

University of Nevada, Reno

Succession in a post-fire world:
Bunchgrass seedling dynamics after wildfire in sagebrush steppe ecosystems

A thesis submitted in partial fulfillment of the
requirements for the degree Masters of Science in
Natural Resources

by

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prepared under our supervision by

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Bunchgrass seedling dynamics after wildfire in sagebrush steppe ecosystems**

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MASTER OF SCIENCE

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ABSTRACT:

Native plant communities experience a constant cycle of disturbance and recovery, and many disturbance regimes are expected to increase in frequency and severity with global change. Altered disturbance regimes can lead to drastic changes in plant community structure and shifts to alternate states. Ecosystem restoration plays a key role in attempting to return those communities to the appropriate successional trajectory. The Great Basin ecoregion of North America has experienced increasing frequency and size of wildfires coupled with increasing non-native annual grass establishment and widespread domestic livestock grazing. Native bunchgrasses are commonly seeded as restoration treatments after wildfire to stabilize soils and limit annual grass establishment; however, seedings often fail. Appropriate post-fire livestock management plays an essential role in increasing long-term restoration treatment efficacy.

My first chapter examined changing post-fire plant community dynamics over time in the absence of disturbance over two years on two seeded Wyoming big sagebrush sites. Plant community dynamics examined included community composition by functional group, bunchgrass spatial relationships, and factors affecting seedling bunchgrass growth and survival. Seeded functional groups increased with time, suggesting seedings were effective at altering plant community composition. Bunchgrass spatial relationships initially reflected artificial structure associated with drill seeding; however, spatial patterns shifted over time to reflect plant-plant interactions

occurring. Bunchgrass seedling growth and survival were negatively affected by increasing neighbor density, and species differed in their responses in year one but not in year two.

My second chapter examined the interaction between post-fire plant community structure and timing of initial post fire defoliation over two years on the same sites. We altered plant community structure using removal treatments, and implemented defoliation treatments starting in the first fall after fire. Seedling removal delayed senescence and decreased bunchgrass cover and density, while adult removal did not have consistent effects. Spring defoliation shortened senescence, and decreased inflorescence production, leaf production, stem length, and total bunchgrass foliar cover. Fall defoliation exhibited mixed effects; however, fall year-two defoliation exhibited fewer negative effects as compared to fall year-one. Seedling removal and spring defoliation interacted to produce the most negative effects, suggesting that defoliating when seedling density is low may be unwise.

General management recommendations include: 1) promoting bunchgrass seedling growing conditions the first year after fire, 2) avoiding spring defoliation all together and delaying fall defoliation until at least the second year after. If initial seedling density is low, delaying livestock further or implement additional restoration treatments. We acknowledge intrinsic differences across sites, and the need for informed and broad management recommendations; however, a site-specific approach is recommended rather than a one-size-fits-all strategy. Lastly, a conservative approach

to reintroducing livestock is appropriate when one is uncertain about possible negative effects on restored species.

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GENERAL INTRODUCTION

Native plant communities experience a constant cycle of disturbance and recovery, and many disturbance regimes are expected to increase in frequency and severity with global change (Spracklen et al. 2009). Altered disturbance regimes can lead to drastic changes in plant community structure and composition and possible shifts to alternate dominant species. Ecosystem restoration plays a key role in attempting to return those communities to the correct successional trajectory after disturbance and reestablishing communities resilient to future disturbances. Additionally, appropriate post-disturbance management is essential to increase the efficacy of these restoration treatments by allowing seeded species to establish and limit the establishment of non-native species.

The Great Basin ecoregion of North America has experienced drastic shifts in wildfire frequency and size. This shift coupled with increasing presence of non-native annual grasses has created a grass-fire feedback loop, leading to the loss of native sagebrush steppe communities and further increasing fire and annual grass invasion. The most common post-fire restoration technique in this region is to plant native perennial bunchgrasses to thereby stabilize soils and compete with non-native grasses; however, seedling establishment and long-term treatment efficacy is highly variable. Additionally, many of these areas are active rangelands, and land managers must decide how long to postpone livestock grazing after fire and restoration. The standard duration of livestock rest is two growing seasons or until specified management objectives are met; however, there is debate in the current literature about the most appropriate

grazing strategy and management objective. Varying post-fire restoration treatment efficacy and post-fire livestock management approaches allow for much uncertainty when providing management recommendations.

This thesis asks two main research questions: 1) what are the plant community dynamics of post-fire seeded sagebrush shrublands in the absence of domestic livestock grazing, and 2) how do post-fire plant community structure and timing of post-fire defoliation interact. My first question informs the second by examining plant interactions in the absence of additional disturbance; thereby contextualizing results observed when defoliation is implemented. I utilize field experiments on two Wyoming big sagebrush sites in the northwestern Great Basin, and focus primarily on the dynamics of planted perennial bunchgrass seedlings, as this functional group is the most frequently seeded in this system.

CHAPTER ONE: Community and spatial dynamics of seeded *Artemisia tridentata* ssp. *wyomingensis* shrublands two years after wildfire

Abstract

Restoration ecology provides an avenue for restoring ecosystem resistance and resilience after landscape level disturbances; however, restoration treatments often fail due to multiple factors. Understanding how restoration treatments affect plant community composition and structure can shed light on factors determining short- and long-term treatment success. We assessed the effects of wildfire and seeding on community characteristics (foliar cover, species diversity, species richness), within a functional group (spatial patterns of seedling and adult perennial bunchgrasses), and at the individual level (bunchgrass seedling growth and survival). Sites were located in two historic *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) communities in the northwestern Great Basin ecoregion of western North America, both of which burned and were drill seeded in 2014. Total foliar cover differed by site, year, and functional group; however, only perennial grasses, annual forbs and perennial forbs increased between years. Both sites exceeded the recommended 20% perennial bunchgrass foliar cover benchmark for reintroduction by the end of the second growing season. Species diversity and richness increased with time on both sites and richness differed by site. Spatial patterns reflected direct competitive interactions among seedlings, as well as between seedlings and adult bunchgrasses. Seedling bunchgrass

year-one growth and probability of survival to year-two differed by species and was negatively correlated with increasing neighbor density. Year-two seedling size did not differ by species but was positively correlated with year-one size and was mediated by increasing neighbor density. Our study suggests that post-fire seeding can reestablish desired species and increase species diversity and richness within two years after fire. We observed changes in bunchgrass spatial relationships over time, with seedlings becoming more dispersed from one another and adult bunchgrasses exhibiting dispersive effects on seedlings. Additionally, surrounding neighbor density was the dominant factor limiting bunchgrass seedling growth and survival in the first two years; however, grass species differed in sensitivity to neighbor density. This aspect of density dependence should be accounted for when selecting potential restoration species and monitoring treatments over time.

Keywords

Fire; spatial mapping; spatial point pattern analysis; seeding; sagebrush steppe; perennial bunchgrass; Great Basin; restoration.

Introduction:

Plant communities experience a cycle of repeated disturbance and ecosystem recovery, which results in changes in community composition and structure over time as successional processes occur. Availability of critical ecosystem services, such as wildlife

habitat, watershed health, and livestock forage, shift along with changing plant community composition (Loreau et al. 2001). Global climate change is forecasted to increase frequency and severity of large-scale disturbances, including wildfire (Spracklen et al. 2009), which may threaten the integrity of these critical processes. Resilient ecosystems have the ability to recover to pre-disturbance community structure and function, with higher levels of resilience denoting a faster return (Holling 1973). Therefore, maintaining and restoring resilient plant communities may provide an approach to coping with changing disturbance regimes and adapting to future climate scenarios (Holling 1986, Chambers et al. 2014).

Predicting plant community responses to disturbance is not as easy as summing up individual plant responses. Plant-plant interactions can be competitive, where plants are negatively affected, or facilitative, where plants are positively affected by the presence of other plants (Callaway and Walker 1997). Competition with adult plants can have negative effects on seedling emergence, survival, and performance (Aguilera and Lauenroth 1993, Callaway and Walker 1997). However, facilitative interactions may reduce abiotic stress on seedlings and increase survival in systems with harsh abiotic conditions, such as semi-arid shrublands (Bertness & Callaway 1994). Additionally, plant-plant interactions may change over time, with initial facilitative interactions shifting to competitive interactions (Bertness and Callaway 1994). These interactions affect plants' access to essential resources and therefore their ability to grow and survive; individual plant survival and reproduction over time cascades to affect plant community composition and structure (Brooker 2006).

Disturbance severity, presence of non-native species, and subsequent restoration treatments can alter post-disturbance community dynamics and successional trajectories (Bates et al. 2009, Bates and Davies 2014). For example, higher wildfire burn severity can lead to more frequent plant mortality (Boyd and Davies 2010), non-native annual species may out compete native perennial species and become dominant in the community (Balch et al. 2013), and restoration treatments may plant novel species to compete with those non-native annuals (Hobbs et al. 2009). Disturbance and non-natives may shift communities to degraded states with altered ecosystem structure and function (Hobbs et al 2009), which may directly affect restoration success (Cortina et al. 2006). Long-term seedling survival may vary by bunchgrass species and depend on annual weather, neighbor community, and disturbance frequency and intensity (Salihi and Norton 1987, Lauenroth et al. 1997, Bates et al. 2009, Mazzola et al. 2012, Bates and Davies 2014, Boyd and Lemos 2015). Post-fire management is essential to successful ecosystem restoration and utilizing established benchmarks for ecosystem recovery will facilitate success (Knutson et al. 2014). Additionally, assessing spatial patterns of vegetative communities can help to determine the effects of disturbance and competition on community structure (Rayburn and Monaco 2009).

