AN ABSTRACT OF THE THESIS OF

Dallas Hall Defrees for the degree of Master of Science in Rangeland Ecology and Management presented on May 25, 2018.

Title: Ungulates and Forest Management: Understanding Interactions Between Large Herbivores and Fuels Reduction Treatments on Shrub Assemblages in the Intermountain West

Abstract approved: ____

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Deciduous shrubs are an integral component of mixed conifer forests of the interior Pacific Northwest by providing structural complexity, forage, and niche habitat. Currently, these species are under pressure from high levels of ungulate herbivory and forest management activities such as fuels reduction treatments. Ungulate herbivory is influential in the suppression of shrubs by maintaining low levels of abundance and shrub diversity that can eventually contribute to the alteration of species composition. Beyond herbivory, episodic disturbances such as prescribed fire and stand thinning can also influence the shrub layer and forest dynamics. Over a century of fire suppression has increased the occurrence of fuels reduction treatments across the interior Pacific Northwest. The aim of this study was to 1) evaluate the effects fuels reduction treatments as well as the effects of herbivory by wild (*Cervus elaphus, Odocoileus hemionus*) and domestic (*Bos taurus*) ungulates on shrub diversity, richness, and height; and 2) examine the relationship

between the amount of protection by physical barriers (coarse woody debris and conifer trees) on shrub architecture and height.

Concerning the first objective, we measured shrub richness, frequency, diversity, and height in four treatments in the mixed conifer forests of the interior Pacific Northwest, USA: 1) ungulate herbivory in fuels treated forest stands, 2) no herbivory in fuels treated stands, 3) herbivory in untreated forest stands and 4) no herbivory in untreated forest stands. We found that ungulate herbivory decreased shrub richness, diversity, and height in both fuels reduction treated and untreated stands. We also found that fuels reduction treatments decreased overall shrub richness, diversity, and height with and without ungulate herbivory. Furthermore, the interaction of ungulate herbivory and fuels reduction treatments had compounding negative effects on shrub diversity and height.

Regarding objective two, we measured the height and architecture of highly preferred shrubs with and without herbivory in untreated forest stands. We examined how well shrubs were protected from herbivory by coarse woody debris and conifer trees, and how that protection may influence the height and architecture of the shrub. Goodness-of-fit tests and multiple linear regressions showed that shrubs exposed to herbivory with a lesser degree of physical protection had more strongly influenced growth form as evidenced by reduced height and an increased proportion of arrested individuals.

This research explored how two of the most common forest disturbances (ungulate herbivory and fuels reduction treatments) influence shrub composition and structure, and specifically how forest structural elements may harbor preferred shrub species and protect them from herbivory. Interactions between the increasing amount of acres of forest undergoing fuels reduction treatments and the high levels of ungulates within the interior Pacific Northwest may contribute to a loss in biodiversity and resources that are provided by deciduous shrubs.

Ungulates and Forest Management: Understanding Interactions Between Large Herbivores and Fuels Reduction Treatments on Shrub Assemblages in the Intermountain West

by
Dallas Hall Defrees

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented May 25, 2018
Commencement June 2018

Master of Science thesis of Dallas Hall Defrees presented on May 25, 2018

APPROVED:

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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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ACKNOWLEDGEMENTS

I am thankful to Bryan Endress for taking me on as a graduate student and guiding me throughout my graduate school experience. I would like to sincerely thank Josh Averett, who was a constant source of mentorship and encouragement in many aspects of my degree. I thank the U.S.D.A Forest Service Pacific Northwest Research Station for their collaboration and guidance through this research, specifically Mike Wisdom, Mary Rowland, and Bridgett Naylor. I would like to acknowledge Patricia Kennedy, Ricardo Mata-Gonzalez and Barbara Lachenbruch as they aided me throughout my graduate school process.

This research would not have been feasible without the hard work of the field technicians, Kent Coe, Walker Powell, Brogan Watson, Kolby Haliewicz, Tyler Dungannon, Reid Endress, Keegan Dutto and Tony Clay. I sincerely thank you for all of your hard work as members of my field team.

I would like to thank my family and friends for their unending support. A sincere thank you to Di O’Bryan who gave me a welcoming place to stay as I completed my course work. To my parents, who have always been supportive and emboldened me to attain my goals. Most importantly I would like to thank my husband, Riley. Riley’s excitement and love in watching me pursue my passions was the most valuable source of encouragement.

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Chapter 1 Introduction

Episodic disturbances frequent the mixed conifer forests of the interior Pacific Northwest of the USA and Canada. Fuels reduction treatments and ungulate herbivory are two of the most pervasive disturbances, both of which contribute to alterations of ecosystems (Hobbs 1996, Augustine and McNaughton 1998, Boerner et al. 2006, Willms et al. 2017). Ungulate herbivory is known to affect an assortment of ecosystems by altering species composition and plant productivity throughout the world (Hobbs 1996, Strauss and Agrawal 1999, Bernes et al. 2018). Although ungulate herbivory is part of the natural trophic cycle of ecosystems and in some instances increases plant productivity (Augustine and McNaughton 1998, Stewart et al. 2006); under high levels of abundance, ungulate herbivores can negatively influence plant fitness, diversity, and ecosystem productivity (Hester et al. 2000, Riggs et al. 2000). More specifically, high abundances of ungulate herbivores can greatly reduce the understory shrub layers in the forest systems of North America (Beschta and Ripple 2012, Endress et al. 2016).

Shrubs are vital to the biodiversity and health of forested ecosystems (Johnson 1992, Hobbs 1996, Moser and Witmer 2000, Rooney 2001, Kleintjes Neff 2007, Endress et al. 2012). Shrubs provide important sources of forage for elk, cattle, and deer (Canon 1987, Clark 2013) especially late in the season. Other wildlife species also benefit from the fruit produced by shrubs such as *Amelanchier alnifolia*, *Arctostaphylos uva-ursi*, *Prunus virginiana*, and *Vaccinium* spp. (Johnson 1998). Besides acting as food sources, shrubs are integral to other ecosystem services. Shrubs contribute to soil health through the input of organic matter or through nitrogen fixation (e.g., *Ceanothus velutinous* and *Alnus incana*; Hobbs 1996, Johnson 1998, Pastor 1998). Furthermore, shrubs are some of the only species that exist in the lower to mid forest canopy layers contributing to ecosystem structural complexity. Shrubs are pivotal to the maintenance of forest biodiversity, thus a decrease in their abundance could result in cascading ecological effects (Augustine and McNaughton 1998, Rooney 2001, Vavra et al. 2007, Rooney 2009).

As important forage for ungulate herbivores, shrubs are susceptible to negative responses as a result of over-browsing. Woody understory vegetation and shrub abundance and richness decline when exposed to native and introduced livestock across an array of temperate and boreal forest landscapes (Berne et al. 2018). Ungulate herbivory can alter the growth form of shrubs by arresting them to heights below the browse level (Hester et al. 2000, Riggs et al. 2000, Beschta and Ripple 2012) and removing vegetative tissue. With less photosynthetic material due to herbivory, the shrubs allocate resources away from reproductive growth, ultimately affecting reproductive success. Beyond the direct effects of herbivory, ungulate herbivores can contribute to modification of ecosystems indirectly by altering soil processes (Stewart et al. 2006), increasing invasive species (Vavra et al. 2007, Berne et al. 2018), and shifting forest stand composition (Pastor et al. 1988, Randall and Walters 2011, Kribell et al. 2011, Freker et al. 2013).

As wildfires continue to threaten our forested areas, land managers are using fuels reduction treatments as a preferred method to try and decrease the severity of fires throughout the region (Agee and Skinner 2005). Fuels reduction treatments can impact forest stands beyond just the removal of overstory canopy and decrease conifer biomass (Boerner et al. 2006, Abella and Springer 2015, Willms et al. 2017). As more forest stands are being slotted for fuels reduction treatments, there may be implications on the forest understory. Fuels reduction treatments decrease the risk of wildfire by removing surface, ladder, and canopy fuels. As surface and ladder fuels, shrubs may be removed from the system (Brown et al. 2004, Agee and Skinner 2005, Hunter et al. 2007). Fuels reduction treatments along with prescribed burning has been noted to change understory communities (Wayman and North 2007) and decrease shrub cover (Willms et al. 2017). Along with mechanical removal of shrubs, fuels reduction treatments may be inhibiting the establishment of shrub species post disturbance with the removal of coarse woody debris that would facilitate the growth of a shrub seedling (Vavra et al. 2007). Structural components of the forest understory can provide favorable microsite conditions for woody species (Gray and Spies 1997, Beschta and Ripple 2007, Gómez-Aparicio et al. 2008) and may also furnish physical protection from ungulate herbivory for palatable species (Smit et al. 2006, Smit et al. 2012).

Despite the frequency of fuels reduction treatments and ungulate herbivory in forest systems, little is still known about how these disturbances interact and influence deciduous shrubs. Disturbance sites can create conditions that promote the growth of highly nutritious and palatable plants. Due to this influx of preferred forage, disturbance sites often become focal points for ungulate herbivores which selectively consume those highly palatable species (Vavra et al. 2007). Beyond this initial interaction, little is known as to how the combination of fuels reduction treatments and ungulate herbivory influence shrubs over the long term, despite the knowledge that both disturbances alone can influence biotic and abiotic components of the forest system.

This study had two objectives that are covered in two separate chapters: 1) increase our understanding of how ungulate herbivory and fuels reduction treatments interact to alter the composition and structure of shrub assemblages in mixed conifer forests of the interior Pacific Northwest, USA (addressed in chapter 2); and 2) characterize the immediate physical barriers associated with palatable shrub species and relate those to the growth form of the shrub (addressed in chapter 3).

Chapter 2 Ungulates and Forest Management: Understanding Interactions Between Large Herbivores and Fuels Reduction Treatments on Shrub Assemblages in the Intermountain West

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For submission to *Forest Ecology & Management*

Abstract

Deciduous shrubs represent species that are important contributors to the biodiversity of conifer forests of the interior Pacific Northwest. As important forage species, they are also highly targeted by wild (*Cervus elaphus, Odocoileus hemionus*) and domestic (*Bos taurus*) ungulates. Ungulates can act as keystone species in these forests and be influential contributors to the prolonged suppression of deciduous shrubs as well as alter species composition of the forest stand. Beyond herbivory, episodic disturbances such as prescribed fire and stand thinning can also influence the shrub layer and forest dynamics. More than a century of fire suppression has increased the occurrence of fuels reduction treatments across the interior Pacific Northwest. We evaluated the effects of two of the most prominent disturbances in this system, ungulate herbivory and fuels reduction treatment, and their subsequent impacts on deciduous shrub composition and structure in mixed-conifer forests of the interior Pacific Northwest. We measured the height and presence of deciduous shrub species in areas that have undergone fuels reduction treatments 15-17 years ago as well as untreated forest stands. Shrubs were also measured in areas with and without ungulate herbivory. Ungulate herbivory ($F_{[2,44]}$ = 14.25, p= 0.0002) and fuels reduction treatments ($F_{[2,44]}$ = 13.17, p= 0.0002) both negatively affected shrub composition. Overall richness, diversity, frequency, and height of shrub species declined in forests stands that had undergone fuels reduction treatments and were exposed to ungulate herbivory. With an increasing amount of land undergoing fuels reduction treatments and the current high levels of ungulates within the interior Pacific Northwest,

interactions between these two disturbances may contribute to a loss in biodiversity and other resources that are provided by deciduous shrubs.

1. Introduction

Deciduous woody species are common and integral understory component of conifer forests by contributing to species richness, structural complexity, and wildlife habitat (Johnson 1992, Hobbs 1996, Moser and Witmer 2000, Rooney 2001, Kleintjes Neff 2007, Endress et al. 2012). Shrubs are important to the maintenance of forest biodiversity and reductions in their abundance can result in cascading ecological effects such as altering vegetation communities (Augustine and McNaughton 1998, Rooney 2001, Vavra et al. 2007, Rooney 2009). Additionally, shrubs provide important forage for both wild and domestic ungulates (Canon 1987, Clark 2013), particularly in late summer and winter months, following senescence of herbaceous vegetation. Areas exposed to high levels of herbivory by ungulates may display drastic declines or even the elimination of highly preferred forage species, leaving behind fewer, less palatable plants on the landscape (Endress et al. 2012, Freker et al. 2013). Consequently, strong herbivore pressure is considered a major contributor to the decline of a number of deciduous woody species in western North America (Woodward et al.1994, Baker et al.1997, White et al. 1998).

Beyond contributing to the decline in shrub abundance and richness, ungulates may also affect shrub architecture by maintaining shrub heights below browse level (< 2.5m), resulting in hedged or ‘arrested’ shrubs (Hester et al. 2000, Riggs et al. 2000, Beschta and Ripple 2012, Endress et al. 2016). Growth of preferred forage species can be negatively affected by browsing to such a degree that even low herbivore densities may be sufficient to prevent browse sensitive species from escaping the browse zone (Hester et al. 2000, Endress et al. 2016). Arrestment of woody species due to herbivory can result in large scale changes to stand composition of forest systems by altering size class distribution (Kribell et al. 2011), modifying competitive interactions among species (Pastor et al. 1988, Randall and Walters 2011), impeding regeneration of palatable shrubs (Beschta and Ripple 2008), and decreasing the amount of understory shade (Woodward et al. 1994). Suppression of shrub establishment and growth due to herbivory can result in a decrease in fruit production of browsed species (Kay 1995) as well as impact nesting habitat and food sources for birds, insects, and other woodland species (Beal et al. 1915, Hobbs 1996, Johnson 2000, Roberson et al. 2016).

Other forest disturbances such as fire, insect outbreaks, and forest management regimes (e.g. fuels reduction treatments) can influence the shrub layer as well. Forest management activities, such as fuels reduction treatments, have the capacity to interact with ungulate herbivory, resulting in shifts of shrub abundance, diversity, composition and structure (Wisdom et al. 2006, Endress et al. 2012, Pekin et al. 2014). In the semi-arid conifer forests of the interior Pacific Northwest of the USA and Canada, fuels reduction treatments have expanded greatly in the past decade as land managers increase efforts to reduce fuel loads that have accumulated due to more than a century of fire suppression. Fuels reduction protocols include clearing standing dead and down wood, removing ladder fuels, burning after thinning, and increasing space between trees

(Agee and Skinner 2005). Elimination of such structures may facilitate arrestment and decrease the abundance of shrubs by removing physical barriers such as standing dead and down wood (Smit et al. 2006, Smit et al. 2012, Defrees et al., Chapter 3) that may protect these species from ungulate browse. Structural components may also provide favorable microsite conditions for woody species establishment (Gray and Spies 1997, Beschta and Ripple 2007, Gómez-Aparicio et al. 2008). Moreover, episodic disturbances such as prescribed fire and stand thinning can create conditions that facilitate heavy use by large herbivores due to increases in the abundance of highly preferred and nutritious vegetation following disturbance events (Vavra et al. 2007).

