in the litter expedite the process of decomposition (Chadwick 1998).

This project is focused on two scenarios that have the potential to affect decomposition: the presence or absence of endophytes and the presence or absence of fire. Comparing decomposition rates among litter in bags that have been exposed to these conditions will indicate how important these contexts are. We predicted that the litter samples in burned prairie will decompose less, as the presence of fire will decrease the number of decomposer species (Semenova-Nelsen 2019). We also predicted that the litter containing live endophytes will have higher decomposition rates relative to sterilized litter because endophytes help expedite the decomposition process.

Decomposition is an essential process in our biosphere, and fungi are an essential part of it because they alone can break down plant lignin (Salvachua et al. 2020). Restoration in these prairies is returning to the use of fire to maintain prairies, as was done by Indigenous communities in the Willamette valley for at least 10,000 years (Boyd 1999; Christy & Alverson 2011; Hamman et al. 2011) prior to colonization. However, we don't know how fire affects decomposition in these prairies, which have changed in composition in historical time due to invasive species. Increasing fire risk as a result of climate change could also have dramatic effects on the decomposition done by fungi in burned areas. By measuring the weights of litter samples that have been buried at burned and unburned sights, we can begin to understand if the presence of fire affects decomposition. By weighing litter with and without endophytes, we can begin to understand their function within plant cells, by seeing if they play a role in decomposition. Both of these treatments, burned and without endophytes, will help us to understand fungal decomposition overall.

What is decomposition? Why do we care?

Decomposition is the process by which nutrients are returned to the environment. When organic material dies, its structure is slowly broken down into smaller pieces by larger organisms like worms, then by smaller organisms like bacteria and fungi (Kleinman 2019). Breaking the large organic material into smaller pieces allows for bacteria and fungi to better access the nutrients held within the tissue. These microorganisms feed on the organic tissue and break them down into their simplest components. These components are then returned into the soil, where they can be taken up and utilized by other, still living, organisms (Kleinman 2019). Without decomposition, all the nutrients contained within living creatures would be lost forever as soon as they died. Decomposition allows for nutrient cycling and the continued existence and growth of life on planet earth.

Methods

Site Description

The samples were placed on the surface of three prairies around Eugene, Oregon (Table 1). Each prairie had a section that was burned either in the concurrent year or within the last two years, and a section that was unburned. For record keeping purposes the different sections are given separate directional names (e.g., East, West) but the prairies with the same names are more or less contiguous, just burned in blocks. In this case, fires were controlled burns, set intentionally to control woody plant invasion and to return the prairies to pre-settler condition. The study sites were a prairie on the East side of Mt. Pisgah and two locations within the Fern Ridge natural area: North and South Eaton and East and West Spire (see Supplemental Figures 1-5). The prairies themselves were mostly composed of grasses and forbs (see Table 1 for specific species), with incursions of blackberry bushes and shrubs/trees. The samples were initially placed on the surface in July, which is the time when most of the prairie grass above-ground biomass is starting to die back naturally in this Mediterranean climate with little to no summer rain. Samples were recovered at three different times: after three months (October 5, 2023), six months (February 4, 2024), nine months (May 5, 2024) post placement in the prairie.

Table 1. Localities. Information about each replicate site. Pictures of each in Supplemental Figures 1-5. Elevations and coordinates from Google Earth. Common species from observations taken at each site at the time of litter collection.

Site Name	**Burned?**	**Common Plant species**	**Lat** (dd)	**Long** (dd)	**Elevation** (m)
North Pisgah	No	*Vulpia* sp., *Aira caryophyllaea*, *Festuca roemeri*	N 43.999809	W 122.943102	529 ft
South Pisgah	Yes	*Daucus carota*, *Vulpia sp.*, *Festuca roemeri*	N 43.996911	W 122.944631	529 ft
South Eaton	No	*Hypochaeris radiata*, *Aira caryophyllaea*, *Vulpia sp.*, *Daucus carota*, *Eriophyllum lanatum*, *Lupinus spp.*, *Agrostis sp.*	N 44.101167	W 123.259355	371 ft
North Eaton	Yes	*Aira caryophyllaea*, *Vulpia sp.*, *Hypochaeris radiata*, *Daucus carota*, *Arrhenatherum elatius*, *Linum bienne*	N 44.102437	W 123.259369	371 ft
East Spire	No	*Anthoxanthum odoratum*, *Vulpia sp*, *Arrhenatherum elatius*, *Festuca roemeri*	N 44.100123	W 123.262949	371 ft
West Spire	Yes	*Vulpia sp*, *Festuca roemeri* , *Daucus carota, Eriophyllum lanatum*	N 44.098619	W 123.264431	371 ft