The sagebrush steppe ecosystem of western North America has been heavily affected by the proliferation of non-native species and increasing wildfire (Billings 1994, Westerling et al. 2006, Miller et al. 2009, Balch et al. 2013). Wildfire, livestock grazing, and restoration treatments can all alter post-fire plant community composition and

structure and post-fire subsequent successional trajectories in this ecosystem (Bates et al. 2009, Bates and Davies 2014). Post-fire restoration treatments focus on reestablishing native perennial bunchgrasses to stabilize soils and prevent non-native species establishment (Pyke et al. 2013). This approach aims to bolster ecosystem resilience by attempting to direct the successional trajectory back towards pre-disturbance community structure rather than allowing it to convert to a degraded state (Palmer et al. 1997). Seeding with rangeland drills is common post-fire in the sagebrush steppe. Many seedings unfortunately fail due to low initial seedling emergence (James et al. 2011); however, once seedlings emerge, survival is typically high (James et al. 2012).

Examining plant community structure and plant-plant interactions can help to understand potential barriers to restoration success. Wildfire causes variable plant mortality, which may alter surviving bunchgrass density. Drill seeding treatments create significant soil disturbance and plant seeds in regularly spaced rows, which initially creates high densities and regular spacing of seedlings (Munkholm et al. 2003). Subsequent competitive interactions between planted seedlings and surviving adult plants will structure the plant community over time (Aguilera and Lauenroth 1993). Finally, the reintroduction of livestock grazing several years after fire is expected to further alter community structure via increased disturbance, including herbivory and trampling. Examining spatial relationships between seedling bunchgrasses and neighboring plants and factors that affect these patterns may contribute to

understanding restoration treatment success or failure in *A. tridentata* ssp. *wyomingensis* ecosystems.

In a field experiment, we examined changes in plant individuals and communities over time after wildfire and post-fire drill seeding. We expected foliar cover, species diversity, species richness, and the presence of seeded species to increase over time. We predicted initial spatial patterns to reflect the spatial structure associated with drill seeding, including high seedling density within regularly spaced drill furrows; however, these patterns would decrease over time as community interactions play out. Lastly, we expected seedling growth and survival to be negatively affected by higher density and foliar cover of neighboring plants due to increased competition for limited soil resources. These dynamics may help inform future post-fire restoration actions by allowing managers to forecast potential community composition and structure based on initial post-fire seedling emergence.

Materials and Methods

Study Areas

We examined changes in community composition and spatial relationships over the first two years after fire on two *A. tridentata* ssp. *wyomingensis* communities that burned in summer 2014 in the northwestern Great Basin. The Coleman fire (Lat/Long: 41.811614, -119.726065) was ignited by lightning on July 1, 2014. Site elevation was 1350m, had gravely loam soils, and received 270mm of annual precipitation (NRCS

2017). The Saddle Draw fire (Lat/Long: 43.359154, -118.017108) was ignited by lightning on July 13, 2014. Site elevation was 1350m, on clayey soils, and receives 280mm of annual precipitation (OSWRB 1969). Combined winter and spring precipitation for both 2015 and 2016 was at or above the 30-year normal on both sites (Fig. 1). A mix of native forbs and perennial grasses was drill seeded between October 2014 and March 2015 on both sites (Table 1). Both sites had moderate levels of permitted livestock use utilizing a spring/fall rotation schedule prior to the fires occurring.

Field Vegetation Mapping

We examined community dynamics and spatial patterns of seedling establishment on 12-1 m² plots at each field site. These plots were fenced in May 2015 to prevent future grazing disturbance and were not manipulated over the course of the study. We mapped basal and foliar cover of all plants to ± 1 cm accuracy on all plots in mid-July of 2015 and 2015 using a 1 m² quadrat with a 1 dm² grid to map (Hill 1920). All plants were identified to species, if possible. Three deep-rooted, perennial bunchgrass species were seeded, including *Elymus elymoides* (bottlebrush squirreltail), *Elymus lanceolatus* (thickspike wheatgrass), and *Pseudoroegneria spicata* (bluebunch wheatgrass). Additionally, seedlings that we could not identify at the time of mapping due to extremely small stature were recorded as unknown. Maps were scanned and digitized using ESRI ArcGIS software.

Community Composition and Species Diversity

Percent foliar cover by species was calculated for each plot during each sampling year. We grouped species into four major functional groups: 1) annual forbs, 2) annual grasses, 3) perennial forbs, and 4) perennial grasses. Shrubs were present in low densities within burned areas; however, no shrubs or trees occurred in mapped plots during the sampling period. We calculated foliar cover for each functional group present; if canopies within the same functional group overlapped in space, they were only counted once. Species diversity was calculated using the Shannon-Weiner index (H) with species richness calculated using rarefaction species curves for each plot (Shannon and Weaver 1949, Heck et al. 1975). Diversity and richness were calculated using the *diversity* and *rarefy* functions in the *vegan* package in R statistical software (Oksanen et al. 2016, R Core Team 2017).

We examined changing community composition as a function of time (year) using linear mixed models. Foliar cover was modeled as function of functional group, site, and year with all possible interactions. Species diversity and richness were modeled as functions of site and year with a site-by-year interaction, and individual plot was coded as the random effect in all models. Foliar cover data were log-transformed to account for skewness; diversity and richness did not require transformation. Mixed models were fit using the *lmer* function in the *lme4* package in R (Pinheiro and Bates 2000, Bates et al. 2015). We utilized the maximum likelihood approach for fitting models, which involves reducing possible model parameters to minimize the Akaike Information Criterion (AIC) goodness-of-fit metric (Bates et al 2015). We compared

models and tested for fixed effect significance using type-III analysis of variance (ANOVA) (Baayen et al. 2008). We tested for treatment level differences using least squares means comparisons with the *lsmeans* and *diffsmeans* functions in the *lmerTest* package in R (Kuznetsova et al. 2016).

Spatial Patterns of Seedling Establishment

We assessed spatial relationships of establishing perennial bunchgrasses using spatial point pattern analysis. The Ripley's K function examines spatial relationships across a specified range of distances by measuring the lag distance (r) from each individual to every other individual in the sampling area (Ripley 1976). These distances are summed and compared to a theoretical curve to test for spatial association (clustering), complete spatial randomness (no spatial pattern), or spatial dispersion (regularity). The Ripley's K_1 function examines the spatial pattern of a single plant species or group, while the Ripley's $K_{1,2}$ examines the effect of one species or group on the spatial pattern of another species or group (Ripley 1977). We used Ripley's K_1 to examine the spatial relationship of planted perennial bunchgrass seedlings only and Ripley's $K_{1,2}$ to examine the effect of surviving adult bunchgrasses on seedling bunchgrass spatial patterns. Inference decreases after distances surpass half the shortest distance of the sampling window (Hasse 1995); therefore, we set our maximum r at 50cm for our 1 m² sampling plots.

We extracted the spatial location of all adult and seedling bunchgrasses from plot maps using ArcGIS software. We simulated 99 runs of each model fit using Ripley's isotropic edge-correction to test the observed pattern against a 95% confidence envelope in R programming software (Ripley 1976, Hasse 1995). This edge-correction method weights individuals closer to the outside of the sampling window to account for edge effects and is the recommended correction method for isotropic point patterns with rectangular sampling windows (Haase 1995, Baddeley 1999). Ripley's K outputs are visually interpreted with no way to statistically compare patterns across sampled plots. Therefore, we summarized point patterns across all plots within each year to show the percentage of plots demonstrating spatial pattern for all given lag distances. We then visually compared summarized patterns across years to determine changes in seedling spatial relationships over time. We used the *Kest*, *Lest*, *Kcross*, *Lcross*, and *envelope* functions in the *spatstat* package in R (Baddeley et al. 2015).

Neighborhood Effects on Seedling Growth and Survival

We examined the effect of plant neighborhood on 1) end-of-season seedling size in year-one and two and 2) on the probability of seedling survival from year-one to two using mixed models. Seedling survival was determined by comparing mapped plots for both years; seedlings present in year-two in the same geographic location as year-one were considered to have survived. We calculated foliar cover extent for each seedling for both sampling years. We also calculated total foliar cover and plant density for all

plants within both a 10 and 20cm radius of each seedling to quantify surrounding plant neighborhood for each year. We calculated values for both radii as plant-plant interactions may occur at various distances based on existing community structure (Callaway and Walker 1997).

We analyzed plant neighborhood effects on seedling growth and survival using mixed model regression (Van Dongen et al. 2004). We utilized linear mixed effects models and linear regression to analyze end-of-season size (Pinheiro & Bates 2000), while seedling survival required using generalized linear mixed models and logistic regression to account for the binomial response of survival or mortality (McCulloch and Neuhaus 2001, Bolker et al. 2009). Bunchgrass species was included as a fixed effect in all models to test for interspecific differences; however, if species did not differ then that effect was dropped from the final model. Possible other fixed effects included neighbor density and foliar cover within either 10 or 20cm of the target seedling. We sampled both distances to account for potential spatial variation in interactions between individuals; consequently, only one distance was used in the final model. We also used year-one end-of-season plant size as a predictor for year-two end-of-season plant size. Plot was coded as the random effect in all models to account for variance in plant community structure across plots. Plant size data were tested for normality and log-transformed to account for skew. Mixed models were fit using the maximum likelihood approach with the *lmer* and *glmer* functions in the lme4 package in R (Pinheiro and Bates 2000, Bates et al. 2015). We tested for regression fit in mixed models using both marginal and conditional R^2 values with the *sem.model.fits* function

in the *piecewiseSEM* package in R (Lefcheck 2015). Marginal R^2 describes the proportion of variance explained by only the fixed effects, while conditional R^2 describes the proportion explained by fixed and random effects combined (Nakagawa and Schielzeth 2013, Johnson 2014). We selected final models that provided the highest marginal and conditional R^2 values for each response variable.