Fuels reduction treatments are now one of the most ubiquitous silvicultural practices in conifer forests of the interior Pacific Northwest. Despite this, little is known about how such treatments influence shrub assemblages and structural development within these forest ecosystems. The purpose of this study was to increase our understanding of how ungulate herbivory and fuels reduction treatments interact to alter the composition and structure of shrub assemblages in mixed- conifer forests of the interior Pacific Northwest, USA. Specifically, we sought to 1) document browse pressure by ungulates (cattle, elk, deer) and compare browsing rates between fuels-treated and untreated (control) forest stands, and 2) determine how ungulate herbivory and fuels reduction treatments alone, and in concert, affect the structure and composition of shrub communities. By researching these interactions within forests, there will be a greater understanding of the consequences of fuels reduction treatments on this ecologically and economically important component of forest ecosystems. We hypothesized that:

(1) browse pressure would be greater in fuels treated areas; (2) Both herbivory and fuels treatment activities would result in negative impacts on the shrub layer composition, generating overall declines in abundance and diversity of shrub species and as well as stunted height; and (3) fuels treated areas exposed to ungulate herbivores will show the lowest shrub richness, diversity and height.

2. Methods

2.1 Study Area

Research was conducted within the Starkey Experimental Forest and Range (SEFR) located in the Blue Mountain Ecological Province of northeast Oregon. Elevations range from 1200m to 1500m above sea level averaging approximately 510mm of annual rainfall, most of which falls in the form of winter snow or spring rain (Rowland et al. 1997). The 10,000-ha experiment station is representative of the montane forest types that are typical of the interior western United States (Rowland et al. 1997). Our research focused on the mixed-conifer forest stands within SEFR. These forests are dominated by Douglas fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*), but also include Ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), Englemann spruce (*Picea* engelmannii), and lodgepole pine (*Pinus contorta*; Franklin and Dyrness 1988). SEFR has maintained approximately 500 cow-calf pairs from mid-June to mid-October, 200 mule deer and 350 elk from April-November for the last 25 years (Endress et al. 2016). These ungulate densities for cattle (7.15/k m^2), mule deer (1.95/km^2), and elk (4.55/km^2) resemble those outside of SEFR

(Wisdom and Thomas 1996).

In the 1980s an outbreak of spruce budworm infected the majority of the grand fir and Douglas fir stands killing most of the adult trees in SEFR, resulting in large amounts of standing dead and coarse woody debris (Bull 2005). Fuels reduction treatments were applied to randomly selected grand fir and Douglas fir stands between 2000-2003 (mean treatment stand area =26 ha, range = 2–214 ha; Long et al. 2008b) to reduce the amount of fire-hazard debris left over from the outbreak and to research effects of fuels reduction treatments on forest recovery. Stands were mechanically thinned with a feller-buncher to meet a goal of <35 tons/ha. Objectives were to leave live, fire resistant large trees (>51 cm at diameter breast height) standing and to keep 18.4 m^2/ha basal area of standing trees. After thinning treatments, stands were broadcast burned using hand drip torches. A total of 681 hectares of forest was fuels reduction treated, and another 1,474 ha of similar forest was untreated (control) (Long et al. 2008a).

As part of the fuels reduction treatment effort, six ungulate exclosures (~ 7 hectares each) were constructed one year after the fuels reduction treatments occurred. Three of these exclosures were located in fuels reduction treated areas and the other three were located in untreated forest stands. Exclosures were constructed using a 2.4-meter-tall fence that excluded elk, deer, and cattle but allowed other wildlife to pass through. Each exclosure was divided into fenced seven one-hectare subplots that were used for ungulate herbivory studies and included low, moderate, and high densities of elk and cattle for seven years (Endress et al. 2012, Clark 2013, Pekin et al. 2014, Endress et al. 2016). Since the seven-year study was completed (2012), the exclosures have been maintained, and no other ungulate herbivory or treatments have occurred for the past five or six years (depending on the exclosure).

2.2 Data Collection

Sampling took place in two forest stand types within SEFR: (1) control stands that have had no wildfire or silvicultural treatments or in ~ 50 years, and (2) treated forest stands that underwent fuels reduction treatments 14-17 years ago. Within these two treatments, sampling was also conducted inside the six upland exclosures that served as a reference for shrub layer development in the absence of ungulates (Appendix A). Using available GIS layers from the Pacific Northwest Research Station (USDA Forest Service) regarding fuels reduction treatment activity, we calculated that approximately 30% of grand fir and Douglas fir forest stands in SEFR underwent fuels reduction treatments. Using ArcGIS 10.3 we then randomly placed sampling points within fuels treated and control areas approximately proportional to total area of each treatment (70:30 untreated to treated ratio). This resulted in 109 plots in control stands and 58 in treated stands. Sample points were $\geq$ 50 meters apart and $\geq$ 10 meters away from the stand edge (to minimize edge effects). Because the ungulate exclosures were smaller (~ 7 ha each), our approach to selecting sampling points differed slightly. In this case, we placed 21 random plots within each exclosure ($\geq$15 m from each other and $\geq$ 10 m from the edge). This resulted in samples sizes of 63 treated and 63 control plots in areas where cattle, elk, and deer have been excluded for the past six years.

Each plot was located using a Trimble GeoXT GPS unit and sampled in late summer of 2016 or 2017. We sampled in late summer for two reasons: 1) to increase our ability to more accurately capture ungulate browsing pressure –which is thought to peak in late summer-early fall in our study area; and 2) to reduce measurement and species identification error associated with senescence and leaf-drop later in the fall. Circular plots with a 7-meter radius (154 m^2) were divided into four subplots (each a quadrant of the circular plot). Within each subplot, species presence, maximum height for each species present, and browse pressure was measured. We categorized shrubs by their growth/size potential into three different growth forms: subshrub (<0.5m), shrub (0.5-3.0m), or large shrub (>3.0m). Subshrubs were excluded from height and browse measurements. Browse pressure was measured for each species by estimating the proportion of the current (this years') leaders browsed. Estimates were grouped into the following use categories: 0%, 1-20%, 21-40%, 41-60%, 61-80%, 81-100% (Burton et al. 2011). A measurement of the tallest individual plant for each species was taken within each of the subplots and then all height measurements were averaged, thus yielding a mean maximum height for each plot. For each species, we used a relative frequency estimate as a measure of abundance for each plot. To do this, we divided the number of subplots a species was present in by four (e.g., if *Salix scouleriana* was present in 2 of 4 subplots, its abundance value for that plot was 0.5).

2.3 Analysis

Following data collection, we noticed that a number of the plots in our control forest stands occurred on slopes much greater than plots found within the fuels treated areas. Because slope can have a large impact on site conditions and subsequent community composition and structure (Holechek et al. 1989), plots that had slope values greater than 20 degrees were excluded from our analyses. A cutoff of 20 degrees was used because there were not plots in the fuels treated areas or exclosures that had a slope greater than 20 degrees, yet there were control plots with 20 degree and steeper slopes. We also noticed that plots with a slope $\geq$ 20 began to diverge in their species composition. This resulted in the following sample sizes used in our analyses: N=84 Control + Ungulates, N=58 Treated + Ungulates, N=63 Control + Ungulates Excluded and N=63 Treated + Ungulates Excluded.

2.3.1 Effects on browse pressure, richness, diversity, abundance and shrub layer height

To test for differences in browse pressure between treated and untreated plots, we used the midpoint value of each category to calculate the average percent of current leaders browsed for each plot. The data exhibited non-normal distribution and transformations were unsuccessful in correcting this; therefore, differences in median browse among the two treatments were analyzed using the Wilcoxon sign test.

Generalized linear models (GLM) were used to test the effects of fuels reduction and ungulate herbivory treatments on species richness, diversity, and shrub layer height separately. We fit the models with normal distribution and an identity link function and included main effects plus an interaction term. Richness was obtained by summing the total number of shrub species that were present within each plot. We used the Shannon's Index to estimate diversity, which was obtained using the row and column summary of our plot by species matrix (250 x 15) in PC-ORD (McCune and Grace 2002). All of the height measurements of shrubs within each plot were averaged to yield a mean shrub layer height value. Height values were log transformed prior to analysis to yield a normal distribution. Statistical analyses were conducted in JMP Pro 13.0 (SAS Institute, Cary, NC, USA).

Effects of fuels reduction and herbivory on target species frequency were analyzed using multiple logistic regression models (one model for each species) for the two most abundant species within each of the three growth form categories: subshrub (*Arctostaphylos uva-ursi*, bearberry; *Spiraea betulifolia*, birchleaf spirea), shrub (*Symphoricarpos albus*, snowberry; *Rosa* spp., Rose), and large shrubs (*Amelanchier alnifolia*, serviceberry; *Salix scouleriana*, Scouler's willow). Species abundance (plot frequency) was the response variable, and fuels reduction (Yes/No) and herbivory (Yes/No) were the predictors. Both major effects and the two-way interaction were included in each model.

2.3.2 Effects on shrub community assemblage

Nonmetric multidimensional scaling (NMS; McCune and Grace 2002) using a Sorenson (Bray-Curtis) distance measure was used to extract the dominant shrub assemblage composition gradients. We used the slow and thorough NMS autopilot setting and Kruskal' strategy 2 for penalization for ties. Sorenson distance was used because we were interested in relative differences in species cover between plots. We excluded rare species (occurring in < 10% of plots) to reduce noise (McCune and Grace 2002). Plots that were not occupied by shrubs were also excluded from the analysis because the application of Sorenson distance measure is not possible with empty sample units. Multivariate analyses were performed on a final matrix consisting of 250 plots by 15 species. Three-dimensional ordinations were produced with a random starting configuration and a maximum of 500 iterations. Ordinations were rotated by orthogonal principal axes to load the greatest amount of variance on axis 1 while ensuring that axes 1 and 2 were independent of one another. To relate fuels reduction treatments, herbivory, and site environmental variables (slope, aspect, elevation) with shrub community variability, a second matrix containing these variables was overlaid onto the ordination space using joint plots, and linear correlations between those variables and the ordination axes were calculated. Non-parametric permutational ANOVA (PERMANOVA; Anderson 2001) was used (McCune and Grace 2002) with a two-way factorial design to test for differences in shrub assemblage composition as a function of our treatments (fuels reduction, herbivory, and their interaction).

3. Results

3.1 Browse Pressure

The majority of shrubs in both fuels treated and control plots were browsed, with 88.3% of shrubs in treated plots and 88.5% of shrubs in control plots experiencing some level of browse during the year sampled. The overall degree in which plants were browsed was similar in both treatments as evidenced by the lack of significance in the percentage of current leaders browsed between fuels treated and control plots that were exposed to herbivory (treated = 29.2%, control= 23.2%, p=0.1769). However, individual species within each treatment showed differing levels of browse (Table 2.1). *Acer glabrum v. douglasii* and *Populous tremuloides* both displayed the highest average of current leaders browsed at 50%, but *Acer glabrum v. douglasii* was only present in the control plots and *Populous tremuloides* was only found in fuels treated plots. Fuels reduction treated plots and control plots had different species composition. Because of this, even though the overall browse levels were similar between the two treatments, the actual species being browsed were different (Table 2.1).

3.2 Richness, Diversity and Height

A total of 31 shrub species were encountered in our plots. Analysis showed that both fuels reduction and herbivory had significant effects on shrub richness (p <0.001) (Table 2.2, Figure 2.1). Untreated stands exposed to herbivory averaged 6.9 species per plot (SD=3.26), while untreated areas without herbivory averaged 9.5 species per plot (SD=2.59). Fuels treated areas exposed to herbivory averaged 4.5 species per plot (SD=3.44) and treated areas without herbivory averaged 8.0 species per plot (SD=2.33). No interaction was found (p = 0.231).

Shrub diversity was negatively affected by fuels reduction treatments and ungulate herbivory (p <0.001). Furthermore, the fuels reduction treatment x herbivory interaction (p=0.002) indicated that the combination of herbivory and fuels treatment further decreased shrub diversity (Table 2.2, Figure 2.1).

The interaction of herbivory and fuels reduction treatment had the greatest impact on shrub height (p =0.016). Shrubs in the control + ungulate plots were 39% taller than shrubs found in the treated + ungulate plots. Herbivory alone decreased shrub height (p <0.001), with the tallest shrubs found in areas without herbivores. In the control plots there was a 61% increase in shrub height in the absence of herbivores. Shrubs in the fuels treated plots were 115% taller in plots without ungulates compared to plots with ungulates. Shrub height was negatively associated (p < 0.001) with fuels reduction treatments, displaying lower mean heights in these plots.

3.3. Species Specific Responses

Herbivory decreased the frequency of *Arctostaphylos uva-ursi* (p <0.001) in both fuels treated and control plots. Conversely, herbivory had much smaller impacts (p=0.184) on the frequency of *Amelanchier alnifolia* and *Spiraea betulifolia*, but declines for these species (p<0.001 and p=0.005 respectively) were seen in areas of fuels reduction treatment (Table 2.3). *Symphoricarpos albus*, and *Rosa* spp. showed decreases (p <0.001 and p =0.006, respectively) in plots with both herbivory and fuels reduction treatment compared to plots with just one explanatory variable. *Salix scouleriana* (p <0.001; Table 2.3) exhibited a positive correlation with fuels reduction treatment, but only in the absence of herbivory (Figure 2.2).

3.4 Shrub Assemblage Responses

The PERMANOVA indicated that both fuels reduction treatments ($F_{[2,44]}$ = 13.17, *p* <0.001) and herbivory ($F_{[2,44]}$ = 14.25, *p* <0.001) resulted in significant differences in shrub assemblage composition. The interaction term was not found to be significant (*p* =0.071) but may still indicate a potential effect.

The 3-dimensional NMS ordination yielded a stable solution that explained 86.7% of variation in the distance matrix (final stress = 14.69, randomization test, *p* = 0.004). Axis 1 explained 42% of the variation and was most correlated with herbivory (r=0.42; Figure 2.3). Ordered by decreasing strength, *Linnaea borealis, Vaccinium scoparium, Vaccinium membranaceum*, *Arctostaphylus uva-ursi, Chimaphila umbellate,* and *Paxistima myrsinites* had the strongest negative correlations with axis 1 (Table 2.4, Figure 2.4). *Symphoricarpos albus* was the only species included in the NMS ordination that had a positive correlation with axis 1 (Table 2.4, Figure 2.4).

Axis 2 explained 27% of variation and was associated with fuels treatment (r=0.47; Figure 2.3). Species most positively correlated to axis 2 were *Arctostaphylus uva-ursi, Ceanothus velutinus, Ribes cereum, Salix scouleriana,* with *Spiraea betulifolia* and *Mahonia repens* having weaker positive correlations. All other species exhibited negative correlations with axis 2 (Table 2.4).

Axis 3 explained little variation in the distance matrix (r^2 = 0.18) and had relatively low correlations with environmental data so it will not be discussed further.

Herbivory decreased the frequency of most of the shrub species measured in both fuels treated and control plots, impacting both highly abundant generalist species and more scarce species. However, of all the species, subshrubs seemed to be the most impacted (Table 2.5). *Mahonia repens, Arctostaphylos uva-ursi, Linnea borealis,* and *Vaccinium scoparium* frequency was lowest in the presence of herbivores compared to all other species (Table 2.5). In fact, *Linnaea borealis* was found in nearly every control plot without herbivory, but showed up with much less frequency with any form of disturbance (fuels treatment or ungulates). Disturbance prone species: *Salix scouleriana, Ceanothus velutinus,* and *Arctostaphylos uva-ursi* were found in greater frequencies in the fuels reduction treatments plots, but only in the absence of herbivory. *Amelanchier alnifolia* had the greatest negative change in frequency of all shrubs in fuels reduction plots both with and without herbivory.