Litter Bags and Collection

Litter was collected from each site itself, and ultimately put back to the site it was taken from to decompose. 50 grams of litter was taken from both the burned and unburned section of each site, samples from around the flagged areas they were going to decompose at (Figure 3). Burned prairies had been burned a year prior to litter collection, so litter to collect was present on those sites. Once the 50 grams had been taken, the samples were mixed (homogenized) in the lab before half was sterilized, so that there was similar material in each replicate.

Litter bags are a crucial step in testing decomposition rates. These bags must withstand decomposing for a year, keep out other decomposers, and be the correct size to hold the desired material. For this experiment, we used nylon fabric, mesh size <1mm, to make 100x100 mm bags, closed with staples (see Supplemental Figures 6-8). 1.5-2 grams of litter was placed into each bag before it was stapled shut. To keep track of each specific bag, numbers on plastic material labeled #1-48 were placed into each prairie, the count starting over at each unburned vs burned prairie. Each bag was also marked with a fabric paint strip, red for not sterilized and black for sterilized (see Supplemental Figures 6-8). To account for the four staples used to close the bag after initial weighing, 0.13 grams were added to each "before" weight, the average weight of four staples based on five samples.

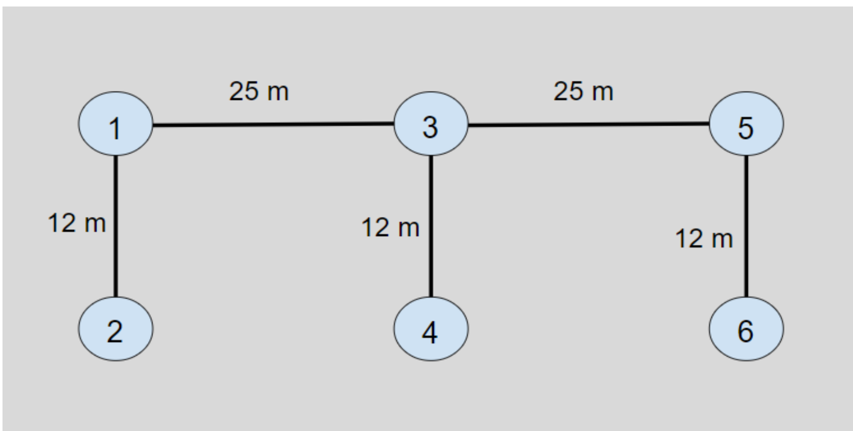
Experimental Design

Table 2. Experimental Design for a single site with burned and unburned sections. The number of bags placed into burned vs unburned and sterile vs unsterile treatments is shown. The total litter bags per site is 96, and for all three sites the total is 288

-	**Burned**	**Unburned**	-
Sterile	6+6+6+6=24	6+6+6+6=24	-
Unsterile	6+6+6+6=24	6+6+6+6=24	-
-	-	-	-
Total	48	48	is 96 x three sites = 288

We used a full factorial design (Table 2) replicated at each of three prairies; within each of three prairies (Pisgah, Eaton, Spires), fire (yes, no) was fully crossed with litter treatment (sterile or not). Litter bags were made from nylon fabric with a mesh size of <1mm, by cutting the fabric and stapling them closed. Litter bags containing either sterilized or unsterilized litter were laid on the surface and pinned to the soil using one hardware cloth U-pin to per two bags in each prairie. The six replicates were laid out in two rows as shown in Figure 3. This layout was chosen because one of the sites (Pisgah) was being monitored for soil and litter fungi in the same locations for a different study (Delevich et al. unpublished, preliminary data in Figure 1). Rates of decomposition were measured based on mass differences of the litter after four different burial periods (three, six, nine, or twelve months). Litter samples were collected from all the prairie sites, half (144) autoclaved (121°C, 15 minutes, liquid setting) to sterilize and kill any decomposers that might already be on or in them. After sterilization, we measured a subset amount into each bag and recorded the weight before putting the bags out. The leaves were then placed into litter bags and staked down to the prairie soil, 24 in each burned site and 24 in each unburned site; i.e., 48 treatment types, spread across six (three burned, three unburned) sites (Table 2). Litter bags were placed at each site according to the specifications laid out in Figure 2. Once placed, a thin litter covering was placed over top of the eight bags. They were initially laid out July 2nd 2023, then samples were removed and weighed on this schedule: October 5th 2023, then the next removed and weighed February 3rd 2024, May 4th 2024, and there will be one more removal at one calendar year after burial July 2024.