Results

Community Composition and Species Diversity

Foliar cover significantly differed by functional group, site, year, and all interactions (Table 2). Total foliar cover significantly increased from year-one to two on both sites; however, total foliar cover at the Coleman fire was significantly higher than at the Saddle Draw fire in year-two (Fig. 2). Perennial bunchgrass cover significantly increased at both sites over time; annual and perennial forb cover increased over time on the Coleman fire (Fig. 2). Annual grass cover did not significantly increase over time at either site (Fig. 2). The difference in total foliar cover between sites in year-two is explained by the significantly higher annual forb cover at the Coleman fire (Fig. 2).

Species diversity differed by year only, while species richness differed by site and year (Table 3). Diversity and richness increased significantly from year-one to year-two at both fires (Fig. 3A & B). The Coleman fire exhibited higher species richness than the Saddle Draw fire in both years (Fig. 3B).

Spatial Patterns of Seedling Establishment

Seedlings exhibited high levels of spatial attraction in year-one with two defined peaks; however, that pattern became muted and peaks shifted in year-two (Fig. 4A). Approximately 80% and 40% of plots exhibited spatial attraction at 8cm and 40cm, respectively, in year-one. These distances represent clusters of seedlings within the same furrow and of seedlings spacing across adjacent drill furrows, respectively. This pattern shifted to approximately 30 and 20% of plots exhibiting spatial attraction at 17cm and 40cm, respectively, in year-two. This shift from 8cm to 17cm represents a loss of clustered seedlings within the same furrow resulting in larger observed lag distances. The 40cm peak decreased in magnitude but did not shift lag distances in year-two, which represents a decrease in ability to detect seedlings across drill furrows.

Adult bunchgrasses exhibited mixed attractive and dispersive effects on seedlings in year-one; however, the dispersive effect on seedlings became more pronounced by year-two (Fig. 4B). Approximately 20% of plots exhibited both attractive and dispersive effects of adults on seedlings at various lag distances in year-one, showing no consistent spatial pattern. This represents the combined natural and artificial structure of seeded communities. Adult location is a function of pre-fire community structure while seedlings location is a function of regularly spaced drill furrows. Dispersive patterns became more pronounced in year-two with approximately 25% of plots exhibiting spatial dispersion with peaks at 14, 30 and 40cm. This shift represents seedling mortality over the first two years, with the closest 14cm distance likely due to competitive interactions between adults and seedlings.

Neighborhood Effects on Seedling Growth and Survival

Year-one end-of-season seedling size differed by species and was negatively correlated with increasing neighbor density within 10cm with these variables explaining 22% of the variance in year-one seedling size (Table 4). All species exhibited decreased growth in response to increasing neighbor density with unidentified seedlings exhibiting significantly lower end-of-season sizes but *Elymus elymoides*, *E. lanceolatus*, and *P. spicata* not differing from one another (Fig 5). Unidentified seedlings exhibited small size across all neighbor densities, which was the main reason that we were unable to accurately identify them.

Seedling survival to year-two differed by species in relation to year-one neighbor density within 10cm (Table 5). Neighbor density explained 46% of the variance in survival, and the top fitting GLMM model had a scale parameter of 0.9788, suggesting the model was not over dispersed (Bolker et al. 2009). *Elymus lanceolatus* exhibited high survival and little sensitivity to increased neighbor density, while *E. elymoides* and *P. spicata* exhibited sharply negative responses to increased neighbor density (Fig. 6). Unidentified seedlings exhibited generally low survival across all neighbor densities (Fig. 6).

Year-two end-of-season seedling size was positively correlated with year-one end-of-season seedling size and displayed an interaction between year-one size and year-two neighbor density within 10cm (Table 6). Year-two size did not vary by species

and was therefore not included in the final model. The top fitting model explained 15% of the variance in year-two size. Year-two size increased with year-one size when year-two neighbor densities were low (0-5); however, high neighbor density (>10) led to decreasing year-two size despite larger year-one sizes (Fig. 7).

Discussion

We found that total foliar cover, perennial bunchgrass foliar cover, species diversity, and species richness all increased with time, which supports restoration goals of reestablishing a diverse and functional plant community. Post-fire seed mixes often include seed from multiple functional groups with the goal of reestablishing diverse communities to support wildlife and livestock forage. Mean perennial bunchgrass foliar cover at both sites exceeded the 20% recommended benchmark for reintroduction of livestock grazing by the end of the second growing season. This suggests that two growing seasons may be suitable in some situations to reestablish a robust native perennial bunchgrasses community on a post-fire seeding with good initial seedling emergence. Perennial forbs remained a minor component of the community through the second year after fire, despite several perennial forb species being included in the seed mix for each site.

Site differences emphasize geographic variation across post-fire restoration treatments within the same dominant plant community. Total foliar cover did not differ across sites in year-one; however the Coleman fire expressed higher total foliar cover in

year-two. Species diversity across sites did not differ while the Coleman fire expressed higher species richness across both years. The only functional group that differed between sites was annual forb cover on the Coleman fire in year-two with *Descurainia pinnata*, *Lepidium perfoliatum*, and *L. lasiocarpum* all readily present. These species often colonize burned areas in sagebrush steppe and can lead to the exclusion of restoration species; however, we still observed suitable establishment of planted species. It is common that annual grass cover is low the first year and expands the second year after fire due to increased resource availability (Young and Evans 1978, Condon et al. 2011); however, annual grass cover did not increase significantly across years despite *Bromus tectorum* (cheatgrass) being present on both sites. Additionally, direct competition with annual forbs and perennial grasses at the Coleman fire may have limited growth for perennial forbs in the second year. Species selection for seed mixes and potential additional restoration actions need to account for this variability in community composition across sites.

Spatial relationships among seedlings only were pronounced in year-one but decreased over time as seedling mortality occurred. Seedling clusters within drill furrows and spacing across drill furrows were easily detectable during the first year. Within-furrow clustering shifted to larger lag distances with less magnitude in year-two, suggesting that seedling competitive interactions have an effect in structuring the community at small spatial scales. This shift was expected as direct competition for limited light and soil resources is intense within densely crowded drill furrows. The attractive peaks at 9 and 17cm for year-one and two, respectively, suggests that these

are the distances below which seedling direct competitive interactions are occurring. Bunchgrasses require more resources as they grow in size; therefore, the radius around each adult where competitive interactions occur should also increase with the size of the plant (Aguilera and Lauenroth 1993). Overcrowding is caused by high seeding rates and high levels of seedling emergence, suggesting that lower seeding rates for perennial bunchgrasses in this situation may reduce within furrow competition and subsequent seedling mortality. Examining seedling density in the context of variable seeding rates may ultimately achieve the same final seedling density with less seed required. Additionally, local adaptation can increase seedling emergence, growth, survival, and reproduction rates across variable precipitation regimes (Joshi et al 2001, Hufford et al. 2008, Rice and Knapp 2008), so using utilizing locally collected seed may further reduce the amount of seed required.

Adult bunchgrass effects on seedlings displayed both attractive and dispersive patterns in year-one but shifted to a more pronounced dispersive pattern in year-two. The initial mixed spatial pattern reflects the artificial community structure associated with post-fire restoration treatments. Drill seeding treatments plant bunchgrass seedlings in regularly spaced furrows, while adults are located based on pre-fire community structure with some mortality due to fire. The dispersive pattern displayed in year-two due is a result of direct competitive interactions between adult and seedling bunchgrasses leading to seedling mortality. The dispersive peak for seedlings within 15cm of adults in year-two suggests that direct competitive interactions leading to seedling mortality occurred within this radius. As with seedlings, the radius around each

adult where competitive interactions occur should also increase with the size of the plant (Aguilera and Lauenroth 1993); however, seedlings will also become more competitive with adults as they grow, and interactions may lead to less frequent seedling mortality. Similar to seedling overcrowding within drill furrows, high densities of adults may lead to high levels of mortality in seedlings. Seeding rates are often high to account for potential variation in adult bunchgrass mortality due to fire; however, reducing seeding rates may be appropriate if adult survival is expected to be high. We expect the move towards a more dispersive spatial pattern between adult and seedling bunchgrasses to continue over time, as Rayburn and Monaco (2009) observed a similar shift towards regular spacing in mature bunchgrasses in the absence of disturbance.

We found that neighbor density was the dominant factor that predicted year-one end-of-season seedling size and probability of survival to year-two. Year-one end-of-season was the strongest predictor for year-two end-of-season size; however, neighbor density mediated year-two growth, with increasing neighbor density leading to smaller year-two seedling size. Species differed in year-one end-of-season size, with all three seeded species exhibited similar response to increasing neighbor density and unidentified seedling exhibiting significantly smaller sizes. This negative response to increasing neighbor density across species suggests that crowding might increase direct competition for resources and results in less year-one growth. Species also differed in probability of survival to year-two, with *E. elymoides* and *P. spicata* having a very similar negative response to increasing neighbor density. This is contrasted with *E. lanceolatus*, where increased neighbor density displayed virtually no effect on survival, and

unidentified seedlings which had low survival rates overall. Seedling survival is critical to successful restoration; therefore, utilizing species that do not exhibit density dependence may be more appropriate. Species did not differ in year-two end-of-season size, with growth strongly influenced by year-one size but mediated by increasing neighbor density. Larger seedlings in year-one produced larger seedlings in year-two, suggesting that year-one end-of-season size may be critical to achieving a robust bunchgrass community two year after fire.