4. Discussion

4.1 Herbivory

Our results indicated there was no detectable difference in ungulate herbivory pressure on shrubs between the fuels treated and control plots with between 20-30% of current leaders being browsed. However, higher levels of current utilization were recorded depending on shrubs species and treatment type and the majority of individuals had accrued some amount of browse. These results indicate a relatively high level of browsing pressure, as evidenced by a decrease in species diversity, richness, and height of shrubs across the landscape, as well as altered species composition in the presence of ungulate herbivory. This amount of high use, signifies that shrubs are an important upland forage resource for ungulate species in our study area. The impacts of ungulate herbivory on shrub layers and deciduous tree species have been well studied, especially in areas of high deer abundance in the eastern United States. Deer over-abundance has spurred studies for the past several decades (Rooney 2001, Côté et al. 2004, Kribell et al. 2011), where researchers found changes in stand composition due to the suppression of existing shrubs and a lack of regeneration owing to herbivory, thereby altering forest stand age gradients, diversity, and species composition. Others have found that native and introduced ungulate species decline understory woody vegetation and shrubs across an array of temperate and boreal forest landscapes (Bernes et al. 2018). Congruent with these studies, we found that the presence of herbivores altered the composition of shrub layers. Other studies in the western United States have examined the ecological impacts of ungulate herbivory (Wisdom 2006, Vavra et al. 2007, Stewart et al. 2009, Endress 2016) in which they looked at individual species responses, aboveground biomass, and the potential for invasion from non-native species. In this study we integrated the entire shrub community into our research including shrub species with different growth forms and palatability. By incorporating the entire shrub layer, we would expect to see differences in the responses of individual species to herbivory and fuels reduction treatment. For instance, species of varying preferences are expected to react differently in the presence of ungulate grazing (Freker et al. 2013). Indeed, we found that *Symphoricarpos albus* and *Spiraea betulifolia* had higher frequencies in control areas with ungulates compared to the other treatments. In fact, *Symphoricarpos albus* displayed a positive correlation with herbivory, implying that it may have a competitive advantage in areas exposed to ungulates compared to the other species that were measured. This pattern did not hold up in fuels treated areas, which may be due to an intolerance of fire, fewer available species for forage, or other abiotic factors.

Despite variations in individual responses, approximately 10% of the total species observed were lost in the presence of ungulates. Ungulate herbivory can remove palatable species to such a degree, that less palatable shrub species are then more highly targeted (Freker et al. 2013). Consistent with these findings, the NMS ordination indicated that all but one species had a negative correlation with herbivory, meaning that the vast majority of shrubs increased abundance in the absence of ungulates. Interestingly, less preferred subshrub species (*Arctostaphylos uva-ursi, Mahonia repens, Paxistima myrsinites,* and *Vaccinium scoparium;* Hayes and Garrison 1960) showed some of the strongest negative correlations to herbivory indicating that the subshrub layer was highly impacted by the presence of ungulates. Apart from the direct alteration caused by browsing, the presence of ungulates is known to decrease vegetation through indirect effects such as trampling and shifting site conditions (Rauzi and Smith 1973, Singer and Schoenecker 2003). The low frequencies of subshrubs found in areas with ungulates suggest that some indirect effects may be playing a role in the loss of species. Treading by ungulates can lead to soil compaction, increased bare ground, and a higher bulk density, creating less hospitable conditions for vegetative growth (Singer and Shoenecker 2003).

The scope in which all shrubs were influenced across our studied landscape reinforces the complexity in which ungulates impact ecological sites. The effects of herbivory may contribute to a loss of late season forage in these forest systems as seen by a decline in shrub frequency and height, resulting in deficiencies not only for ungulate species, but also other wildlife and vegetation. A decrease in these species may cause ungulates to migrate to alternative locations seeking food sources in the absence of shrubs, placing even more pressure elsewhere such as riparian areas and lowland meadows that are already exposed to high levels of ungulate herbivory (Kay 1994, Averett et al. 2017). These consequences can have economic impacts concerning domestic animal owners who rely on late season allotments for their cattle, landowners who see more damage due to elk and deer herbivory in their meadows, as well as stream health and riparian vegetation vigor. We are likely to observe heightened competition between wild and domestic ungulates for diminishing late season forage.

This study measured the combined browse pressure of elk, cattle, and deer and did not separate by species. Shrubs and trees constitute the diets of all three of these species, although the proportion of each diet depends on history of grazing, time of year, and other available forage (Holechek et al. 1982, Stewart et al. 2002, Findholt et al. 2004, Clark 2013). Research within northeastern Oregon exploring diet composition and resource partitioning by mule deer, elk, and cattle found that cattle predominantly consume graminoids (Holechek et al. 1982, Stewart et al., Findholt et al. 2004), but can convert to a higher proportion of shrub use after the senescence of herbaceous vegetation (Holecheck et al. 1982). Elk and deer were found consume larger proportions of shrubs and trees compared to cattle over the course of the entire year (Stewart et al. 2002, Findholt et al. 2004). However, Endress et. al (2016) found that elk and cattle both consume large amounts of *Salix scouleriana* and *Populous balsamifera*, although elk consumed a higher proportion of leaders compared to cattle (Endress et al. 2016). All three ungulate species in our study area contributed to the high browse pressure with potentially a higher percentage being consumed by elk and deer.

4.2 Fuels Reduction Treatment

Episodic disturbance such as fuels reduction treatment can facilitate the recruitment of shrub species (Irwin and Peek 1983). Indeed, this study found that *Populous balsamifera*, *Salix scouleriana*, *Arctostaphylos uva-ursi*, and *Ceanothus velutinus* had their highest frequencies in fuels treated plots, but only when ungulates were excluded. These findings are similar to other studies that found episodic disturbance can increase recruitment of species, but may also result in heavy ungulate herbivory pressure (Vavra et al. 2007, Endress et al. 2012). Fuels reduction treatment also had an effect on species beyond those that favor recruitment post disturbance (e.g., *Salix scouleriana* and *Arctostaphylos uva-ursi*). Although individual shrubs responded to fuels reduction treatment differently; overall, in areas with and without ungulates, fuels reduction treatments decreased total species richness, diversity and abundance. Fuels treated plots had approximately 20% fewer shrub species than the control areas, and lower frequencies of most species. The recovery rate for individual shrubs was influenced by the mechanical thinning and broadcast burning fuels reduction treatments applied to these forest stands, with lower mean maximum heights compared to control stands. The disparity of shrub height between plots, implies that fuels reduction treatment stands have less ideal conditions for recovery from browse and overall growth.

Under equal levels of browse, we found that the majority of shrub species are less likely to recover in areas that have undergone fuels treatment, resulting in decreased abundance, richness, diversity, and shrub height. Despite being nearly twenty years since the implementation of fuels reduction treatments on these forest stands, the understory shrub layer still maintains legacy effects. Either the studied shrub community requires a long recovery period (greater than fifteen years) after fuels treatment, or the treatment itself directionally altered the shrub composition. In either scenario, fuels reduction treatments in similar ecosystems may ultimately decrease the shrub layer by reducing shrub frequency and height compared to control plots, escalating the rate in which late season forage is lost for ungulate species. Ironically, the loss of deciduous woody species may increase woody fuel loads and increase fire risk in subsequent years by eliminating competitive interactions with conifer species and promoting conifer sapling recruitment, thus, increasing the amount of ladder fuels. However, this has yet to be evaluated.

4.3 Ungulate Herbivory and Fuels Reduction Treatments

This research found that the interaction of herbivory and fuels reduction treatments perpetuated the deterioration in species diversity and structure. Fuels reduction treated plots with ungulates had the lowest levels of diversity out of the four treatments as well as the lowest average maximum height. This highlights the potential compounding effects of each factor. Fewer species may be able to regenerate and establish when faced with fuels reduction treatment and the additive effects of herbivory, causing these areas to have a decrease in shrub biodiversity. Furthermore, individuals that are able to establish may have inhibited recovery from herbivory in areas of fuels treatment with lower heights and therefore a decreased biomass and vigor compared to individuals in untreated stands.

Forest structural elements such as down wood have been shown to protect palatable species from herbivory by acting as physical barriers that prevent access to the plant by ungulates or by providing favorable microhabitats (Gray and Spies 1997, Beschta and Ripple 2007, Gómez-Aparicio et al. 2008, Smit et al. 2012). The more robust shrub layer in control plots versus fuels treated areas may indicate that the loss of structural elements due to fuels reduction treatments may be hindering the ability of shrubs species to escape herbivory. This should be further studied in order to better understand the mechanism of shrub establishment when large portions of forested systems are undergoing fuels reduction treatment.

We found clear trends in our study site as to the effects of high use by ungulates and fuels reduction treatments on shrubs. However, responses may vary across mixed-conifer forest stands depending on site conditions, precipitation, and ungulate densities. More productive sites may be better equipped to withstand these levels of ungulate herbivory just as drier forest types, such as our research area, may be at a higher risk for slow recovery. Responses may also vary under different types of fuels reduction treatments. The scope of this study is limited to the combination of mechanical treatments and broadcast burning that was used as a fuels reduction treatment. We were unable to explore the separate effects of mechanical treatments versus broadcast burning alone. Additionally, we may have underestimated the amount of current browse. Since it is difficult to quantify browse pressure, estimates may not fully represent current use on individual plants. Sampling late in the season and not including winter browse measurements would add to the underestimate of browse that occurred over the entire year.

5. Conclusion

Our research identified fuels reduction treatments and ungulate herbivory as key factors in determining shrub composition and height within our study area. Mixed conifer forest stands with more moisture, differing site conditions and lower ungulate densities could show fewer effects of fuels treatment and herbivory on the shrub layer. This research reinforces the need to seek knowledge concerning the combined impacts of ungulates and fuels reduction treatments across the landscape within the Interior Pacific Northwest and beyond. Our results demonstrate the importance in understanding the long-term impacts of fuels reduction treatments on shrub assemblages, especially in concert with ungulate herbivory. Future studies should explore the physical, chemical, and ecological changes resulting from fuels reduction treatments and how the current levels of ungulates may influence those outcomes across different study areas. Slow recovery post fuels reduction treatment may prevent the restoration or succession of mixed conifer forest stands, thereby causing a loss of resources and altering soil composition and stability. Arrestment and low frequencies of shrubs may result in consequences that affect the amount of niche habitat and available forage to other animals in the forest system past ungulates. Shrubs are resources that are integral to forest systems and maintaining populations of these shrubs is important to an array of aspects in forest ecosystems.

Acknowledgements

We thank the U.S.D.A Forest Service Pacific Northwest Research Station for their collaboration and guidance through this research, specifically Mike Wisdom, Mary Rowland, and Bridgett Naylor. I also appreciate the hard work of the field technicians, Kent Coe, Walker Powell, Brogan Watson, Kolby Haliewicz, Tyler Dungannon, Reid Endress, Keegan Dutto and Tony Clay that were are large part of my data collection team. We thank Patricia Kennedy, Ricardo Mata-Gonzalez, and Barbara Lachenbruch for comments on previous versions of this manuscript.

Figures

Figure 2.1 Mean (± Standard Deviation) species richness and diversity (Shannon-Wiener Index H') across control and fuels treated plot (x-axis) and the absence (solid line) or presence (dashed line) of ungulate herbivory.

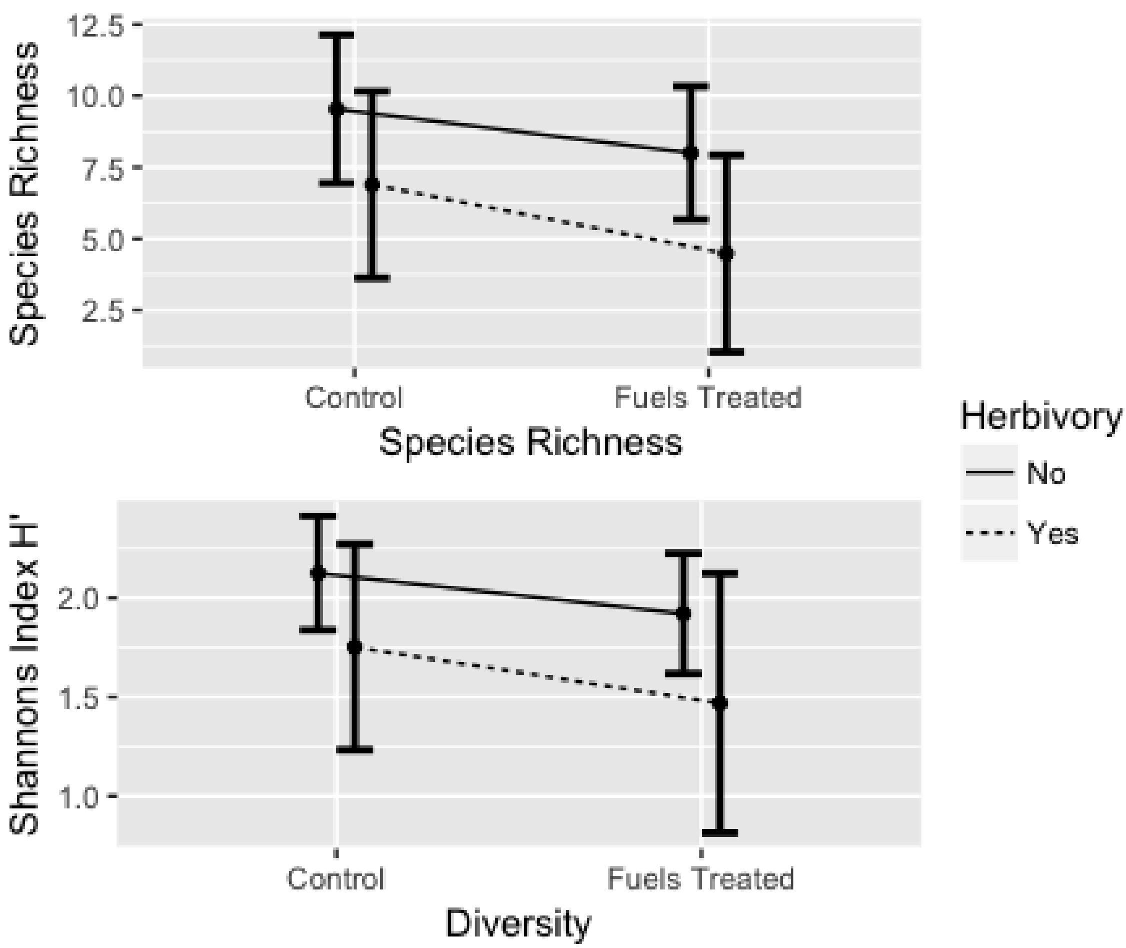


Figure 2.2 Frequencies (± 95 % conifidence intervals) for the two most abundant shrub species in each size class in all four treatments. Solid lines represent areas without ungulates, dotted lines represent areas with ungulates.