Figure 3. Litter bag plot layout. Each unburned vs. burned meadow was laid out the same. The litter bags were thus randomly placed with respect to the environment they were in and there was replication both within and among sites. Four sterile and four unsterile bags were left at each numbered point.



Site management activities during the experiment

Two of the prairies, Eaton and Spires, experienced mowing during the course of the experiment. Because mowing would destroy the litter bags, we picked them up the day before (September 11, 2023) by placing each set of six into a separate clean, dry paper bag. They were returned to the same locations the following day. Managers at the third prairie, Pisgah, hoped to burn it in August or September of 2023. Because conditions for controlled burns must be just right (low wind, sufficient crews, etc.) we were asked to remove our bags on July 22, 2023 and were unable to put them back out until October 12, 2023. Unfortunately, the conditions were never right to burn this prairie.

Nutrient Analysis

Nutrient analyses were done on the 3 month samples to determine if the large differences in decomposition were due to nutrient availability. Samples from Eaton and Spire that had been removed after three months were ground and homogenized, put to dry overnight in an oven at 105 degrees F, then further ground by a bead milling machine (Fisherbrand Bead Mill 24 Homogenizer). Seven milling balls were placed into each sample tube, then run through the machine for two minutes at speed 3.40 m/s. Each tube was run through these settings twice. After bead milling, each sample was run through a Thermo Scientific Flash Smart to get percent composition of carbon and nitrogen for each sample.

Data Analysis

To determine the effects of burning on decomposition, we ran an ANCOVA (analysis of covariance) with the difference in weight (decomposition) as a response variable, burn and sterilization as interacting effects, fresh weight and months since burial as covariates, and site as a random effect. Then, we subsetted each sample collection time and reran the model without months since burial, to measure whether these effects contribute to differences in decomposition across each time period. Finally, to measure whether nutrient differences were contributing to differences in composition, we ran an anova with N and C as responses to decomposition weight, burn, and site. Analyses and graphing were done with R (version 4.2.2), using the following packages: *ggplot, tidyverse, ggpubr, rstatix, emmeans*.

Results

Litter decomposition was affected by both the sterilized (P= 0.003; Fig. 4) and by the burned (P=0.034; Fig. 5) treatments. Litter bags that were sterilized had greater average decomposition amounts than litter bags that had not been sterilized (Fig. 4), and litter bags from burned sections had greater average decomposition amounts than litter bags from unburned sections (Fig. 5).