Intraspecific differences in seedling growth and survival are important considerations when selecting and applying restoration materials. Planting the same species that were present prior to the fire occurring will restore pre-fire ecological structure and function, but those species also need to be competitive with non-native species. *Elymus elymoides* and *P. spicata* were present on both sites prior to fire and are therefore appropriate to use; however, the negative effect of increasing neighbor density on the probability of these species' survival to year-two may present a challenge when sites become heavily invaded. *Elymus lanceolatus* was not present on either site prior to fire; yet, it was more tolerant to neighbor density for across-season survival, suggesting the potential competitive ability to allocate more resources to root production and survive overcrowding (Rowe and Leger 2011). Additionally, seed sourced from locally-adapted populations can increase bunchgrass seedling emergence, growth, survival, and reproduction rates across variable precipitation regimes (Joshi et al 2001, Hufford et al. 2008, Rice and Knapp 2008). Seeding rates are often high in pounds of pure live seed per acre, with the rationale that more seed may lead to higher density of

established bunchgrasses in the context of uncertain future weather. However, increased seeding rates do not always lead to increased bunchgrass density (Launchbaugh and Owensby 1969). Therefore, utilizing locally-adapted native seed in future restoration treatments may require less seed to achieve the same desired community structure and function.

Conclusion

Post-fire restoration on our field sites appears to have been effective in restoring community diversity and structure after the first two growing seasons. Perennial bunchgrass foliar cover increased and surpassed the 20% foliar cover benchmark for livestock reintroduction by the end of the second growing season. Despite this, we do not yet know how resilient these seedlings are to grazing. We recommend a conservative approach to reintroducing livestock on seeded sites as to not inadvertently cause seeding failure. Additionally, assessing year-one end-of-season seedling size and plant community density may provide managers a tool to assess potential bunchgrass growth into year-two and whether suitable forage will be available to reintroducing livestock that year. If year-one growth is slow, any potential disturbance should be avoided. Overall, species diversity and richness increased without non-native annual grasses dominating either site. Non-native annual forbs were highly present on the Coleman fire, which appears to have suppressed seeded perennial forb cover but had no effect on perennial bunchgrass cover. Sites with higher non-native annual cover likely

warrant a different approach to post-fire management and additional restoration actions should be considered, if necessary.

Spatial analysis demonstrated that competitive interactions affected the location of establishing seedlings. High densities of seedlings within drill furrows led to seedling mortality and an increase in within furrow spacing by year-two. Adult-seedling interactions also led to seedling mortality within a specified radius of influence. Individual seedling growth and survival was most impacted by neighbor density; however, responses differed by species. Overcrowding led to more direct competition for resources and subsequently lower end-of-season seedling size and generally lower probability of survival. The eventual reintroduction of livestock grazing and other future management decisions will likely change community and spatial dynamics on these sites. Therefore, longer-term observation will be required to determine continued change in community composition and spatial structure. Bunchgrass species exhibited differences in response to increasing neighbor density in the first year after fire. *Elymus elymoides* and *P. spicata* exhibited larger end of season sizes, with *E. lanceolatus* exhibiting higher probability of survival to year-two. Interspecific differences disappeared by the second year, with year-one end-of-season size positively affecting and increasing neighbor density negatively affecting year-two seedling size. These differences warrant consideration when selecting and applying potential restoration materials in order to achieve the desired restoration outcome.

Our results must be considered in the context of above average cumulative winter and spring precipitation for both years one and two. This pattern allowed for

longer growing seasons due to sustained soil moisture, which may have contributed to higher initial seedling establishment, larger end-of-season size, and higher probability of survival. Seeding failure is often attributed to lack of suitable winter precipitation; however, seedlings must also be able to withstand potential short growing seasons and intense competition with non-natives. Therefore, future restoration materials testing should examine seedling emergence, growth, and survival in the context of variable precipitation regimes and pre-existing cover of non-natives.

Post-fire restoration seeding treatments in *A. tridentata* ssp. *wyomingensis* communities are implemented with the goals of increasing ecosystem resistance and resilience by reestablishing preferred species and limiting non-native annual grass invasion. This goal appears to have been achieved on both of our research sites, supporting the ability to achieve the goal of native species restoration in this system within two years after wildfire. By assessing dynamics at variable scales, we were able to examine factors affecting individual seedlings and scale that upward to explain post-fire community trends. We acknowledge the large amount of variability in pre-fire plant communities, soil, annual weather patterns, non-native species pressure, and land management approaches across the region; therefore, careful consideration should be taken when planning and implementing restoration actions. Successful restoration implementation will lead to the ability of these systems to better handle inevitable future disturbance and forecasted climate change in the region (Dalglish et al. 2011).

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Tables

Table 2. Seeded native species mixes. Species with * represent locally collected accessions. Seeding rates were not available.

Coleman Fire (northwest Nevada)	Saddle Draw Fire (southeast Oregon)
<u>Perennial Bunchgrasses:</u> <i>Elymus elymoides</i> (bottlebrush squirreltail) <i>Elymus lanceolatus</i> (thickspike wheatgrass) <i>Poa canbyi</i> (Canby's bluegrass) <i>Pseudoroegneria spicata</i> (bluebunch wheatgrass)	<u>Perennial Bunchgrasses:</u> <i>Pseudoroegneria spicata</i> (bluebunch wheatgrass) * <i>Elymus elymoides</i> (bottlebrush squirreltail) * <i>Leymus cinereus</i> (basin wildrye) <i>Poa secunda</i> (Sandberg's bluegrass) * <i>Pseudoroegneria spicata</i> (bluebunch wheatgrass) *
<u>Perennial Forbs:</u> <i>Medicago sativa</i> (Ladak alfalfa) <i>Linum lewisii</i> (Lewis flax)	<u>Perennial Forbs:</u> <i>Chaenactis douglasii</i> (Douglas dustymaiden) <i>Eriogonum heracleoides</i> (Wyeths buckwheat) <i>Sphaeralcea munroana</i> (Munroes globemallow)

Table 3. ANOVA for foliar cover by functional group, site, and year. *Bold values were statically significant at $\alpha = 0.05$ and italicized values were significant at $\alpha = 0.10$.*

Effect	df	Foliar Cover	
		<i>F</i>	<i>P</i>
Functional Group	3, 191	40.6	< 0.001
Site	1, 191	12.6	< 0.001
Year	1, 191	89.8	< 0.001
Site x Year	1, 191	2.5	<i>0.056</i>
Functional Group x Site	3, 191	11.8	< 0.001
Functional Group x Year	3, 191	11.0	0.001
Functional Group x Site x Year	3, 191	2.3	<i>0.077</i>

Table 4. ANOVA for species diversity (Shannon's H), and species richness by site and year. *Bold values were statically significant at $\alpha = 0.05$.*

Effect	df	Species Diversity		Species Richness	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Site	1, 24	1.4	0.253	9.8	0.004
Year	1, 24	30.1	< 0.001	44.7	< 0.001
Site x Year	1, 24	0.9	0.894	0.6	0.445

Table 4. Regression results for year one end-of-season seedling size. Values represent coefficient estimates with standard error in parentheses. *Bold values were statically significant at $\alpha = 0.05$ and italicized values were significant at $\alpha = 0.10$.*

	<i>Estimate (SE)</i>
Intercept	-7.25 (0.31)
Species: <i>Elymus elymoides</i>	-0.38 (0.33)
Species: <i>Pseudoregnaria spicata</i>	0.12 (0.220)
Species: Unknown	-1.09 (0.24)
Neighbor Density w/in 10cm	-0.20 (0.05)
Conditional R ²	0.436
Marginal R ²	0.120

Table 5. Regression results for seedling survival to year two. Values represent coefficient estimates with standard error in parentheses. *Bold values were statistically significant at $\alpha = 0.05$ and italicized values were significant at $\alpha = 0.10$.*

	<i>Estimate (SE)</i>
Intercept	0.31 (0.47)
Species: <i>Elymus elymoides</i>	-0.38 (0.33)
Species: <i>Pseudoregnaria spicata</i>	0.12 (0.220)
Species: Unknown	-1.09 (0.24)
Neighbor Density w/in 10cm	-0.20 (0.05)
Marginal R ²	0.621
Conditional R ²	0.507

Table 6. Regression results for year two seedling end-of-season size. Values represent coefficient estimates with standard error in parentheses. Bold values were statistically significant at $\alpha = 0.05$ and italicized values were significant at $\alpha = 0.10$.

	<i>Estimate (SE)</i>
Intercept	0.007 (0.003)
Year One Plant Size	2.91 (0.64)
Year Two Neighbor Density	-0.00001 (0.0004)
Plant Size x Neighbor Density	-.35 (0.20)
Conditional R ²	0.291
Marginal R ²	0.150

Figures

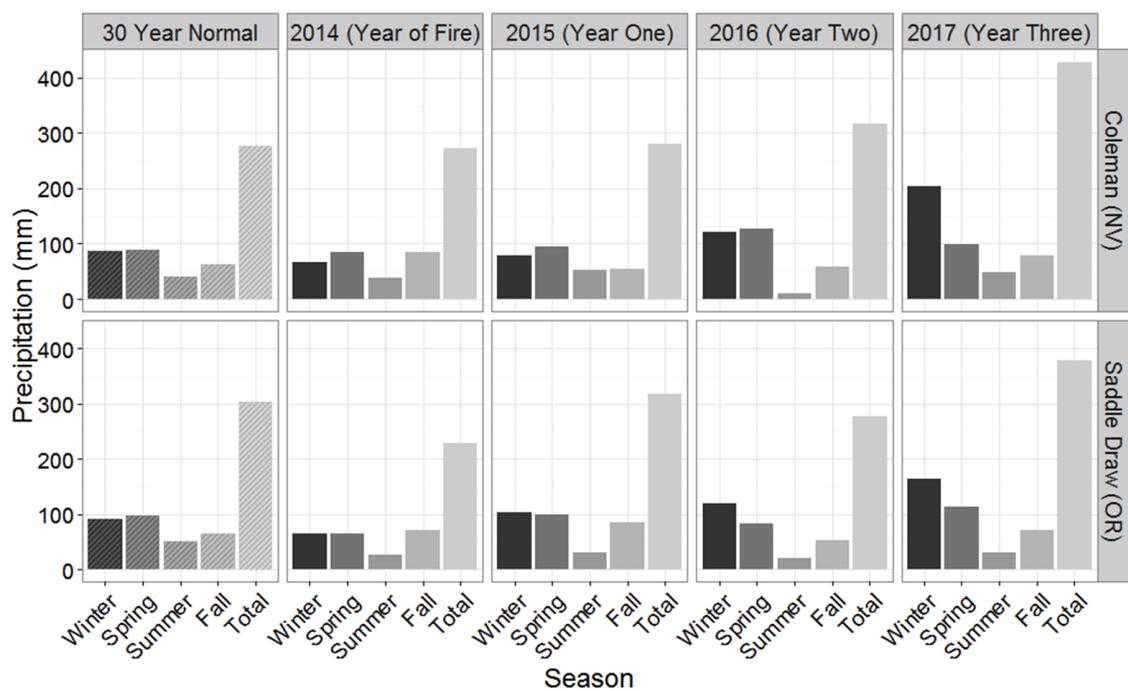


Figure 1. Precipitation for the Coleman (NV) and Saddle Draw (OR) fires (PRISM 2004). Seasons are winter (December of prior year – February), spring (March – May), summer (June – August), and fall (September – November).