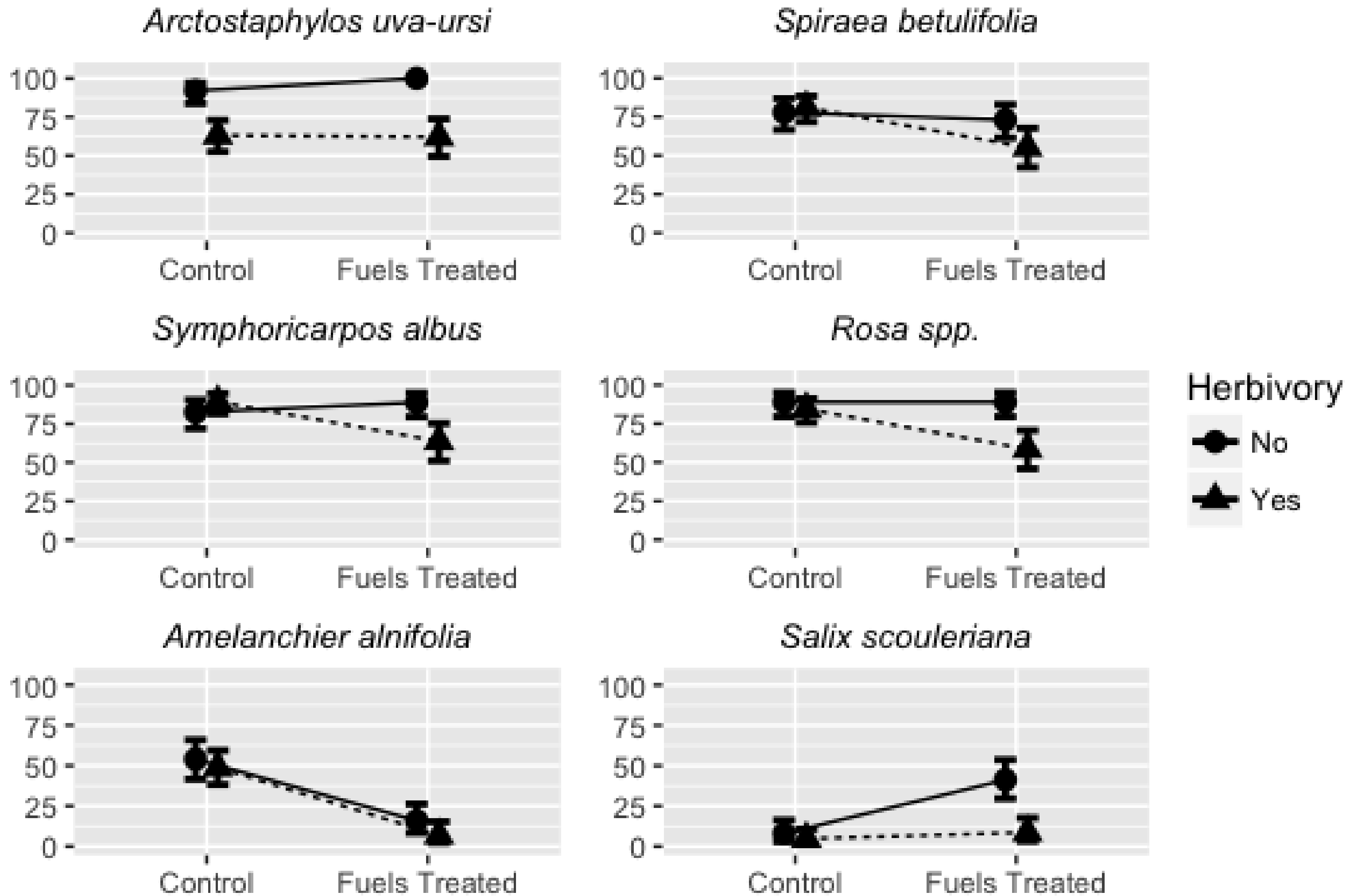


Figure 2.3 Ordination joint plot with the environmental variables overlaid. Orange points represent plots with ungulates, black points represent plots without ungulates, circles represent control plots, crosses represent treated plots. Vector length and direction indicate correlations with the ordination axes vectors with r >0.1 are shown

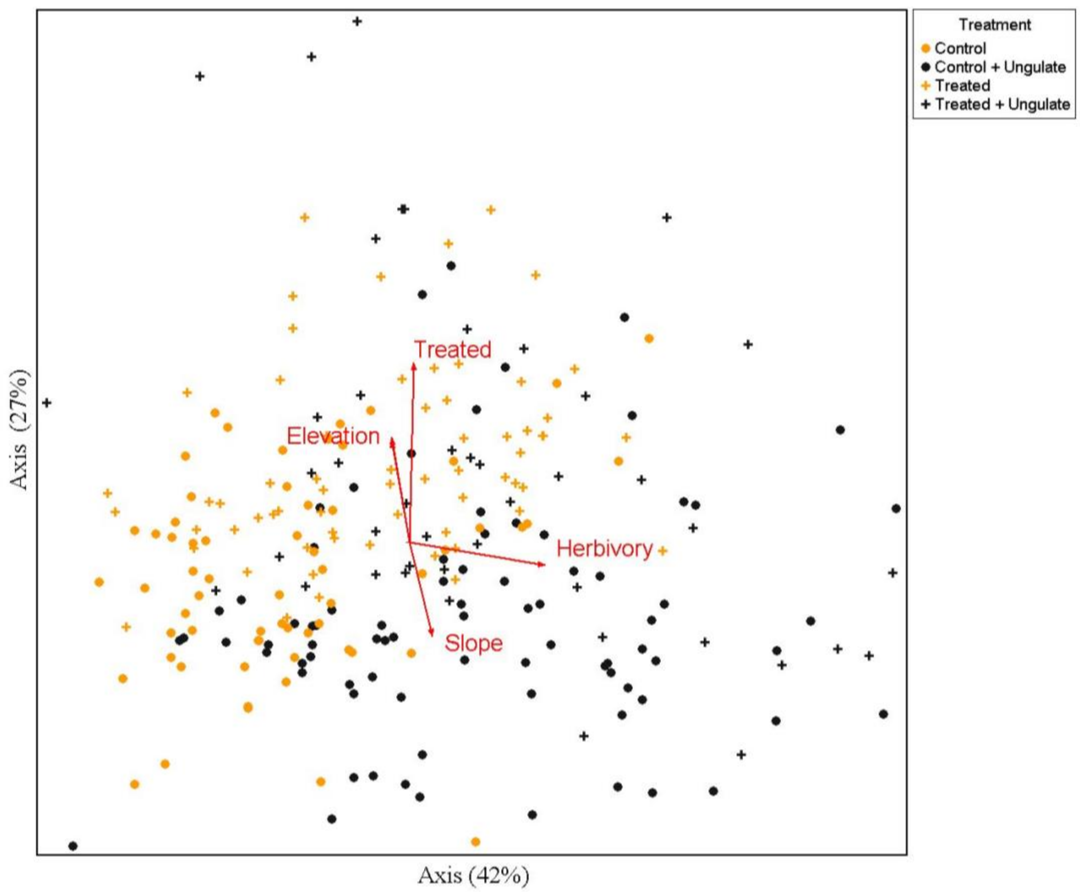
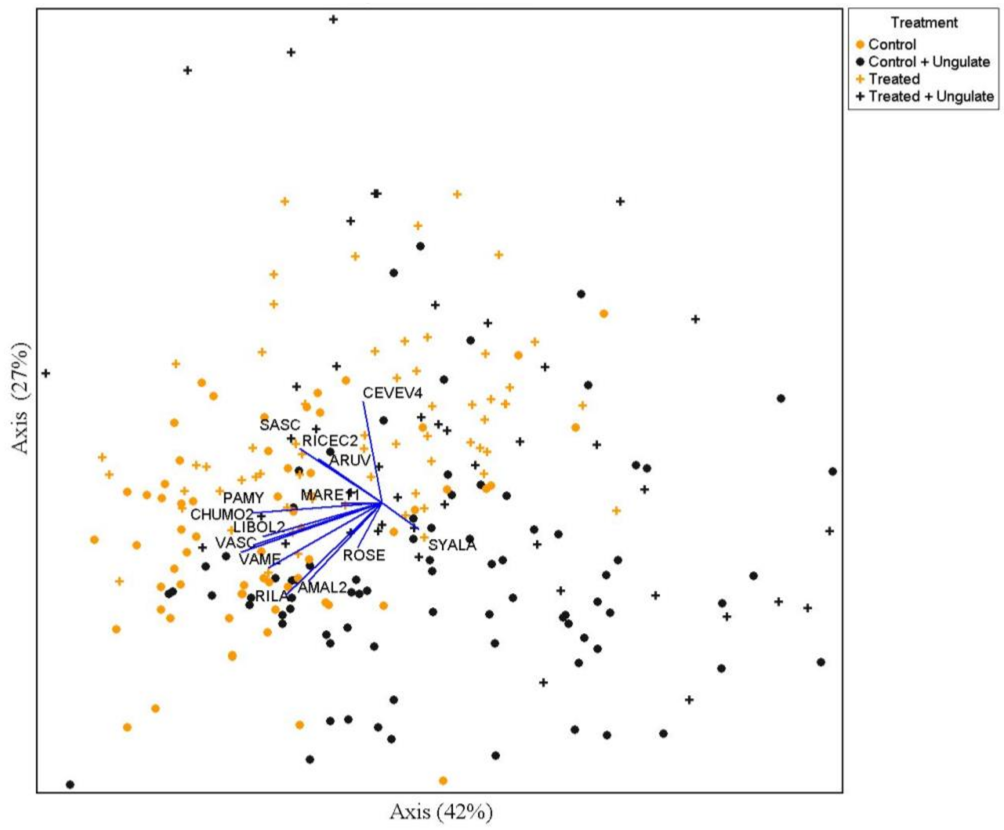


Figure 2.4 Ordination joint plot with species overlaid. Orange points represent plots with ungulates, black points represent plots without ungulates, circles represent control plots, crosses represent treated plots. Vector length and direction indicate correlations with the ordination axes. Species codes are as follows: AMAL2, *Amelanchier alnifolia;* ARUV, *Arctostaphylos uva-ursi;* CEVE4, *Ceanothus velutinus;* CHUMO2, *Chimaphila umbellate;* LIBOL2, *Linnea borealis;* MARE11, *Mahonia repens;* PAMY, *Paxistima myrsinites;* RICEC2, *Ribes cereum;* RILA, *Ribes lacustre;* ROSE, *Rosa* spp.; SASC, *Salix scouleriana*; SYALA, *Symphoricarpos albus*; VAME, *Vaccinium membranaceum;* and VASC, *Vaccinium scoparium.*



Tables

Table 2.1 Average percent of current leaders browsed for shrubs species found in fuel reduction treatments and control areas exposed to herbivory. Species are ordered from the highest average use in both treatments to the lowest. Sample sizes are next to each species.

Species	**% Leaders Browsed**			
	Fuels Treated	**SE**	**Control**	**SE**
Acer glabrum v. douglasii (3)	50	40	-	-
Populous tremuloides (2)	-	-	50	0
Salix scouleriana (40)	30	8.2	54	9.8
Rosa spp. (217)	26	2.5	36	4.3
Crategus douglasii (8)	28	13.2	-	-
Amelanchier alnifolia (89)	28	3.5	15	11.9
Symphoricarpus albus (220)	23	2.1	31	3.5
Artemisia rigida (3)	-	-	23	7.5
Holodiscus discolor (7)	30	11.5	0	-
Rubus leucodermis (10)	25	1.8	10	0
Ribes lacustre (57)	16	4.8	38	12.5
Ceanothus velutinus (56)	37	6.7	16	2.9
Physocarpus malvaceus (19)	16	5.7	-	-
Ribes viscosissium (6)	10	0	10	0
Shepherdia canadensis (4)	10	0	-	-
Ribes cereum (101)	6	2.1	4	1.6
Philadelpheus lewisii (1)	0	0	-	-

Table 2.2 Results from general linear models for the effects of fuels reduction treatments and ungulate herbivory, and their interactions on species richness, Shannon-Wiener diversity indices, and shrub height.

	Richness			
	Estimate	SE	Chi-square	*p*
Fuels treated	0.987	0.181	28.117	<0.0001
Herbivory	1.541	0.181	63.931	<0.0001
Fuels treated * Herbivory	-0.218	0.181	1.436	0.231
	Diversity			
	Estimate	SE	Chi-square	p
Fuels treated	0.174	0.035	23.844	<0.0001
Herbivory	0.290	0.035	61.465	<0.0001
Fuels treated * Herbivory	-0.088	0.035	6.352	0.012
	Height			
	Estimate	SE	Chi-square	p
Fuels treated	0.045	0.013	12.832	0.0003
Herbivory	0.138	0.013	99.271	<0.0001
Fuels treated * Herbivory	-0.030	0.013	5.852	0.016

Table 2.3 Summary of the logistic regression analyses that tested the frequency of shrubs for the top two most abundant species in each size class: subshrub (<0.5), shrub (0.5-3.0), large shrub (<3.0) against ungulate herbivory and fuels reduction treatments. Bold values indicate statistical significance.

	Arctostaphylus uva-ursi				*Spiraea betulifolia*			
	Estimate	SE	t Ratio	*p*	Estimate	SE	t Ratio	p
Fuels treated	-0.017276	0.023349	-0.74	0.46	0.0763547	0.027008	2.83	**0.0051**
Herbivory	0.1672482	0.023349	7.16	**<.0001**	0.0366721	0.027008	1.36	0.1757
Fuels treated * Herbivory	-0.022407	0.023349	-0.96	0.3381	-0.052545	0.027008	-1.95	**0.0528**
	Symphoricarpos albus				*Rosa* spp			
Fuels treated	0.0478585	0.023012	2.08	**0.0385**	0.0647578	0.023251	2.79	**0.0057**
Herbivory	0.0458744	0.023012	1.99	**0.0472**	0.0865832	0.023251	3.72	**0.0002**
Fuels treated * Herbivory	-0.079605	0.023012	-3.46	**0.0006**	-0.064758	0.023251	-2.79	**0.0057**
	Salix scouleriana				*Amelanchier alnifolia*			
Fuels treated	-0.09298	0.020181	-4.61	**<.0001**	0.2000205	0.026517	7.54	**<.0001**
Herbivory	0.0895594	0.020181	4.44	**<.0001**	0.035338	0.026517	1.33	0.1838
Fuels treated * Herbivory	-0.073686	0.020181	-3.65	**0.0003**	-0.009544	0.026517	-0.36	0.7192

Table 2.4 Species correlations with Axis 1 and Axis 2 of the NMS ordination. Axis 1 was mostly highly correlated to herbivory and Axis 2 is most correlated with fuels reduction treatment. Species are ordered from the strongest positive correlation to the strongest negative correlation for each axis.

Axis 1			Axis 2		
	r	Growth Form		r	Growth Form
Symphoricarpus albus	0.41	Shrub	*Arctostaphylus uva-ursi*	0.48	Subshrub
Ceanothus velutinus	-0.05	Shrub	*Ceanothus velutinus*	0.39	Shrub
Spiraea betulifolia	-0.07	Subshrub	*Ribes cereum*	0.20	Shrub
Salix scouleriana	-0.19	Large Shrub	*Salix scouleriana*	0.18	Large Shrub
Rosa spp.	-0.22	Shrub	*Spiraea betulifolia*	0.09	Subshrub
Ribes cereum	-0.26	Shrub	*Mahonia repens*	0.03	Subshrub
Ribes lacustre	-0.27	Shrub	*Paxistima myrsinites*	-0.05	Subshrub
Amelanchier alnifolia	-0.29	Large Shrub	*Chimaphila umbellata*	-0.11	Subshrub
Mahonia repens	-0.35	Subshrub	*Vaccinium scoparium*	-0.31	Subshrub
Paxistima myrsinites	-0.38	Subshrub	*Linnaea borealis*	-0.33	Subshrub
Chimaphila umbellata	-0.43	Subshrub	*Amelanchier alnifolia*	-0.37	Large Shrub
Arctostaphylus uva-ursi	-0.53	Subshrub	*Symphoricarpus albus*	-0.37	Shrub
Vaccinium membranaceum	-0.55	Subshrub	*Vaccinium membranaceum*	-0.37	Subshrub
Vaccinium scoparium	-0.65	Subshrub	*Ribes lacustre*	-0.38	Shrub
Linnaea borealis	-0.74	Subshrub	*Rosa* spp.	-0.42	Shrub

Table 2.5 Frequency, as a percent, of shrub species that were found in at least 10% of the plots. Frequencies are separated by treatment: fuels treatment with and without ungulate herbivory (left) and control plots with and without ungulate herbivory (right). The difference in frequency between no herbivory and herbivory is also included in each column.