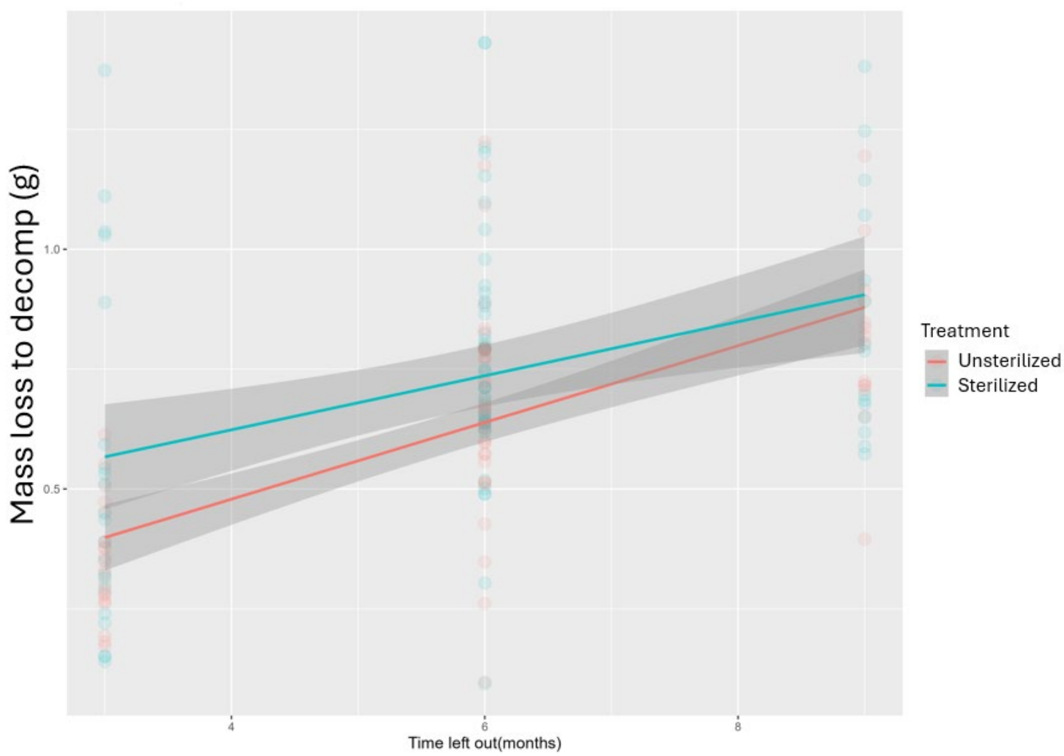


Figure 4. Norms of Reaction diagram showing litter decomposition for sterile treatment over time. Litter bags that had been sterilized had a significantly greater average decomposition than litter bags that had not been sterilized.