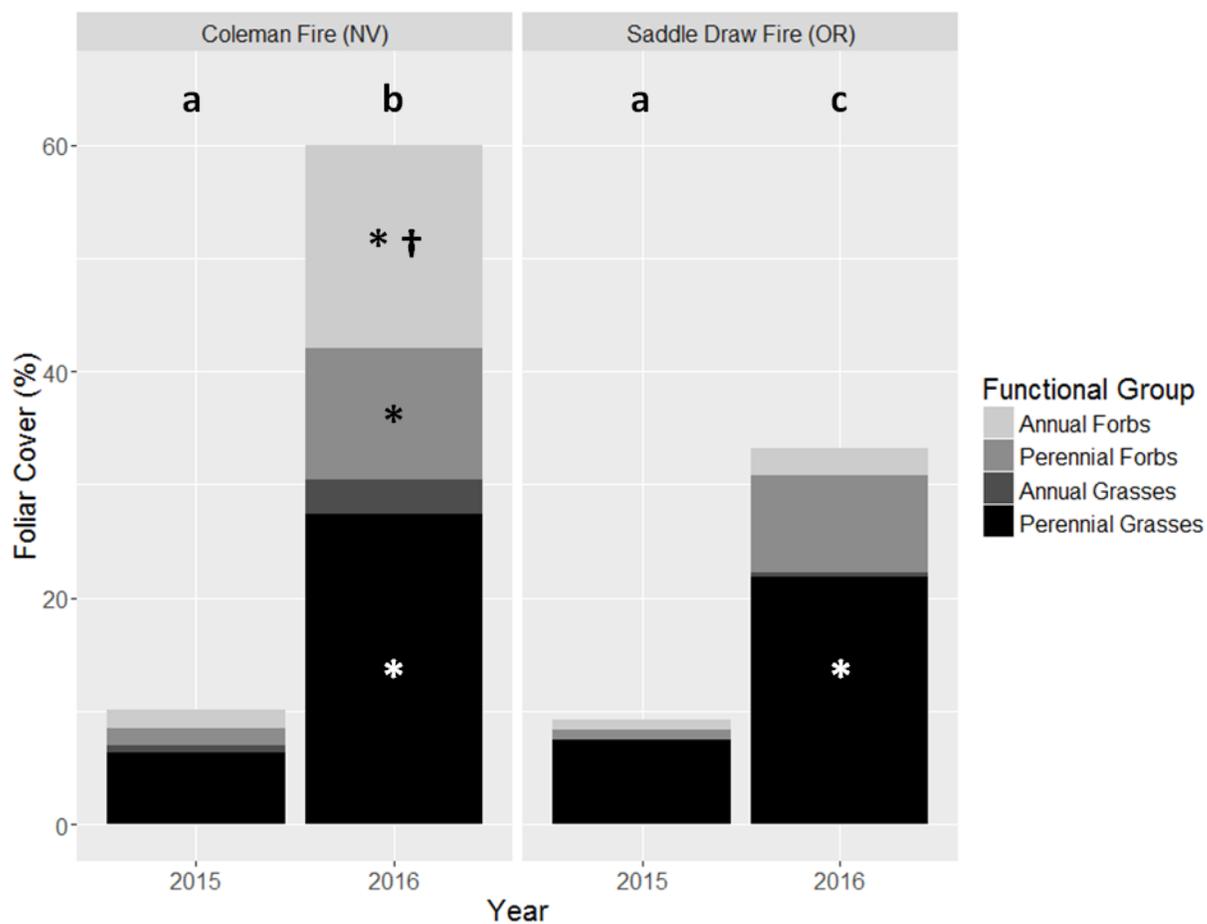


Figure 2. Mean foliar cover by functional group, site, and year. All functional groups summed represent total foliar cover. Letters represent statistically significantly different groups for total foliar cover among years and sites, * represent significant differences for a particular functional group within site across years for a particular functional group within site, and † represent significant differences for a particular functional group across sites within year. All comparisons are statistically significant at $\alpha = 0.05$. Symbols are only shown on the group with a higher mean but represent the appropriately paired group.

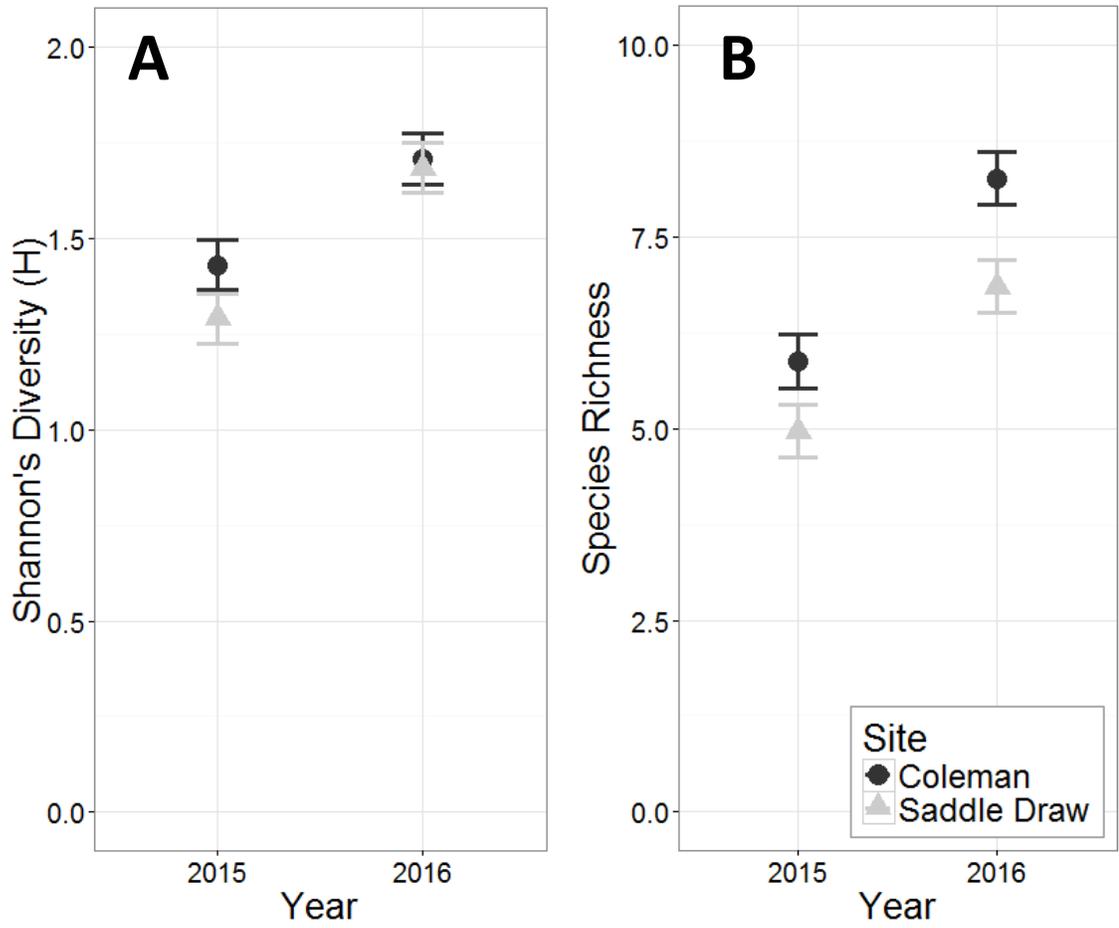


Figure 3. A) Shannon's diversity and B) species richness by site and year. Points represent fitted model estimates with standard errors.