	Fuels Treated			**Control**		
	No herbivory	Herbivory	Difference	No Herbivory	Herbivory	Difference
Subshrubs						
Arctostaphylus uva-ursi	100	62.1	-37.9	92.1	63.1	-29
Chimaphila umbellata	33.3	8.6	-24.7	42.9	31	-11.9
Linnaea borealis	52.4	15.5	-36.9	90.5	38.1	-52.4
Mahonia repens	84.1	43.1	-41	84.1	71.4	-12.7
Paxistima myrsinites	27	13.8	-13.2	28.6	9.5	-19
Spiraea betulifolia	73	55.2	-17.8	77.8	81	3.2
Vaccinium membranaceum	34.9	27.6	-7.3	60.3	45.2	-15.1
Vaccinium scoparium	39.7	15.5	-24.2	74.6	28.6	-46
Shrubs						
Ceanothus velutinus	44.4	25.9	-18.6	17.5	2.4	-15.1
Symphoricarpus albus	88.9	63.8	-25.1	82.5	89.3	6.7
Ribes cereum	50.8	25.9	-24.9	47.6	28.6	-19
Ribes lacustre	4.8	6.9	2.1	49.2	22.6	-26.6
Rosa spp.	88.9	58.6	-30.3	88.9	84.5	-4.4
Large Shrubs						
Amelanchier alnifolia	15.9	6.9	-9	54	48.8	-5.2
Salix scouleriana	41.3	8.6	-32.6	7.9	4.8	-3.2

Chapter 3 Forest Structural Components Influence Shrub Architecture & Height by Mediating Ungulate Herbivory

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For submission to the Journal of Plant Ecology

Abstract

Palatable shrubs are exposed to increasing disturbance pressure from ungulate herbivores and forest management practices throughout much of western North America. We aimed to assess the role of physical barriers (coarse woody debris and conifer trees) in protecting shrubs from herbivory by elk (*Cervus elaphus*), deer (*Odocoileus hemionus*) and cattle (*Bos taurus*). We measured the height and architecture type of palatable deciduous shrubs within the mixed-conifer forests in the interior Pacific Northwest, USA as well as the degree to which individual shrubs were protected by coarse woody debris and conifer trees. We sampled in areas exposed to the large herbivores as well as in ungulate exclosures where ungulate herbivory had been excluded for 5-6 years. Goodness-of-fit tests and multiple linear regressions were performed to test for relationships between the role of coarse woody debris and conifer trees and shrub height and architecture. Results showed that shrubs surrounded by coarse woody debris and trees were less likely to have arrested growth forms and that these structural elements contributed to increased growth of palatable shrubs. We also found that coarse woody debris and conifer trees within 2m of a shrub increased shrub height, with some individuals able to escape the browse zone. This research provides a deeper understanding of the importance of forest structural elements that can act as protective barriers for shrubs against ungulate herbivory. Refugia for shrubs will be an important component of maintaining shrub populations under continued levels of herbivory and other forms of disturbance.

1. Introduction

Mixed conifer forests of the interior Pacific Northwest, USA support large populations of elk, deer, and cattle. These wild and domestic ungulates forage on a wide range of graminoids, forbs, trees, and shrubs. Within these forests, many deciduous shrub species are highly palatable to ungulate herbivores and are preferred as late season forage after the senescence of herbaceous vegetation (Canon 1987, Clark 2013). However, high levels of browsing pressure over the last several decades have contributed to a decline in shrub populations across the west (Woodward et al.1994, Baker et al. 1997, White et al. 1998, Endress et al. 2012). Ungulates are important contributors not only to the decline of shrubs but also to the alteration of shrub architecture and the suppression of shrub height, which can decrease both vertical and horizontal canopy development in forests (Hester et al. 2000, Riggs et al. 2000, Beschta and Ripple 2012, Endress et al. 2016). Ungulate herbivory is a central contributor to the alteration of shrub assemblages within the interior Pacific Northwest mixed conifer forest stands (Riggs et al. 2000, Wisdom et al. 2006) by decreasing shrub height, diversity, richness, and abundance (Hall Defrees et al. in review).

A number of studies across forest ecosystems have indicated that various types of physical barriers can play a role in allowing preferred species to recruit, grow, and maintain a population in over-browsed and over-utilized systems (Banta et al. 2005, Smit et al. 2006, Smit et al. 2012). For example, in the eastern deciduous forests of North America where deer overabundance has altered shrub communities, rocky outcrops and boulders serve as refugia for woody species resulting in higher shrub abundances and diversity when protected (Banta et al. 2005). A similar result was found in wooded pastures in the subalpine forest of the Swiss Jura Mountains in Switzerland where Smit et al. (2006) found that unpalatable nurse plants decreased mortality rates of preferred species in areas of herbivory. Further research found that coarse woody debris played a significant role in the recruitment of oak saplings by providing physical protection from large herbivores ensuring the maintenance of the species within these forests (Smit et al. 2012). Each of these studies suggest that the presence of forest structural elements, or lack thereof, is an important contributor to the abundance, recruitment, and survival of palatable species exposed to high levels of herbivory by ungulates.

Maintaining shrubs in forest ecosystems is integral to supporting biodiversity, structural complexity, and habitat for birds, insects, and mammals (Hobbs 1996, Moser and Witmer 2000, Rooney 2001, Kleintjes 2007). Furthermore, many shrubs produce fruit that provide an important food source for birds and mammals (Rogers and Applegate 1983, Bairlein 2002). Arrestment of shrubs by herbivory not only contributes to a loss in structural complexity, but can also cause significant declines in fruit production (Kay 1992), affecting population dynamics and impacting the food supply and habitat of wildlife species (Beal 1915, Hobbs 1996, Rooney 2001, Moser and Witmer 2000, Kleintjes 2007, Roberson et al. 2016). Additionally, arrestment of shrubs and trees may eventually alter the stand composition of these forest ecosystems by changing environmental factors (e.g., solar radiation) in the understory and altering competitive interactions among species (Pastor et al. 1988, Woodward et al. 1994, Randall and

Walters 2011, Kribell et al. 2011).

Despite the fact that ungulates are important contributors to plant community regulation resulting in numerous cascading effects (Riggs et al. 2000, Vavra et al. 2007, Endress et al. 2012), there has been little research on the role of physical barriers in mediating herbivore pressure on shrubs and how this may affect shrub abundance, structure or size in these forest systems. Forest managers are implementing management activities that seek to reduce the amount of structural elements within the forest systems in an effort to reduce fuel loads and fire severity. Because of these efforts, examining the role of structural elements and the success of shrubs may become even more relevant. Fuels reduction treatments are now one of the most widespread and common forest management treatments throughout the region. Hall Defrees et al. (2018) found that shrub abundance, richness and height were strongly influenced by both fuels reduction activities and herbivory prompting concerns about the ability of shrubs to persist (Hall Defrees et al. 2018). If coarse woody debris or other physical barriers do protect these species from herbivory, increased fuels reduction treatments may result in a substantial loss of microhabitats (or refugia) that aid their establishment, growth, and persistence.

In this study, we assessed the structural traits of a suite of large, palatable shrub species in order to assess the relationship between the amount of protection offered by coarse woody debris, conifer trees, and other physical barriers and individual shrub architecture and height. We hypothesized that individual shrubs with a lesser degree of physical protection will have reduced height and altered shrub architecture with a large proportion of shrubs classified in an arrested state. We measured shrubs in areas exposed to cattle, elk, and deer as well as in three exclosures where ungulates have been excluded for 5-6 years in order to see how the relationship between physical barriers and shrub size/architecture varies with and without exposure to herbivory. Knowledge as to how the success of palatable shrubs relate to the physical protection offered by forest structural components may deepen our understanding of how current management practices can influence our forest ecosystems in ways that have not been highly researched thus far.

2. Methods

2.1 Study Area

Research was conducted in the Blue Mountain Ecological Province of northeast Oregon within the Starkey Experimental Forest and Range (SEFR). The forest stands of SEFR are predominantly mixed conifer forest dominated by Douglas fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*), with smaller populations of ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), Englemann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*; Franklin and Dyrness 1988). SEFR is between 1200 and 1500m in elevation and averages 510mm of annual rainfall, mostly in the form of winter snow or spring rain (Rowland et al. 1997). The 10,000-ha experiment station is representative of the montane forest types that are typical of the interior western United States (Rowland et al. 1997). As an experiment station, SEFR has maintained approximately 500 cow-calf pairs from mid-June to mid-October, 200 mule deer and 350 elk from April-November for the last 25 years (Endress et al. 2016).

Ungulate densities within SEFR for cattle (7.15/km^2), mule deer (1.95 km^2), and elk (4.55 km^2) are similar to densities found outside of the fence in surrounding areas (Wisdom and Thomas 1996).

Within the mixed conifer forests of SEFR, three (~7 hectares each) ungulate exclosures were constructed as part of the management plan in SEFR between 2001-2004 (Bally Camp, Bee Dee, and Doug Prairie). Exclosures were constructed using a 2.4-meter-tall fence that prevent elk, deer, and cattle from entering but allowed other wildlife to pass through. Between 2004-2012, these exclosures were used to conduct research on the effects of cattle and elk herbivory on forest dynamics (Endress et al. 2012, Clark 2013, Pekin et al. 2014, Endress et al. 2016). Since then, the exclosures have been maintained, and ungulates have been excluded from the sites for the past five or six years (depending on the exclosure).

2.2 Data Collection

We focused our sampling on palatable shrub species able to grow above the browse line (2.5m in height; Table 3.1). Sampling took place within mixed conifer forest stands that have not undergone any silvicultural treatments in ~50 years. We also collected data within the three upland exclosures to use as a reference for shrub growth and architecture in the absence of herbivory. Circular (7m diameter) plots were randomly placed throughout mixed-conifer forest stands using ArcGIS 10.3 to identify the random locations. Points were at least 50 m apart and at least 10 m away from the edge of each forest patch. Because the exclosures were smaller, our approach to placing sampling points differed slightly. In this case, we randomly placed 21 plots within each exclosure (≥15 m from each other and > 10 m from the edge). Sampling took place in the summers of 2016 and 2017 and we sampled 109 plots exposed to herbivory and 63 plots within the exclosures where herbivory has been excluded for 5-6 years (total N= 172).

Within each plot we recorded the presence of any of the species on our target list and then measured a series of plant attributes and physical barriers. Measurements to characterize individual shrubs included plant height and architecture type. We used architecture types described by Keigley and Frisnia (1998) and included: Arrested (chronic intense browsing), Released (browsing changed from intense to light/moderate), Retrogressed (browsing changed from light/moderate to intense), and Uninterrupted (majority of each year's stem growth is unbrowsed). We encountered a total of 284 shrubs (161 in areas exposed to herbivory and 123 within the ungulate exclosures). Prior to analysis we removed five (4 in areas exposed to herbivory, 1 in ungulate exclosures) shrubs from the data set whose heights were considered to be outliers based off of the Tukey box plots in JMP Pro 13.0 (SAS Institute, Cary, NC, USA) leaving a total of 279 shrubs for the final analysis.

We also identified and measured a series of potential structural barriers associated with each of our sampled shrubs. First, we collected data on any coarse woody debris (≥ 30cm tall) and conifer trees that were within a 2m radius of each shrub. Protocols were based on those described by Smit et al. (2012) and modified for our forest systems. Within the circle we measured the distance to the edge of all coarse woody debris and conifer trees. We then grouped distance measurements into categories

(0-50cm, 51-100cm, 101-150cm, 151-200cm, >200cm). Additional measurements included the height of any down logs or stumps, the number of coarse woody debris units and individual trees, tree species, tree DBH, and a measurement of total tree basal area within the 2m radius.

The degree to which the individual shrub was protected by coarse woody debris or trees was quantified as an estimate of encirclement based off of a 360° circle in increments of 60°. Thus, we classified the degree of protection for each shrub into six categories: 0- 60°, 61-120°, 121-180°, 181-240°, 241-300°, 301-360°. The midpoint value for each category for degrees surrounded was used for analysis. An estimate of the total amount (cumulative) of 'protection' included obstructions by both coarse woody debris and trees (both may be present surrounding a shrub). Other structural elements that could protect shrubs from herbivory other than coarse woody debris or trees (i.e., boulders) were also included in the initial data collection, but were absent or so rare (n=3) that we were unable to analyze due to small sample sizes.

We also measured the degree to which individual shrubs were embedded/covered by other vegetation (e.g., branches of conifer saplings). This foliar overlap was estimated using the following categories: 0%, 1-25%, 26-50%, 51-75%, 76-100% and was considered when portions of the shrub that were below the browse zone (2.5m), were growing in between or through the vegetation and branches of unpalatable species (e.g., *Abies grandis, Pinus ponderosa,* etc.). Topographical variables for each plot including slope, aspect, and elevation were extracted from digital elevation models (DEM) accessible through the NRCS Soil Data Viewer and ARCGIS 10.3 and were included in the multiple linear regressions.

2.3 Analysis

2.3.1 Architecture

Two goodness-of-fit tests were performed to examine if the actual distribution of shrub architecture types were significantly different than if foliar overlap and total protection did not have any effect on shrub architecture. We pooled the degrees of total protection categories (0- 60°, 61-120°, 121-180°, 181-240°, 241-300°, 301-360°) into two groups due to low sample sizes in the cells of the contingency table. To pool categories in an objective manner we conducted a classification and regression tree analysis (CART) in JMP Pro 13.0 (SAS Institute, Cary, NC, USA) to determine the best split of categories. The analysis indicated that a cutoff of 300° was the best split, so we grouped total protection into low (<300°) and high (>300°) levels of protection. Similarly, we pooled foliar overlap groups into two categories based on CART analysis and measured the differences in the proportion of individuals with different shrub architecture types without foliar overlap (0%) and shrubs with foliar overlap (1-100%).

2.3.2 Height

To explore the role of structural components in influencing shrub height, we performed a series of multiple linear regression models. Shrub height was log transformed prior to analysis to meet the assumption of normal distribution. Predictor variables were screened for correlations using nonparametric Spearman’s correlation. If two predictor variables were highly correlated (rho>0.80 and $p<0.001$), one of them was removed prior to analysis. The remaining variables included: slope, aspect, elevation, number of coarse woody debris units, percent foliar overlap, distance to coarse woody debris, mean height of course woody debris, distance to nearest tree, sum basal area of trees, coarse woody debris degrees protection (30˚, 90 ˚, 150 ˚, 210 ˚, 270 ˚, 330 ˚), and tree degrees protection (30˚, 90 ˚, 150 ˚, 210 ˚, 270 ˚, 330 ˚). Interaction terms were not included in the model. A stepwise regression was ran using backwards selection in which explanatory variables with an alpha value of >0.25 were removed. The final model was determined by using the *p*- value (alpha <0.10).

To explore differences in shrub height response in areas with and without ungulate herbivory, we ran two separate multiple linear regression models in JMP Pro 13.0 (SAS Institute, Cary, NC, USA): one on shrubs exposed to ungulate herbivory and the other on the shrubs found within the exclosures that were not exposed to herbivory. We included both models in our analysis to compare model strength. We would expect the model of shrubs not exposed to recent herbivory to explain much less of the variation in shrub height because there is no advantage of physical barriers protecting them from herbivory. Instead, we would expect other variables such as slope, aspect, and elevation to be a greater predictors of shrub height.