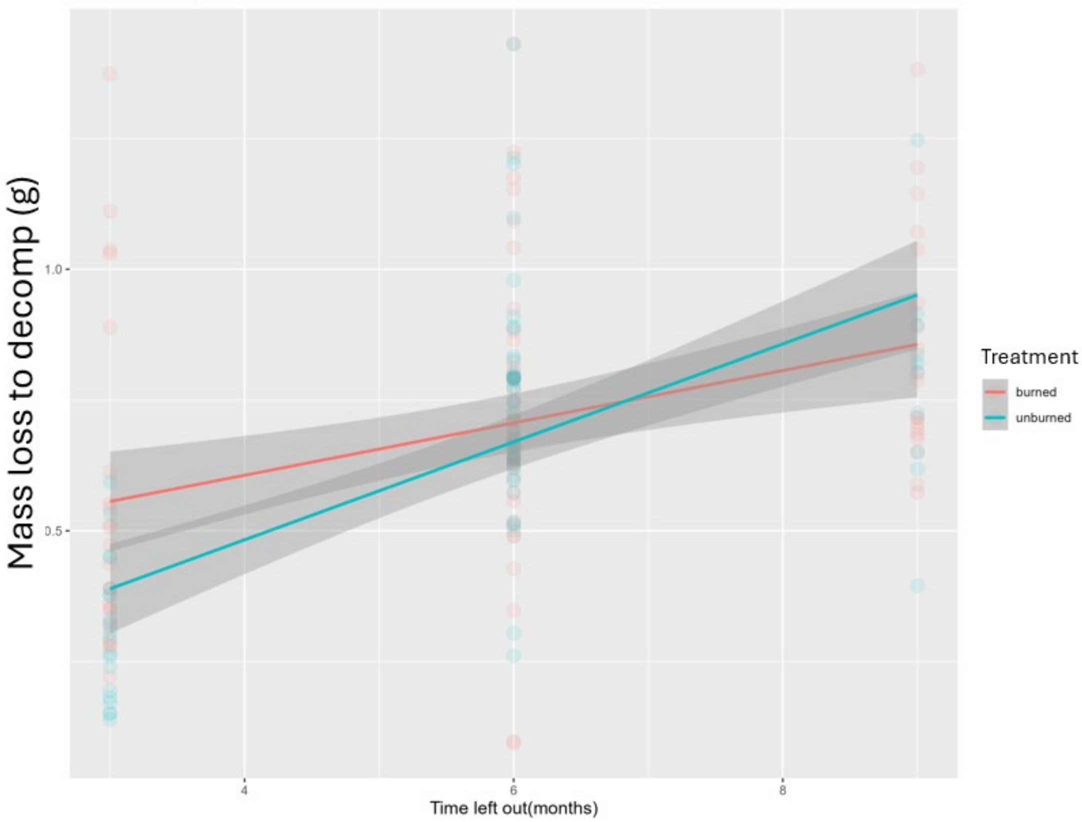


Figure 5. Norms of Reaction diagram showing litter decomposition for the burned treatment and an interaction with time. Litter bags from burned sites had a significantly greater average decomposition than litter bags from unburned sites, but at nine months the unburned showed a larger difference than the burned.

Decomposition was not constant. Litter bags removed after three months had a larger difference between treatments than litter bags removed after six months and nine months for both burned (P_{3m} = 0.0008, P_{6m} = 0.47, P_{9m} = 0.29; Fig. 7) and sterile treatments (P_{3m} = 0.018, P_{6m} = 0.027, P_{9m} = 0.069; Fig. 6).

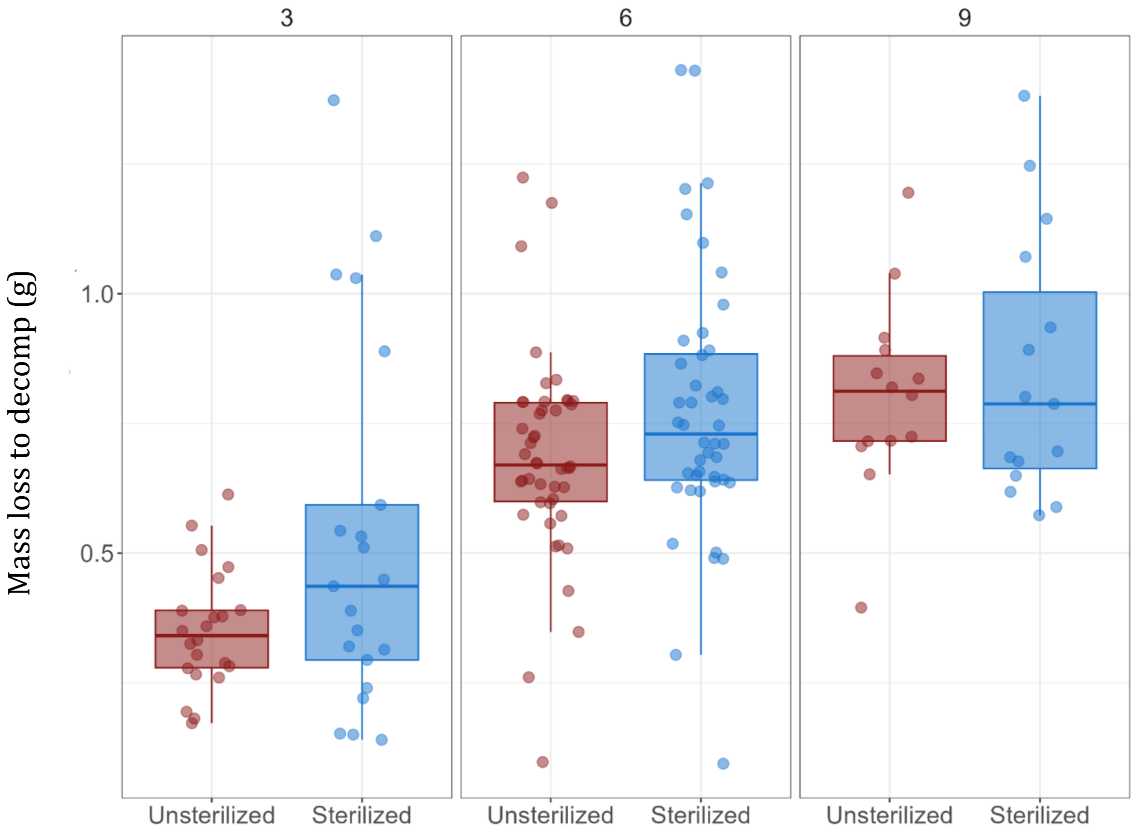


Figure 6. Litter decomposition for sterile treatment separated by sample removal time. Differences between sterilized and unsterilized litter bags were greater in bags removed after three months than in litter bags removed after six and nine months.