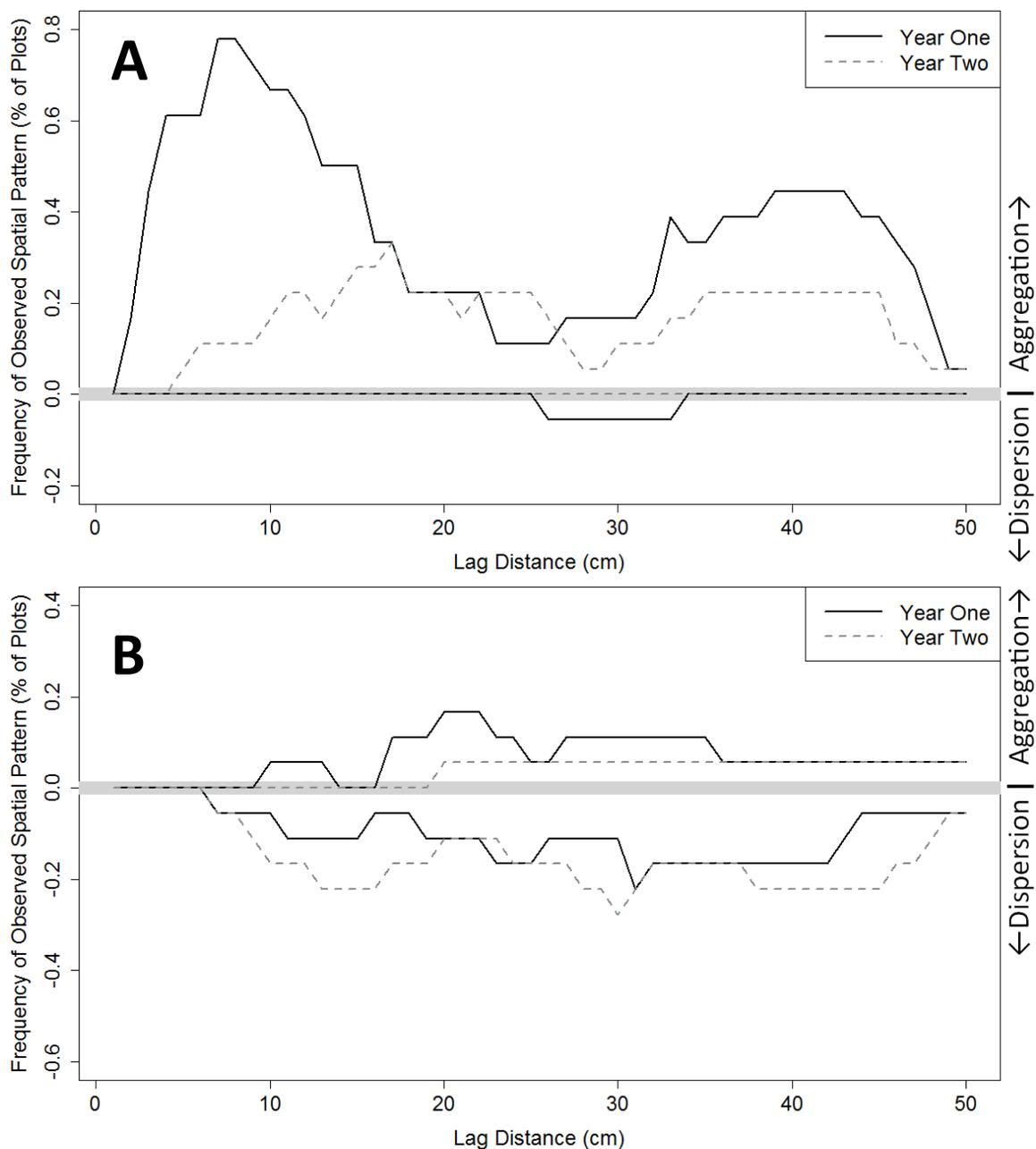


Figure 4. Percentage of plots exhibiting spatial patterns by lag distance in year one and year two for A) seedling bunchgrasses only, and B) adult effects on seedlings. Positive values signify spatial aggregation, negative values signify spatial dispersion for any given lag distance, and values of 0 signify complete spatial randomness for a given lag distance. If both positive and negative values are exhibited at a particular lag distance, the combination represents a ratio of spatial aggregation to dispersion for that lag distance.

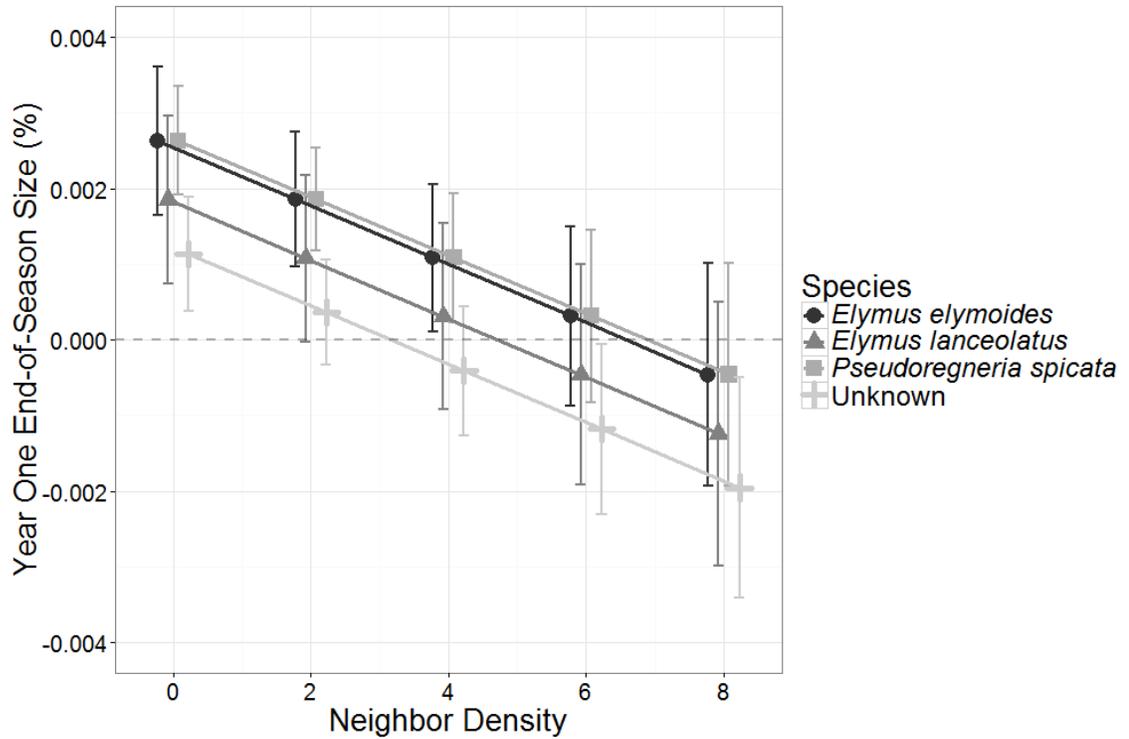


Figure 5. Year one end-of-season seedling size in percent cover by species as a function of neighborhood density within 10cm of seedling. Points represent fitted model estimates and error bars represent 95% confidence intervals.

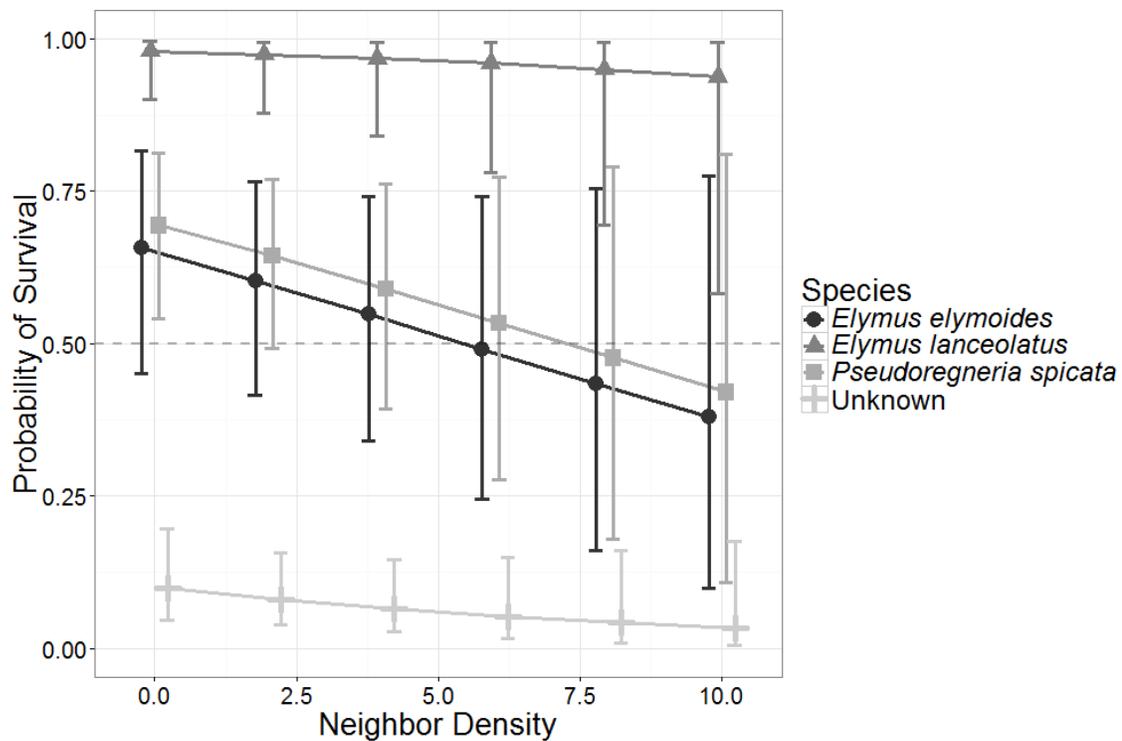


Figure 6. Probability of seedling survival from year one to year two by species as a function of neighborhood density within 10cm of seedling. Points represent fitted model estimates and error bars represent 95% confidence intervals.