3. Results

3.1 Architecture

In areas exposed to herbivory, shrub architecture was heavily influenced by the amount of total protection (likelihood ratio chi-square =35.9; d.f. =3; p <0.0001). There was a 56% increase in the proportion of Arrested shrubs in areas of low protection compared to areas with high protection (> 300˚). Conversely, the proportion of Uninterrupted shrubs increased by 74% in areas of high protection compared to low protection (Table 3.2; Figure 3.1). The vast majority of shrubs (120/121=99.2%) within the exclosures were Uninterrupted with only single shrub having a Retrogressed architecture type (Figure 3.1).

Foliar overlap also influenced shrub architecture in the presence of herbivores (likelihood ratio chi-square=16.44; d.f.=3; p<0.0001). Arrested shrubs were more often associated with 0% foliar overlap than 1-100% foliar overlap (88/97=91% and 33/64=52%, respectively). Uninterrupted shrubs were nearly absent (3/97=3% of individuals) when there was no foliar overlap, while nearly 25% (16/64 individuals) were classified as Uninterrupted with any level of foliar overlap (Table 3.2; Figure 3.1). Analysis was not performed on shrubs inside the exclosures due to all but a single shrub being classified as Uninterrupted.

3.2 Height

When exposed to ungulate herbivores, total protection by coarse woody debris and trees influenced shrub height. Shrubs that had greater than or equal to 270˚ protection were much taller (median =110cm, SD = 82.47) than those with lower levels of protection, and a number of individuals (7/40=17.5%) were able to escape the browse zone and grow over 2.5m (Figure 3.2). No shrubs with less than 270˚ of protection were taller than 121 cm (median=43, SD=24.5), well below the browse line (Figure 3.2). As the amount of protection increased, shrub height increased.

The relationship between shrub height and the level of protection differed within the ungulate exclosures. Although there were differences in median heights across the categories of protection (median range = 93.5–215.5, SD range =65.5–150.5); no matter the level of protection, some shrubs within the exclosures were able to grow above the browse line (Figure 3.2). Foliar overlap did not have a clear relationship with shrub height. Shrubs grew above the browse zone under both low and high percentages of foliar overlap (Figure 3.3).

The multiple linear regression indicated that a number of physical barriers affected shrub height (R^2*adj*=0.38, p<0.001; Table 3.3) in the presence of ungulate herbivores. The final model included a number of environmental variables (aspect and elevation) as well as tree surroundedness and coarse woody debris surrounded. All variables were statically significant. Shrub height was increased with increasing protection by coarse woody debris and/or trees (Table 3.3).

The model for shrub height in the absence of herbivores explained much less of the variation (R^2 *adj*=0.17, p<0.001; Table 3.3), yet was significant. Significant predictors included slope and foliar overlap. Coarse woody debris surrounded was also included in the model but was not statistically significant (p-value =0.0538). Similar to the first model, shrub height was positively correlated with coarse woody debris surrounded and foliar overlap, but the strength of the relationship was much weaker.

4. Discussion

Our study is one of the first to explore the role of forest structural elements acting as protective barriers from ungulate herbivory within the interior Pacific Northwest, USA. Our results showed that shrubs surrounded by coarse woody debris and trees were less likely to have Arrested growth forms due to herbivory, and that these structural elements can contribute to increased growth of palatable shrubs.

Preferred shrub species are highly targeted and negatively affected by browsing to such a degree that even low densities of ungulates can prevent escape past the browse zone (Hester et al. 2000, Endress et al. 2016). Indeed, this study found that the majority of shrubs were arrested when exposed to herbivory from elk, cattle, and deer. In areas of high browse pressure, refugia can be critical in the survival and population dynamics of highly targeted plant species (Banta et al. 2005, Smit et al. 2006, Gómez-Aparicio et al. 2008). We found that shrubs with growth forms less influenced by herbivory existed only under the highest levels of protection. Small abundances of coarse woody debris or trees may not be sufficient to protect these species.

The marked differences in the height of shrubs outside of the exclosures compared to those inside of the exclosures, signifies to what extent herbivory is impacting shrub growth. Shrubs within the exclosures were able to grow above the browse line regardless of the level of protection, and have done so after just a few years of ungulates being excluded. We also found that shrub architecture was able to recover in the exclosures, with the vast majority of shrubs having Uninterrupted growth forms.

In excluded areas the overall model was weaker, though coarse woody debris protection and foliar overlap were still predictors of shrub height. There are two potential explanations for this even in the absence of ungulates. 1) Shrubs are still recovering from the legacy effects from the browsing treatments that occurred within the exclosures six years ago. 2) Coarse woody debris and foliar overlap may be creating advantageous microhabitat conditions for shrub growth by providing understory shade, nutrients through decay or increased soil moisture content (Harmon et al. 1986, Gray and Spies 1997). Regardless of the reason, coarse woody debris and foliar overlap were found to be beneficial for shrub growth. Variation is shrub height both with and without ungulate herbivory was not completely explained by our models. Other variables (i.e., plant traits, secondary metabolites, etc.), most likely also play a role in shrub height variation and should be examined in future studies.

Mammals, invertebrates, and vascular plants all benefit from the unique structural elements and nutrients offered by standing dead and coarse woody debris (Andersson and Hytteborn 1991, Bull et al. 2005, Stevenson and Rogers 2006, Bunnel and Houde 2010). Our research indicates that coarse woody debris may also be integral to the protection of stressed populations of palatable shrubs of the interior Pacific Northwest. Plants often partition resources between reproduction and vegetative growth (Bazzaz and Grace 1997), therefore when plants are defoliated by herbivory and maintained below browse level they may allocate more resources towards vegetative growth, reducing fruit production (Watson and Casper 1984). While we did not measure reproductive output, this is another important element that should be explored as an effect of herbivory. Decrease in fruit production not only contributes to a decline in the fitness of the plant but may also affect food sources for animals in the upland forests. Although browsing may not directly affect survival of established palatable woody species (Endress et al. 2016), the high levels of Arrested shrubs negatively impacts these deciduous woody species, ultimately diminishing their frequency and distribution across the landscape.

Increased occurrence and severity of fire as well as insect and disease outbreak contribute to the need for management within our forest systems (Agee and Skinner 2005, Parker et al. 2006). Currently, fuels reduction treatments are a preferred tool to prevent further loss of resources due to forest fire or disease. However, fuels reduction treatments are decreasing the amounts of coarse woody debris and conifer saplings within our forest systems, which may ultimately impact forest stand dynamics and available forage and habitat for wildlife. Managers are now maintaining patches of natural forest in their fuels reduction treatments, due to the evidence that these are of great importance to the local fauna (Tiedemann et al. 2000, Brown et al. 2004, Bull et al. 2005). Despite this, the scope in which managers need to leave coarse woody debris and other structural elements for the protection and regeneration of palatable species is poorly understood. We are currently experiencing high levels of ungulate pressure within the Pacific Northwest and witnessing declines in shrub abundance, richness, and diversity within the mixed conifer forests (Hall Defrees et al. 2018) and this research shows that higher amounts of protection offered by coarse woody debris and surrounding trees may act as a type of refugia for deciduous shrubs.

Within our study area we found that the proportion of shrubs with Arrested growth forms decreased with greater degrees of protection and foliar overlap, and that height increased with the higher levels of protection offered by nearby coarse woody debris and trees. In areas of higher productivity, shrub response may differ due to more available resources and the ability to withstand herbivory at a greater rate. Our research was conducted in relatively dry forest stands which could hinder a shrub’s ability to recover. Differing densities of ungulate herbivory could also influence these findings. Although low levels of ungulate herbivory can still have large impacts on the shrub layer, with less competition and more resources due to fewer individuals, large herbivores may spend less energy seeking out food sources that are more protected. Further research across various landscapes and with different levels of herbivory need to occur in order to fully understand the type and importance of refugia within our forested ecosystems.

5. Conclusion

Maintaining shrub populations is not only important for the biodiversity of the system, but it also provides important forage for wild and domestic livestock. Without these species, late season forage can decline and ungulates would be forced to find food elsewhere, placing pressure other systems (Averett et al. 2017). Preserving shrubs may become increasingly important as fuels reduction treatments expand across the landscape and ungulate herbivory remains high. Understanding how palatable shrubs are able to escape herbivory under these types of disturbance pressures is important as land managers make decisions into the future. Whether coarse woody debris is increasing shrub height through protection, creating favorable conditions for growth, or a combination of the two, it is positively influencing shrub growth under the conditions measured in this study and is therefore may be an important component of forest ecosystems. Retaining the diversity and population dynamics of these shrub species will be ever more essential as we continue to evolve with our land practices and decisions into the future.

Acknowledgements

We thank the U.S.D.A Forest Service Pacific Northwest Research Station for their collaboration and guidance through this research, specifically Mike Wisdom, Mary Rowland, and Bridgett Naylor. I also appreciate the hard work of the field technicians, Kent Coe, Walker Powell, Brogan Watson, Kolby Haliewicz, Tyler Dungannon, Reid Endress, Keegan Dutto and Tony Clay that were are large part of my data collection team. We thank Patricia Kennedy, Ricardo Mata-Gonzalez, and Barbara Lachenbruch for comments on previous versions of this manuscript.

Figures

Figure 3.1 Proportion of arrested, retrogressed, released, or uninterrupted shrubs with low (<300˚) and high (>300 ˚) levels of protection by coarse woody debris, trees, or other structural elements (top), and in areas with and without foliar overlap (bottom).

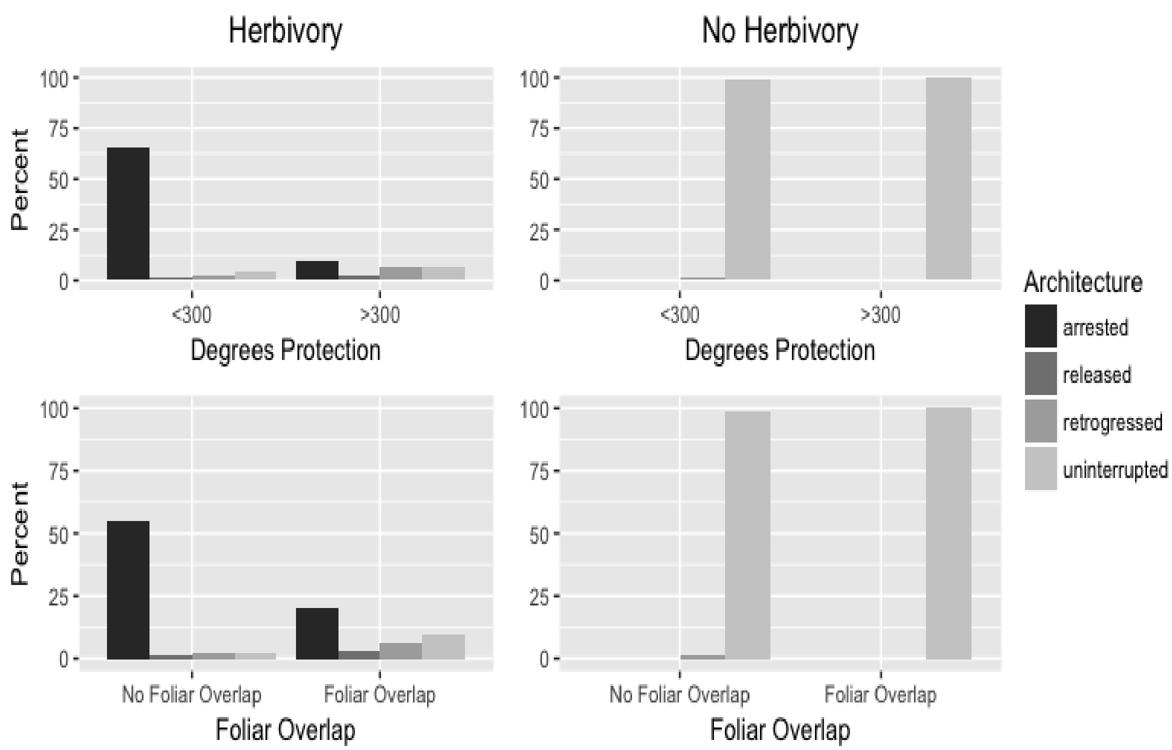


Figure 3.2 Heights of individual under different levels of protection (With Ungulate Herbivory; Left) and heights of individual shrubs within the exclosures (Right). Shapes represent what type of physical barrier that constituted the majority of the protection: Trees, open circles; Coarse woody debris and trees have equal protection, crosses; and coarse woody debris, open triangles.