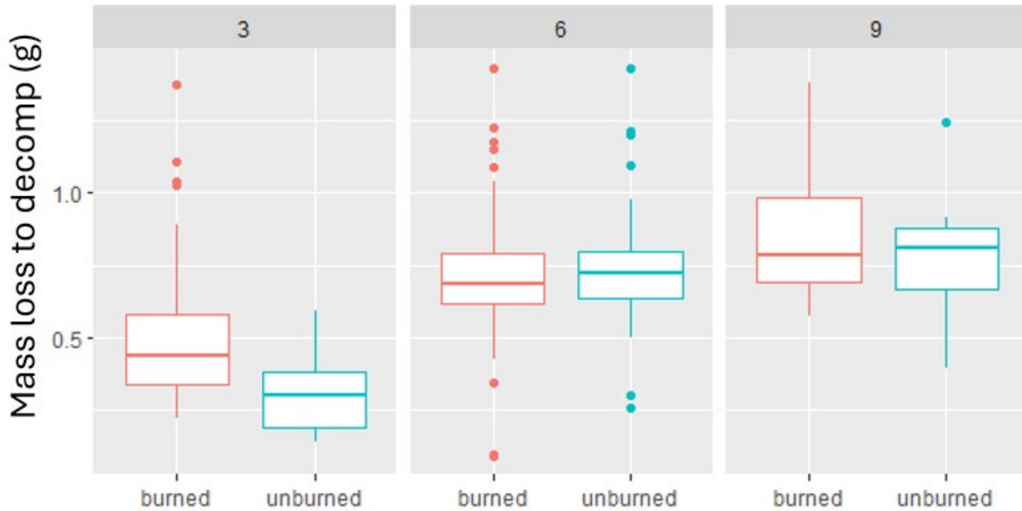


Figure 7 Litter decomposition for burned treatment separated by sample removal time. Differences between burned and unburned litter bags was greater in bags removed after three months than in litter bags removed after six and nine months.

Nutrient Analysis Results

Measuring nitrogen and carbon amounts in samples removed after three months did not help to explain differences in decomposition. Differences in the C:N ratio between burned and unburned treatments were minimal (P = 0.13, Fig. 8). Differences in mass lost to decomposition between burned and unburned litter are the result of something other than differing nutrient availabilities.