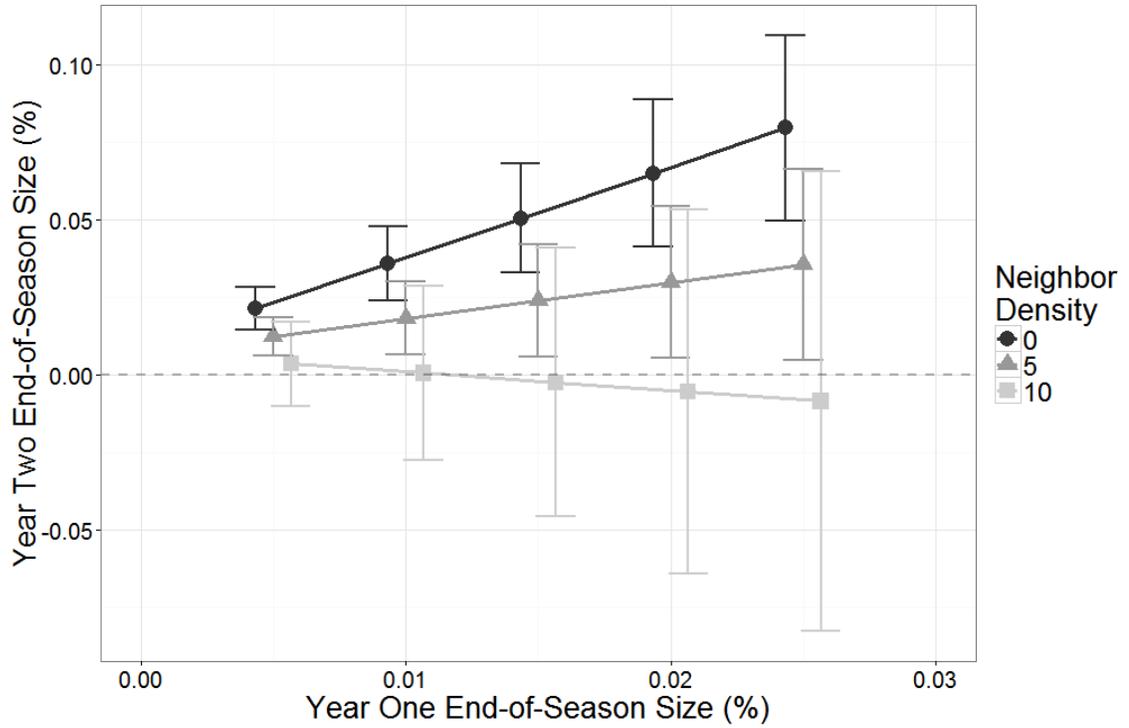


Figure 7. Year two end-of-season seedling size by species as a function of year one end-of-season size and year two neighbor density within 10cm. Points represent fitted model estimates and error bars represent 95% confidence intervals.

CHAPTER TWO: Effects of neighboring plants and defoliation on perennial bunchgrass seedlings after fire in sagebrush communities.

Abstract

Native perennial bunchgrass species are often seeded after wildfire in the Great Basin to stabilize soils and resist invasive species establishment. Domestic livestock grazing is typically postponed for two growing-seasons to allow for seedling establishment. Seeding failures may occur due to unsuitable abiotic conditions or inappropriate post-fire grazing management leading to seedling mortality. We explored how neighboring plant communities and post-fire defoliation affected the efficacy of post-fire seeding treatments in *Artemisia tridentata* ssp. *wyomingensis* communities. We implemented plant removal treatments at the beginning of the first growing-season to vary the relative density of adult and seedling perennial bunchgrasses. Spring and fall defoliation treatments were used to simulate livestock grazing and examine the appropriate time to reintroduce livestock after fire. We repeatedly sampled perennial seedling tiller timing of senescence, leaf and inflorescence production, and stem length during the first three growing-seasons to quantify plant-level responses. We also sampled end-of-season perennial bunchgrass plant density and foliar cover for the first three years to quantify treatment effects on community structure. Fall and spring defoliation within seedling removal hastened senescence following defoliation, while spring defoliation decreased leaf production, stem length, and inflorescence production.

Adult and seedling removal both decreased plant density and foliar cover in the first year after fire. Foliar cover with adult removal recovered as compared to neighbor removal controls by the second year, while seedling removal cover and density remained reduced in through the duration of the study. Seedling mortality did not differ by treatment, and none of our treatments reached the recommended benchmark for livestock reintroduction of 20% bunchgrass foliar cover after three growing-seasons. Our results suggest that post-fire plant community structure affects restoration efficacy, and that spring and fall defoliation differ in their effects on seedling perennial bunchgrasses. We suggest a conservative approach to reintroducing livestock after wildfire and restoration, especially if initial seedling establishment is low or growing-season rainfall is below average. Additionally, we suggest assessing livestock reintroduction foliar cover benchmarks by site rather than utilizing a regional standard of 20%.

Keywords

Post-fire; restoration; growth; survival; Great Basin; semi-arid; rangeland; neighborhood; defoliation

Introduction

Native ecosystems face constant pressure from shifting natural and anthropogenic disturbance regimes, which threaten ecosystem structure and function, wildlife habitat, and economic land uses (Bunting 1985, Billings 1994). Restoration treatments seek to return disturbed ecosystems to pre-disturbance structure and function; however, many barriers present challenges to achieving treatment success. Treatment failure is often attributed to high initial disturbance severity, low post-disturbance precipitation, and high non-native species pressure (Arkle et al. 2014). Once initial seedling establishment is determined, the post-restoration disturbance regime can affect long-term treatment efficacy. Examining how this disturbance regime interacts with restoration treatments may inform decision-making and improve the likelihood of success for future restoration treatments.

Wildfires in North America's Intermountain West have increased in size and frequency in recent decades (NIFC 2014), due to changing climate, historical land use, and the proliferation of non-native species (Billings 1994, Westerling et al. 2006, Miller et al. 2009, Balch et al. 2013). This pattern is particularly evident in the sagebrush steppe ecosystem, where a positive feedback cycle with wildfire and invasive annual grasses has led to landscape-level community shifts and habitat degradation across half of the ecosystem's historic extent (Whisenant 1990, Billings 1994, Miller et al. 2011, Balch et al. 2013). *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) is not fire-adapted and native perennial bunchgrasses are often seeded after wildfire to stabilize soils and resist invasive species establishment (Pyke et al 2013, Chambers et al

2014a, Knutson et al. 2014). Unfortunately, long-term treatment success is variable, and seeding treatments may fail due to unsuitable abiotic conditions limiting initial seedling establishment or severe post-fire disturbance leading to seedling mortality (Pyke et al. 2013, Arkle et al. 2014, Knutson et al. 2014).

Post-fire plant community structure may vary based on pre-fire condition, burn severity, and rehabilitation treatment (Taylor & Skinner 2003, Boyd et al. 2015). Degraded pre-fire communities may have low perennial bunchgrass density, leading to low post-fire bunchgrass density. Increasing burn severity can increase native species mortality, leading to variable post-fire plant density (Boyd et al. 2015). Post-fire seeding treatments are applied at different times and with variable seeding rates and seeded species. Seedling establishment, growth, and survival may be affected by abiotic (soil, climate, slope, and aspect) and biotic (neighboring community, soil microbial community, and herbivory) factors. Plant-plant interactions have been shown to affect seedling establishment by modifying abiotic stressors, such as soil water availability and solar radiation exposure (Callaway and Walker 1997). Competition between seedlings and surviving adults for limited resources may affect seedling growth and survival (Callaway and Walker 1997); in contrast, surviving adults may facilitate seedling establishment by ameliorating harsh environmental conditions (Bertness & Callaway 1994). Variable bunchgrass plant community structure may have implications for post-fire seeding treatment efficacy (Boyd and Svejcar 2011).

The concepts of ecosystem resistance and resilience are helpful in understanding *A. tridentata ssp. wyomingensis* community response to wildfire (Chambers et al.

2014a). Resistance denotes an ecosystem's ability to limit invasive species establishment (D'Antonio & Thomsen 2004); resilience denotes an ecosystem's inherent ability to recover to pre-disturbance structure and function (Holling 1973). *Artemisia tridentata ssp. wyomingensis* communities have intrinsically low resistance and resilience levels and are highly prone to invasion by non-native annual grasses (Chambers et al. 2007). Post-fire communities with higher abundance of native perennial bunchgrasses can stabilize soils, resist annual grass invasion, and facilitate subsequent sagebrush reestablishment faster than sites without this functional group (Condon et al. 2013, Pyke et al. 2013, Chambers et al. 2014b). In contrast, degraded communities can shift to annual grass dominated systems, which burn as frequently as five years on average (Balch et al. 2013). Restoring degraded sagebrush ecosystems is therefore important to reestablishing resilient communities across the region.

Domestic livestock grazing is an important economic land use in the Great Basin, and land managers make an effort to reintroduce livestock in a timely manner after wildfire. Perennial bunchgrasses require time to recover to pre-fire conditions (Knutson et al. 2014), and improper domestic livestock grazing can be detrimental to recovering plant communities after fire (Pellant et al. 2004). Effects of livestock grazing on semi-arid rangelands vary based on frequency, intensity, and seasonality of grazing (Jones 2000) and can alter plant community composition, ecosystem structure, and plant productivity (Fleischner 1994, Bunting et al. 1998, West and Yorks 2002, Roselle et al. 2010). Growing-season defoliation can decrease bunchgrass growth, recruitment, and long-term survival (Olsen and Richards 1988a and 1988b, Zhang and Romo 1995);

however, moderate dormant-season grazing may have limited effects (Bates and Davies 2014, Vermiere et al. 2014). Livestock grazing is typically postponed for two growing seasons after wildfire to allow for plant species recovery (BLM 2007); however, there is little research addressing the effects of timing of post-fire livestock grazing on seedling perennial bunchgrasses planted in post-fire restoration treatments. Bunchgrass seedlings are less resilient to grazing as compared to adult bunchgrasses (Bates et al. 2009), and resuming livestock grazing prematurely may lead to seedling mortality and overall seeding failure. Land managers are moving toward using management benchmarks for livestock reintroduction (3 perennial bunchgrasses / m² or 20% perennial bunchgrass foliar cover), which may represent ecologically appropriate metrics of plant community recovery. However, proper post-fire grazing rest and subsequent management are still essential to restore resilient sagebrush ecosystems (Pellant et al. 2004, Miller et al. 2011, Chambers et al. 2014a).