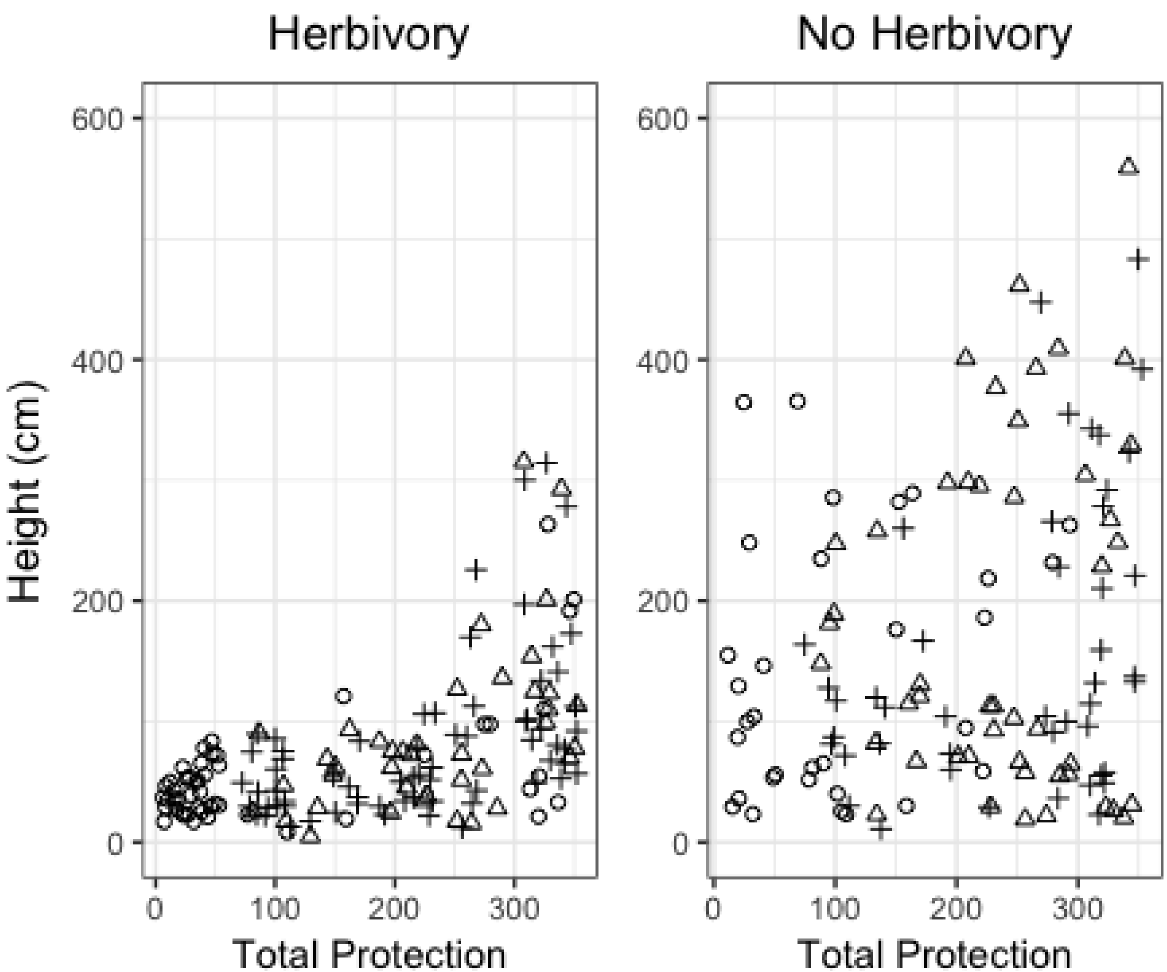
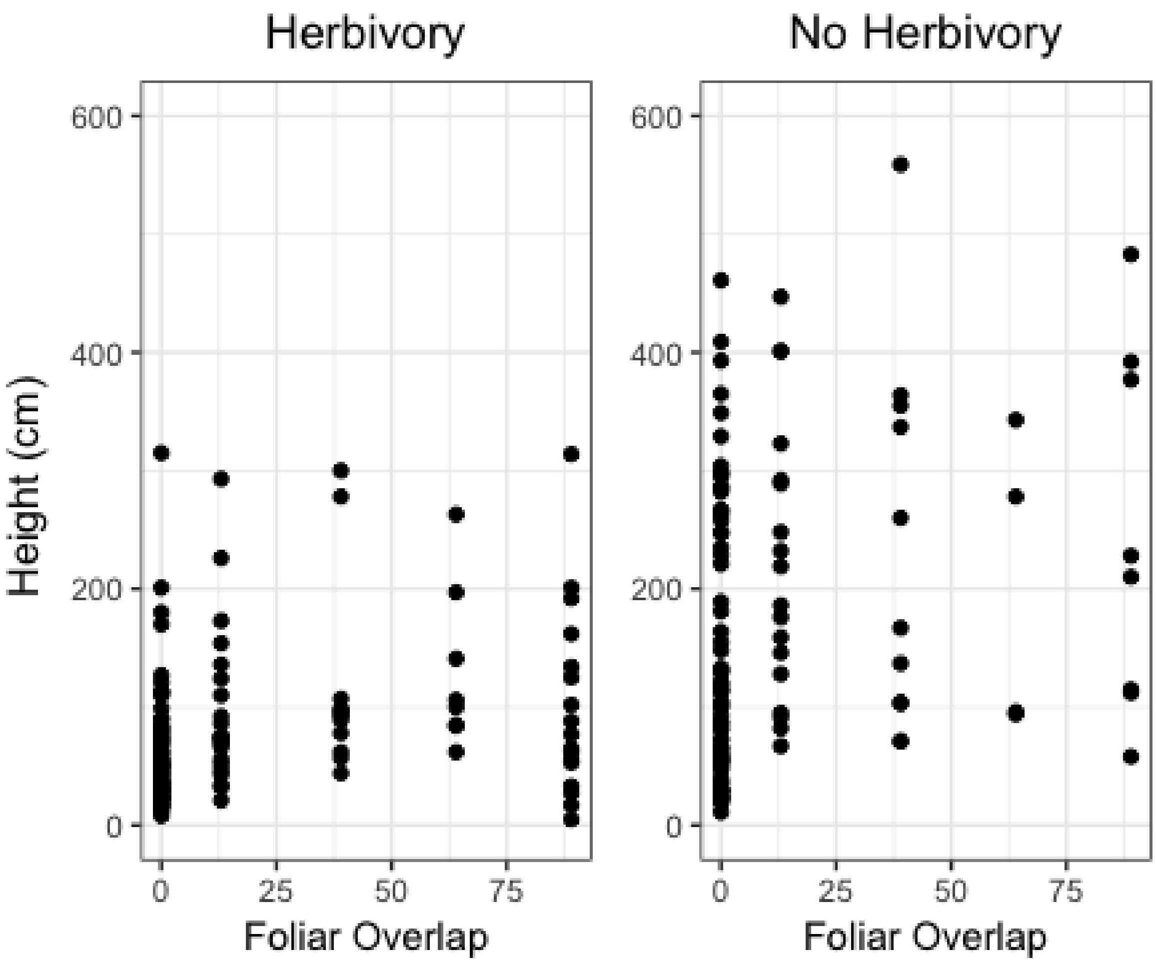


Figure 3.3 Heights of individual shrubs exposed to herbivory (Left) and heights of individual shrubs within the exclosures (Right) with different percent of foliar overlap.



Tables

Table 3.1 Shrub species included in the study.

Latin Name	Common Name
Acer glabrum v. douglasii	Rocky Mountain Maple
Alnus incana	Thin leaf Alder
Amelanchier alnifolia	Serviceberry
Cornus sericea v. sericea	Red-osier Dogwood
Crategus douglasii v. douglasii	Black Hawthorn
Holodiscus discolor	Oceanspray
Philadelpheus lewisii	Mock-Orange
Populous balsamifera	Black Cottonwood
Populous tremuloides	Quaking Aspen
Prunus virginiana	Chokecherry
Rhamnus alnifolia	Alder Buckthorn
Salix monochroma	Onecolor Willow
Salix scouleriana	Scouler's Willow
Sambucus nigra ssp. cerulea	Blue Elderberry
Sambucus racemose	Black Elderberry
Sorbus scopulina v. scopulina	Mountain Ash

Table 3.2 Percent of shrub species observed in each architecture type in areas with low (<300°) and high (>300°) levels of protection and with no foliar overlap (0%) or some foliar overlap (1-100%).

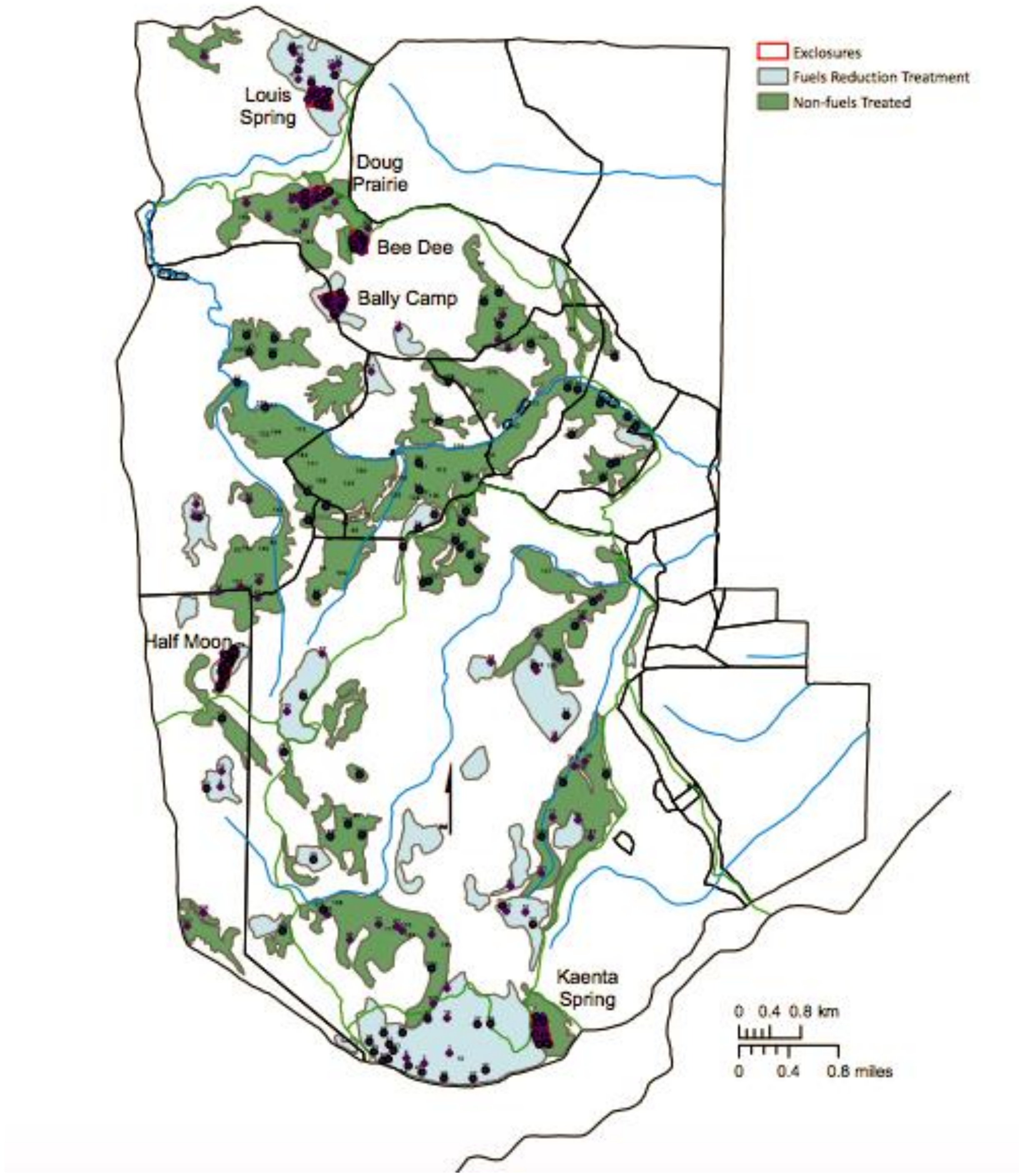
	Arrested	Retrogressed	Released	Uninterrupted
Low Protection	65.2	2.5	1.9	5.0
High Protection	9.9	6.2	2.5	6.8
No Foliar Overlap	90.7	4.1	2	3.1
Foliar Overlap	51.6	15.6	7.8	25

Table 3.3 Results of multiple linear regression models for each parameter included in the final models. Results for shrub height in areas exposed to ungulate herbivory (Extant), and the best fit model for shrub height in areas with no herbivores (Exclosure). Bold values indicate statistical significance. CWD Surrounded, Degrees protected by coarse woody debris; # CWD, the number of coarse woody debris units found within 2m of the shrub. Only significant terms are included.

Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
(A) Exposed to herbivores				
Aspect	-0.001328	0.000466	-2.85	**0.0205**
Elevation	-0.0024835	0.000553	-5.13	**<.0001**
Tree Surrounded	0.0019848	0.000535	3.71	**<.0001**
CWD Surrounded	0.0014848	0.000533	2.79	**0.0029**
(B) Herbivores excluded				
Slope	0.0994149	0.026993	3.68	**0.0004**
CWD Surrounded	0.0023556	0.000983	2.40	**0.0182**
Foliar Overlap	0.0096336	0.002952	3.26	**0.0014**

Appendix A. Supporting Figures

Map of study area including the 268 plots (purple circles) included in final analysis.



Chapter 4 Conclusion

This thesis explores the impact of herbivory and fuels treatment on shrub species of the mixed conifer forests of the interior Pacific Northwest, USA. We measured landscape wide responses of the entire shrub community to ungulate herbivory from elk (*Cervus elaphus)*, deer *(Odocoileus hemionus*), and cattle (*Bos taurus*) alone and in concert with fuels reduction treatments. We also measured individual shrub responses to immediate protection from herbivory in the form of forest structural elements. I discuss the contributions of each chapter below as well as an overall summary.

Chapter two focused on the analysis of fuels reduction treatment and ungulate herbivory on deciduous shrub assemblages. Shrub composition analysis showed differences in shrub community due to the effects of ungulate herbivory and fuels reduction treatments, as well as the combination of the two. Similar with other studies we found that ungulate herbivory decreased shrub diversity, richness, and abundance (Woodward et al.1994, Baker et al.1997, White et al. 1998, Endress et al. 2012, Freker et al. 2013, Berne et al. 2018). Individual species responses varied with pressures of herbivory and fuels reduction treatments; several shrubs reacted positively to these disturbances. Some species have a more competitive advantage against herbivores (Freker et al. 2013) and other species have high regeneration rates after disturbance such as fuels reduction treatments (Irwin and Peek 1983). However, we found that although some shrubs increased frequency under one or the other of these disturbances, the combination of the two decreased the abundances of all species and also further declined species diversity.

Chapter three results indicated that nearby coarse woody debris and conifer trees can increase shrub height and improve shrub architecture in the presence of ungulate herbivory. Shrubs surrounded by 270˚ or more by coarse woody debris or trees were taller and some individuals were able to escape the browse zone. Both coarse woody debris and trees were significant in explaining variation in shrub height, implying that both are important in providing protection. In areas of high browse pressure, refugia can be critical in the growth and survival of palatable species (Banta et al. 2005, Smit et al. 2006, Gómez-Aparicio et al. 2008). Congruent with these studies, we found that shrubs with growth forms less influenced by herbivory existed only under the highest levels of protection.

Shrubs in the absence of ungulate herbivory also showed positive correlations with shrub height and coarse woody debris protection and foliar overlap, although the model was weaker. Coarse woody debris may facilitate shrub growth by contributing to favorable growth conditions by providing nutrients and increasing soil moisture but we were not able to explore that in this research (Harmon et al. 1986, Gray and Spies 1997).

Ungulate herbivory and fuels reduction treatments are omnipresent disturbances within the forests of the interior Pacific Northwest. We found that both of these disturbances alone can have negative effects on overall shrub composition and structure. When these two disturbance occur simultaneously the negative effects can be further exacerbated with less species diversity and shorter plants. Furthermore, we found that the effects of fuels reduction treatments maintain a legacy for at least fifteen years after the application of the treatment. Either the mixed conifer forest stands are slow to recover, or these disturbances altered the forest succession.

We took a closer look at how some individual shrubs within this forest system may be able to escape the pressure of herbivory and grow above the browse zone. Shrub arrestment can have negative effects not only on the shrub itself, but also the ecosystem as a whole (Kay 1995, Hester et al. 2000, Riggs et al. 2000, Beschta and Ripple 2012, Endress et al. 2016). Coarse woody debris and conifer trees increased shrub growth and helped mitigate the pressures of ungulate herbivory. Fuels reduction treatments often remove surface and ladders fuels such as coarse woody debris and trees (Brown and others 2004, Agee and Skinner 2005, Hunter et al. 2007). The removal of these forest structural elements that can act as a physical barrier for ungulates may help explain why fuels reduction treatments have lower shrub richness, diversity, and shrub height compared to treated stands and why the shrub layer has not been able to recover for more than fifteen years.

Shrubs are important forage for ungulates especially after graminoids and forbs have senesced in late summer through winter. As fuels reduction treatments continue to increase across the landscape, we may see a loss in resources in the current level of ungulate herbivory persists. This research can help inform land managers as to how current practices are influencing the shrub assemblage. Further research needs to explore the scope in which these two disturbances as well as their interaction is influencing the shrub layer. Broadening this research over different landscapes and levels of herbivory pressure will be necessary to have a more comprehensive idea of land management and the states of our forest ecosystems.

Bibliography

Abella, S.R. and Springer, J.D., 2015. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. *Forest Ecology and Management*, *335*, pp.281-299.

Agee, J.K. and Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *Forest ecology and management*, *211*(1-2), pp.83-96.

Andersson, L.I. and Hytteborn, H., 1991. Bryophytes and decaying wood–a comparison between managed and natural forest. *Ecography*, *14*(2), pp.121-130.

Augustine, D.J. and McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *The Journal of wildlife management*, pp.1165-1183.