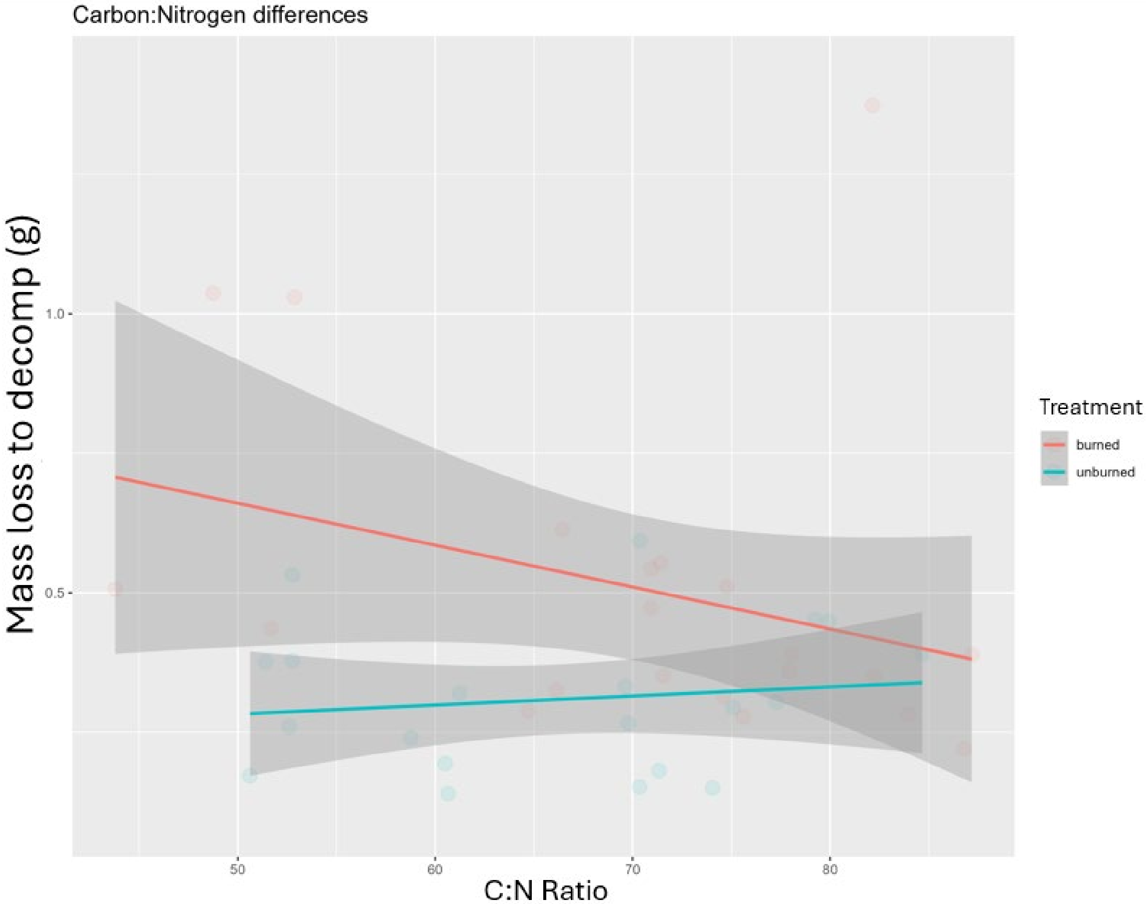


Figure 8. C:N Ratio in burned vs unburned litter. Shows minimal difference between treatments. Relationship does not explain differences in decomposition.

Discussion

Litter decomposition was affected by both sterilization and fire treatments, but the magnitude of these differences diminished after the first removal. Litter bags removed after three months had a significantly greater weight loss in litter bags that had been sterilized and in litter bags that contained burned material (Figures 6, 7). After the first three months decomposition rates were very similar across all treatment types.

Our first hypothesis was that litter in burned prairie would decompose less, as the presence of fire would decrease the number of decomposer species (Semenova-Nelsen 2019). Our results showed the opposite. In an attempt to explain this relationship, nutrient analyses were done on the litter bags removed after three months to see if nutrient availability could account for the significant decomposition rate differences between treatments. This analysis showed that the differences in the C:N ratio between burned and unburned litter was not significant. (Figure 8). This indicates that the differences in mass loss to decomposition between burned and unburned litter are result of something other than nutrient availability. The lack of relationship between fire presence and nutrient availability is different to other studies into fire effects on decomposition (e.g., Kohmann et al. 2020), where there was a measured relationship. While differences in decomposition between burned and unburned sites in those studies were a result of fire affecting nutrient availability and ratios, our data indicates that was not the case here. Our differences were likely the result of something else, possibly differences in fungal community.

Another relationship we saw in the data was that sterilized samples had greater rates of decomposition than the unsterilized samples (Figures 4, 6). We had initially predicted that unsterilized litter would have greater decomposition rates, as the endophytes inside the plant cells that remained alive would begin to start the decomposition process. The data showed the opposite, with the sterilized treatment having greater decomposition than the unsterilized (with endophytes). One possible explanation for this relationship is that the autoclave treatment did more than kill the endophytes, it also changed the tissue composition, making it easier to decompose. In fact, there are many studies that have examined the effect of autoclaves on cellular composition, many of which have found that the process of sterilization by autoclave can cause tissue to break down (Beaudet 2011; Wang 1995; Howard 1974). This tissue breakdown could account for the greater amount of decomposition seen in the sterilized samples than in the unsterilized samples (Figures 4, 6). To properly determine if endophytes are playing a role in decomposing the tissue they are housed in, other sterilization methods would have to be compared.