Averett, J.P., Endress, B.A., Rowland, M.M., Naylor, B.J. and Wisdom, M.J., 2017. Wild ungulate herbivory suppresses deciduous woody plant establishment following salmonid stream restoration. *Forest Ecology and Management*, *391*, pp.135-144.

Bairlein, F., 2002. How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds. *Naturwissenschaften*, *89*(1), pp.1-10.

Baker, W.L., Munroe, J.A. and Hessl, A.E., 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. *Ecography*, *20*(2), pp.155-165.

Banta, J.A., Royo, A.A., Kirschbaum, C. and Carson, W.P., 2005. Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of over browsing.

Bazzaz, F.A. and Grace, J. eds., 1997. *Plant resource allocation*. Academic press.

Beal, F. E. L. 1915. Food of the robins and bluebirds of the United States. Bulletin No. 171. Washington, DC: U.S. Department of Agriculture. 31 p. [24990]

Bernes, C., Macura, B., Jonsson, B.G., Junninen, K., Müller, J., Sandström, J., Lõhmus, A. and Macdonald, E., 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. *Environmental Evidence*, *7*(1), p.13.

Beschta, R.L. and Ripple, W.J., 2008. Wolves, trophic cascades, and rivers in the Olympic National Park, USA. *Ecohydrol*

Beschta, R.L. and Ripple, W.J., 2012. Berry-producing shrub characteristics following wolf reintroduction in Yellowstone National Park. *Forest Ecology and Management*, *276*, pp.132-138.

Boerner, R.E., Waldrop, T.A. and Shelburne, V.B., 2006. Wildfire mitigation strategies affect soil enzyme activity and soil organic carbon in loblolly pine (Pinus taeda) forests. *Canadian Journal of Forest Research*, *36*(12), pp.3148-3154.

Brown, R.T., Agee, J.K. and Franklin, J.F., 2004. Forest restoration and fire: principles in the context of place. *Conservation biology*, *18*(4), pp.903-912.

Bull, E.L., Clark, A.A. and Shepherd, J.F., 2005. *Short-term effects of fuel reduction on pileated woodpeckers in northeastern Oregon: a pilot study* (p. 17). US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Bunnell, F.L. and Houde, I., 2010. Down wood and biodiversity—implications to forest practices. *Environmental Reviews*, *18*(NA), pp.397-421.

Burton, T.A., Smith, S.J. and Cowley, E.R., 2011. *Multiple Indicator Monitoring (MIM) of Stream Channels and Streamside Vegetation: Technical Reference 1737-23*.

Canon, S.K., Urness, P.J. and DeByle, N.V., 1987. Habitat selection, foraging behavior, and dietary nutrition of elk in burned aspen forest. *Journal of Range Management*, pp.433-438.

Clark, A., DelCurto, T., Vavra, M. and Dick, B.L., 2013. Stocking rate and fuels reduction effects on beef cattle diet composition and quality. *Rangeland Ecology & Management*, *66*(6), pp.714-720.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C. and Waller, D.M., 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.*, *35*, pp.113-147.

Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L. and Pasteris, P., 2002. A knowledge-based approach to the statistical mapping of climate. *Climate research*, *22*(2), pp.99-113.

Endress, B.A., Wisdom, M.J., Vavra, M., Parks, C.G., Dick, B.L., Naylor, B.J. and Boyd, J.M., 2012. Effects of ungulate herbivory on aspen, cottonwood, and willow development under forest fuels treatment regimes. *Forest ecology and management*, *276*, pp.33-40.

Endress, B.A., Naylor, B.J., Pekin, B.K. and Wisdom, M.J., 2016. Aboveground and belowground mammalian herbivores regulate the demography of deciduous woody species in conifer forests. *Ecosphere*, *7*(10).

Findholt, S., Johnson, B., Damiran, D., DelCurto, T. and Kie, J., 2004. Diet composistion, dry matter intake, and diet overlap of mule deer, elk, and cattle.

Franklin, J.F., Dyrness, C.T., 1988. Natural vegetation of Oregon and Washington. Portland, Or., Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Dept. of Agriculture.

Frerker, K., Sonnier, G. and Waller, D.M., 2013. Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. *Forest Ecology and Management*, *291*, pp.55-64.

Gómez-Aparicio, L., Zamora, R., Castro, J. and Hódar, J.A., 2008. Facilitation of tree saplings by nurse plants: Microhabitat amelioration or protection against herbivores?. *Journal of Vegetation Science*, *19*(2), pp.161-172.

Gray, A.N. and Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology, 78*(8), pp.2458-2473.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R. and Lienkaemper, G.W., 1986. Ecology of coarse woody debris in temperate ecosystems. In *Advances in ecological research* (Vol. 15, pp. 133-302). Academic Press.

Hayes, D.W. and Garrison, G.A., 1960. Key to important woody plants of Eastern Oregon and Washington. *Key to important woody plants of Eastern Oregon and Washington.*

Hester, A.J., Edenius, L., Buttenschøn, R.M. and Kuiters, A.T., 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry*, *73*(4), pp.381-39

Hobbs, N.T., Baker, D.L., Bear, G.D. and Bowden, D.C., 1996. Ungulate grazing in sagebrush grassland: mechanisms of resource competition. *Ecological Applications*, *6*(1), pp.200-217.

Holechek, J.L., Vavra, M., Skovlin, J. and Krueger, W.C., 1982. Cattle diets in the blue mountains of Oregon II. Forests. *Journal of Range Management*, pp.239-242.

Holechek, J.L., Pieper, R.D. and Herbel, C.H., 1989. *Range management. Principles and practices*. Prentice-Hall.

Hunter, M.E., Shepperd, W.E., Lentile, L.B., Lundquist, J.E., Andreu, M.G., Butler, J.L., Smith, F.W., 2007. A comprehensive guide to fuels treatment practices for ponderosa pine in the Black Hills, Colorado Front Range, and Southwest.

Irwin, L.L. and Peek, J.M., 1983. Elk habitat use relative to forest succession in Idaho. *The Journal of Wildlife Management*, pp.664-672.

Johnson, C.G. and Clausnitzer, R.R., 1992. *Plant associations of the Blue and Ochoco Mountains*. US Department of Agriculture, Forest Service, Pacific Northwest Region, Wallowa- Whitman National Forest.

Johnson, C.G., 1998. *Common plants of the inland Pacific Northwest*. USDA Forest Service, Pacific Northwest Region.

Johnson, Kathleen A. 2000. Prunus virginiana. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/tree/pruvir/all.html [2016, November 10].

JMP®, Version *13*. SAS Institute Inc., Cary, NC, 1989-2007.

Kay, C.E. and Chadde, S., 1992. Reduction of willow seed production by ungulate browsing in Yellowstone National Park. In *Proceedings-Symposium on Ecology and Management of Riparian Shrub Communities. Gen. Tech. Rep. INT-289. US Forest Serv* (pp. 92-99).

Kay, C.E., 1995. Browsing by native ungulates: effects on shrub and seed production in the Greater Yellowstone Ecosystem.

Kay, C.E., 1994. The impact of native ungulates and beaver on riparian communities in the Intermountain West. *Natural Resources and Environmental Issues*, *1*(1), pp.23-43.

Keigley, R.B. and Frisina, M.R., 1998. *Browse evaluation by analysis of growth form*. Montana Fish Wildlife and Parks.

Kleintjes Neff, P.K., Fettig, S.M. and VanOverbeke, D.R., 2007. Variable response of butterflies and vegetation to elk herbivory: an exclosure experiment in ponderosa pine and aspen-mixed conifer forests. *The Southwestern Naturalist*, *52*(1), pp.1-14.

Kribel, J.R., Kolman, K.B. and Ware, S., 2011. Rapid change in sapling and seedling layers in an otherwise stable hardwood forest: an effect of deer browsing. *Castanea*, *76*(2), pp.140-148.

Long, R.A., Rachlow, J.L. and Kie, J.G., 2008. Effects of season and scale on response of elk and mule deer to habitat manipulation. *Journal of Wildlife Management*, *72*(5), pp.1133-1142.

Long, R.A., Rachlow, J.L., Kie, J.G. and Vavra, M., 2008. Fuels reduction in a western coniferous forest: effects on quantity and quality of forage for elk. *Rangeland ecology & management*, *61*(3), pp.302-313.

McCune, B., Grace, J.B. and Urban, D.L., 2002. *Analysis of ecological communities* (Vol. 28). Gleneden Beach, OR: MjM software design.

Moser, B.W. and Witmer, G.W., 2000. The effects of elk and cattle foraging on the vegetation, birds, and small mammals of the Bridge Creek Wildlife Area, Oregon. *International biodeterioration & biodegradation*, *45*(3), pp.151-157.

Parker, T.J., Clancy, K.M. and Mathiasen, R.L., 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agricultural and Forest Entomology*, *8*(3), pp.167-189.

Pastor, J., Naiman, R.J., Dewey, B. and McInnes, P., 1988. Moose, microbes, and the boreal forest. *BioScience*, *38*(11), pp.770-777.

Pekin, B.K., Wisdom, M.J., Endress, B.A., Naylor, B.J. and Parks, C.G., 2014. Ungulate browsing maintains shrub diversity in the absence of episodic disturbance in seasonally-arid conifer forest. *PloS one*, *9*(1), p.e86288.

Randall, J.A. and Walters, M.B., 2011. Deer density effects on vegetation in aspen forest understories over site productivity and stand age gradients. *Forest ecology and management*, *261*(3), pp.408-415.

Rauzi, F. and Smith, F.M., 1973. Infiltration rates: three soils with three grazing levels in northeastern Colorado. *Journal of Range Management*, pp.126-129.

Riggs, R.A., Tiedemann, A.R., Cook, J.G., Ballard, T.M., Edgerton, P.J., Vavra, M., Krueger, W.C., Hall, F.C., Bryant, L.D., Irwin, L.L. and DelCurto, T., 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. *USDA Forest Service Research Paper PNW*, *527*.

Roberson, E.J., Chips, M.J., Carson, W.P. and Rooney, T.P., 2016. Deer herbivory reduces web-building spider abundance by simplifying forest vegetation structure. *PeerJ*, *4*, p.e2538.

Rogers, Lynn L.; Applegate, Rodger D. 1983. Dispersal of fruit seeds by black bears. Journal of Mammalogy. 64(2): 310-311. [5941]

Rooney, T.P., 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry: An International Journal of Forest Research*, *74*(3), pp.201-208.

Rooney, T.P., 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecology*, *202*(1), pp.103-111.

Rowland, M.M., Bryant, L.D., Johnson, B.K., Noyes, J.H., Wisdom, M.J. and Thomas, J.W., 1997. *Starkey Project: history facilities, and data collection methods for ungulate research*. Portland, Or.: US Dept. of Agriculture, Forest Service, Pacific Northwest Research Station.

Schedule of Proposed Actions (SOPA)10/01/2016 to 12/31/2016Wallowa-Whitman National Forest [WWW Document], 2016. [WWW Document]. Schedule of Proposed Action- 10/01/2016 to 12/31/2016 - Wallowa-Whitman National Forest. URL http://www.fs.fed.us/sopa/components/reports/sopa-110616-2016-10.html (accessed 11.10.16).

Singer, F.J. and Schoenecker, K.A., 2003. Do ungulates accelerate or decelerate nitrogen cycling?. *Forest Ecology and Management*, *181*(1-2), pp.189-204.

Skovlin, J.M., 1991. Fifty years of research progress: a historical document on the Starkey Experimental Forest and Range. *Gen. Tech. Rep. PNW-GTR-266. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 54 p*, *266*.

Smit, C., Den Ouden, J.A.N. and MÜLLER-SCHÄRER, H.E.I.N.Z., 2006. Unpalatable plants facilitate tree sapling survival in wooded pastures. *Journal of Applied ecology*, *43*(2), pp.305- 312.

Smit, C., Kuijper, D.P., Prentice, D., Wassen, M.J. and Cromsigt, J.P., 2012. Coarse woody debris facilitates oak recruitment in Białowieża Primeval Forest, Poland. *Forest Ecology and Management*, *284*, pp.133-141.

Stewart, K.M., Bowyer, R.T., Kie, J., Dick, B.L. and Ben-David, M., 2003. Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche?. *Ecoscience*, *10*(3), pp.297-302.

Stewart, K.M., Bowyer, R.T., Ruess, R.W., Dick, B.L. and Kie, J.G., 2006. Herbivore optimization by North American elk: consequences for theory and management. *Wildlife Monographs*, pp.1-24.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Dick, B.L. and Ruess, R.W., 2009. Population density of North American elk: effects on plant diversity. *Oecologia*, *161*(2), pp.303-312.

Strauss, S.Y. and Agrawal, A.A., 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution*, *14*(5), pp.179-185.

Stevenson, S.K., Jull, M.J. and Rogers, B.J., 2006. Abundance and attributes of wildlife trees and coarse woody debris at three silvicultural systems study areas in the Interior Cedar-Hemlock Zone, British Columbia. *Forest ecology and management*, *233*(1), pp.176-191.

Tiedemann, A.R., Klemmedson, J.O. and Bull, E.L., 2000. Solution of forest health problems with prescribed fire: are forest productivity and wildlife at risk?. *Forest Ecology and management*, *127*(1-3), pp.1-18.

Vavra, M., Wisdom, M.J., Kie, J.G., Cook, J.G. and Riggs, R.A., 2004. The role of ungulate herbivory and management on ecosystem patterns and processes: future direction of the Starkey Project. In *Transactions of the 69th North American Wildlife and Natural Resources Conference* (pp. 785-797).

Vavra, M., Parks, C.G. and Wisdom, M.J., 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecology and Management*, *246*(1), pp.66-72.

Waller, D.M., Johnson, S.E. and Witt, J.C., 2017. A new rapid and efficient method to estimate browse impacts from twig age. *Forest Ecology and Management*, *404*, pp.361-369.

Wang, T., Hamann, A., Spittlehouse, D., and Murdock, T.N. 2012. ClimanteWNA-High-resolution spatial climate data for western North America. *Journal of Applied Meteorology and Climatology 61:16-29.*

Watson, M.A. and Casper, B.B., 1984. Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics*, *15*, pp.233-258.

Wayman, R.B. and North, M., 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. *Forest Ecology and Management*, *239*(1-3), pp.32-44.

White, C.A., Olmsted, C.E. and Kay, C.E., 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin*, pp.449-462.

Willms, J., Bartuszevige, A., Schwilk, D.W. and Kennedy, P.L., 2017. The effects of thinning and burning on understory vegetation in North America: A meta-analysis. *Forest Ecology and Management*, *392*, pp.184-194.

Wisdom, M.J., J.W. Thomas. 1996. Elk. Pages 157-181 *in* P.R. Krausman, editor. Range land wildlife. Society for Range Management, Denver, Colorado, USA.

Wisdom, M.J., Vavra, M., Boyd, J.M., Hemstrom, M.A., Ager, A.A. and Johnson, B.K., 2006. Understanding ungulate herbivory–episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. *Wildlife Society Bulletin*, *34*(2), pp.283-292.

Woodward, A., Schreiner, E.G., Houston, D.B. and Moorhead, B.B., 1994. Ungulate-forest relationships in Olympic National Park: retrospective exclosure studies. *Northwest Science*, *68*(2).

Youngblood, A., Metlen, K.L. and Coe, K., 2006. Changes in stand structure and composition after restoration treatments in low elevation dry forests of northeastern Oregon. *Forest Ecology and Management*, *234*(1-3), pp.143-163.