Data for this thesis was analyzed both including and excluding the data collected from the Pisgah location. This is because the litter samples for Pisgah were not set out until the other bags had been out for three months already, because of site management happening at Pisgah. When Pisgah data was excluded from overall analysis, the difference between burned and unburned samples was not very different ($P_{excl} = 0.0025$, $P_{incl} = 0.034$). The lack of difference when Pisgah is included compared to when it's excluded indicates the removal of the bags due to site management did not have that great of an effect on the amount of decomposition happening in the samples. This makes sense, as even in removal the samples in the litter bags would have been decomposing. They were simply held in paper bags, but still could have decomposed similarly to the samples still out at the sites, as shown in the lack of difference..

Prescribed burns are a key part of maintaining native Oregon prairies; fire keeps trees and shrubs from turning them into forests, and fire may also encourage growth of some native species, such as camus that have evolved under thousands of years of native American prairie burning practices (Pendergrass 1995; Hamman et al. 2011). Outside of prescribed, intentional burns, wildfires are expected to increase under anthropogenic climate change conditions (Abatzoglou 2018). Fires in general are predicted to become larger, more intense, and happen with greater frequency (Aparicio 2022). With the understanding that fire is something these prairies will be regularly exposed to, whether intentional or not, it's important to understand the effects of fire across different taxa. Having insight into how decomposition might change in areas that have been burned can give managers of these landscapes tools to be ready for the larger scale implications of these changes in decomposition. For example, our data suggest that the decrease in decomposition rates as a result of fire are relatively short-lived, a year or two. Whether this is a result of differing nutrient composition or a different factor, it provides a good starting point for allowing site managers and teams to understand consequences of burning and come up with methods for dealing with any consequences ahead of time. Our future work on fungal community composition will add more information for site managers to use.

Future Work

Work on this project will continue after this thesis. There will be one more collection of litter bags, at the one year mark, and community composition of the litter will be examined. All litter samples collected will be sequenced using the fungal ITS region of ribosomal DNA to detect fungal community differences among locations, and potentially between litter that had been collected at burned and unburned sites. This information will provide a fuller picture of the effect fire has on decomposer organisms within prairie ecosystems. It could also help to explain some of the discrepancies between what we hypothesized and what we saw in our results. Our hypothesis was that burned samples would decompose slower than unburned because the fire would cause a decrease in decomposers. However, there are certain fungal families that are known to increase in abundance post fire disturbance. Some ascomycetes, for example, have been detected in greater numbers after fire disturbance (Wicklow & Hirschfield 1979; Holden 2013). Certain Ascomycete genera like *Aspergillus* and *Phoma* degrade plant biomass faster than others (Challacombe et al. 2019), and decomposition being done by ascomycetes has been found to decrease over time, slowly being replaced by basidiomycetes (Purahong et al. 2016). In our results, we saw that burned litter decomposed at a greater rate than unburned, and that the difference between burned and unburned was much greater after three months than it was after six and nine months. Sequencing data could provide an explanation for these results if samples are found to have ascomycete genera like *Aspergillus* and *Phoma* that are known to decompose faster, and if we see a greater abundance of ascomycetes in samples removed after three months than we do after six months and nine months. We can hypothesize that these things are true based on the results we saw, but the sequencing work that will continue after the publication of this thesis will give us a clearer picture of the relationships happening in these litter samples. Understanding how intentional burning may affect decomposition on Oregon prairies can help prairie managers mitigate wider scale consequences as a result of differing decomposition rates.

Supplemental Materials

Supplement Figure 1. Eaton burned site. This particular burn took place Oct 2015, but the one in our study occurred Sept 2022. Picture from Wes Messinger, Fern Ridge site manager.

Supplemental Figure 2. Unburned Eaton prairie July 2023. Image from Bitty Roy.

Supplemental Figure 3. Spire Prairie. Image from Bitty Roy.

Supplemental Figure 4. Pisgah burned prairie. Picture taken November 2023 by Bitty Roy.

Supplemental Figure 5. Pisgah unburned prairie. Picture taken November 2023 by Bitty Roy.

Supplemental Figure 6. Examples of litter bags pre-decomposition. Red stripe indicates not sterile, black stripe indicates sterile. Picture from Ellen Ralston.

Supplemental Figures 7 (left) and 8 (right). Closer view of decomposition bags. Red stripe indicates not sterile, black stripe indicates sterile. Figure 7 shows a clear view of the numbering system. Pictures from Ellen Ralston.

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