We examined how varying post-fire plant community structure and timing of defoliation affected post-fire seedling perennial bunchgrass growth, reproduction, and survival, as well as overall plant community structure. In a field experiment, we applied neighbor removal treatments (no, adult, and seedling removal) to manipulate plant community structure and simulate potential restoration scenarios. We then applied defoliation treatments to simulate domestic livestock grazing (spring and fall) starting the first fall after wildfire in burned *Artemisia tridentata* ssp. *wyomingensis* communities. Seedling senescence, leaf and inflorescence production, stem length, and survival addressed plant-level effects, while total perennial bunchgrass foliar cover and

density addressed community-level effects of post-fire grazing. We predicted that 1) adult removal would increase length of the growing-season, growth, reproduction, and survival for seedlings due to reduced competition with mature neighbors, 2) spring defoliation would lead to earlier plant senescence and increase seedling mortality due to increased resource stress, and 3) delaying defoliation to the second year would decrease negative effects on seedlings due to plants having more resource reserves available for recovery.

Materials and Methods

Site Descriptions

The study was conducted on two *A. tridentata ssp. wyomingensis* communities that burned in summer 2014 in the northwestern portion of the Great Basin. The Coleman fire occurred in northwestern Nevada and was ignited by lightning on July 1, 2014. Site elevation was 1350m, had gravely loam soils, and received 270mm of annual precipitation (NRCS 2017). The Bureau of Land Management (BLM) drill seeded a mix of native perennial grasses and forbs in November 2014. The Saddle Draw fire occurred in southeastern Oregon and was ignited by lightning on July 13, 2014. Site elevation was 1350m, on clayey soils, and receives 280mm of annual precipitation (OSWRB 1969). The BLM drill seeded a mix of native perennial grasses and forbs between October 2014 and March 2015. Pre-fire precipitation was below average, while post-fire winter and spring precipitation was above the 30-year average on both sites for all three years after fire,

while summer precipitation was below average in year-two only (Figure 2). Both sites were in good ecological condition and experienced moderate levels of livestock use utilizing a rest and differed rotation grazing schedule prior to fire occurring.

Pseudoregnaria spicata (bluebunch wheatgrass) and *Elymus elymoides* (bottlebrush squirreltail) were planted at both sites; additionally, *Elymus lanceolatus* (thickspike wheatgrass) was planted on the Coleman fire. All three species are deep-rooted perennial bunchgrasses, native to sagebrush steppe communities in the Great Basin, and are commonly used in post-fire restoration treatments. *Elymus elymoides*, *P. spicata*, and *E. lanceolatus* represented the third, sixth, and seventh most commonly seeded bunchgrass species respectively in northern Nevada between 2006-2009 (Leger and Baughman 2015). These species represented 12, 42, and 11% of sampled plants at our sites, respectively. Thirty-five percent of bunchgrass seedlings were unidentifiable to species by the second year due to mortality, small stature, and/or lack of seed head development.

Vegetation Treatments and Measurements

We examined potential post-fire restoration scenarios by varying the density of adult and seedling bunchgrasses using plant removal treatments. These treatments were applied at the start of the first growing-season after fire to emulate potential variability in initial seedling establishment. We implemented three treatment levels that represent potential post-fire scenarios: 1) no neighbor removal (control) representing

variable density of surviving adult and seedling bunchgrasses; 2) adult removal representing high adult bunchgrass mortality with variable seedling density; and 3) seedling removal representing high adult bunchgrass survival and low initial seedling establishment. Adult removal treatments killed all surviving adult bunchgrasses within each 1m² sample plot. Seedling removal killed all but four seedling bunchgrasses with a minimum of 10cm spacing to reduce seedling-seedling interactive effects. Treatments were implemented by cutting target plant stems below the meristematic root crown, thereby killing plants while minimizing soil disturbance. Cut plant biomass was removed from the plots to eliminate potential fertilization effects. Six replicates of each neighbor removal treatment (macro-plot type) were placed at each study site using a random grid-cell method. These plots were 16 m² in size and surrounded by livestock exclusion fencing.

Four defoliation treatment levels were nested within removal treatments to assess the effect of defoliation at various times post-fire on seedling growth with a full 3 x 4 factorial design. Treatments were: 1) no simulated grazing (control), 2) fall year-one, 3) spring year-two, and 4) fall year-two defoliation. Defoliation treatments were implemented during the boot stage (early-mid May) and after plant senescence (early-mid October) starting in spring 2016 and fall 2015 and 2016. We used defoliation treatments as opposed to actual livestock in order to control for a uniform 50% utilization level across all sampled plants. We estimated that 50% utilization was equal to defoliating plants at approximately 40% of plant height using a height-weight regression. We could not identify many seedlings during the first year so the 40% plant

height was applied to all bunchgrasses regardless of species. Cut biomass was removed from the plots to eliminate potential fertilization effects. Four defoliation treatment subplots representing all treatment levels were randomly placed within each neighbor removal macro-plot. Defoliation plots were 1 m² and had a minimum of 50 cm spacing between subplots.

We used 20-gauge colored wire to mark two tillers on three perennial grass seedlings per subplot. New focal tillers were marked at the beginning of each sampling season. If a marked seedling died over the course of the study, another seedling was marked and sampled unless there were less than three possible focal seedlings within the plot. Marked tillers were measured approximately every 14 days from the beginning of June through the middle of August in 2015 and 2016, and approximately every 30 days from the middle of May through middle of September in 2017. We measured timing of senescence, leaf and inflorescence production, and stem length for each target tiller to quantify within-season plant-level treatment effects. We tracked seedling survivorship over three years to quantify across-season plant-level treatment effects. Tillers were considered senesced when all current year's leaves and stems were brown. Seedlings were considered dead if above ground biotic material was broken off during the growing-season and did not regrow the following year. We also visually estimated perennial bunchgrass foliar cover and plant density by age class (adult or seedling) in each subplot at peak greenness (mid-July) during each sampling year to examine community-level treatment effects.

Statistical Analyses

We grouped data across bunchgrass species to draw generalized conclusions, to address difficulties identifying all seedlings to species, and to account for the differing percentage of individuals sampled by species across treatment levels. We analyzed the timing of individual tiller senescence as a proxy for overall within-season seedling senescence. This metric allowed us to compare the percent of actively growing tillers for all treatments at regular time steps during the growing-season. The number of sampling events in year-one was not suitable to calculate senescence curves; therefore, only year-two and three senescence data were used. We calculated timing of senescence using Kaplan-Meier survival estimates (Kaplan and Meier 1958) and calculated curves to quantify the decrease in percent of actively growing tillers throughout the growing-season. We then compared senescence curves across treatments using log-rank comparisons (Harrington and Fleming 1982, Pyke and Thompson 1986). The log-rank method compared mid- and endpoints of the Kaplan-Meier senescence curves to determine whether those curves were statistically different along a chi-square distribution. We compared across removal treatments using no defoliation treatments to examine effects of neighbor removal, and we compared defoliation treatments within neighbor removal treatment to examine effects of timing of defoliation. We also compared across years within treatment to determine interannual difference in senescence. We utilized the *Surv* and *survdifff* functions in the Survival package in R program software to generate and compare senescence curves (Therneau and Grambsch 2000, Therneau 2015).

We used mixed models to assess treatment effects on leaf and inflorescence production, stem length, seedling survival, foliar cover, and plant density. Mixed models account for variation associated within each sampling unit (plot) when determining the final model (Pinheiro & Bates 2000). Linear mixed models (LMMs) were used to analyze leaf production, stem length, foliar cover and plant density (Pinheiro & Bates 2000), and generalized linear mixed models (GLMMs) were used to account for the binomial response associated with within-season inflorescence production and across-season seedling survival (Bolker et al. 2009). We used the *lmer* and *glmer* functions in the lme4 package in the R statistical software for fitting mixed models (Bates et al. 2015, R Core Team 2017). Separate models were fit for each response variable using the maximum likelihood approach; this involves minimizing Akaike Information Criterion (AIC) goodness-of-fit weights for each possible model. Potential predictor variables for all models included neighbor removal treatment, defoliation treatment, age class date, and year with all possible interactions included; individual plot was a random effect. Models were by fit by dropping out interactions and fixed effects until the lowest AIC values were achieved.

Results

Tiller Senescence, Growth, Reproduction, and Seedling Survival

Timing of senescence differed by neighbor removal, defoliation, and year (Table 1). Seedling removal delayed senescence as compared to no removal in both years two

and three; in addition, defoliation treatments differed within the seedling removal treatment (Fig. 2). Fall year-one and spring year-two treatments in year-two and spring year-two and fall year-two treatments in year-three accelerated senescence as compared to no defoliation within seedling removal (Fig. 2). However, these treatments did not differ in percent senescence from the same defoliation treatment within no and adult removal within either sampling year. Overall, senescence occurred later in year-three as compared to year-two, despite less overall growing-season precipitation occurring at either field site in the third year (Fig. 1).

Leaf production differed by defoliation treatment in years two and three. Date and the neighbor by defoliation interaction were significant in all three years (Table 2A). Leaf production was highest in year-one across treatments and lowest in year-three (Fig. 3). Neighbor removal did not affect leaf production during the three years. Fall year-one defoliation increased leaf production in year-one and year-two, while spring year-two defoliation decreased leaf production in year-three (adult and seedling removal) (Fig. 3).

Tiller stem length differed by defoliation treatment and the neighbor by defoliation interaction in all three years; date was significant in years two and three (Table 2B). Year-one tillers were shorter than in other years, with the tallest tillers occurring in year-two (Fig. 4). Fall year-one plots exhibited longer tillers within adult removal in year-one; however, the fall year-one defoliation treatment had not yet occurred (Fig. 4). Spring year-two defoliation decreased stem length across all three neighbor treatments in year-two and in seedling removal only in year-three; fall year-two defoliation decreased stem length in year-three in seedling removal only (Fig 4).

Inflorescence production differed by defoliation treatment in all three years, as well as by date and the neighbor by defoliation interaction (Table 2C). Neighbor removal did not affect inflorescence production during the three years. All treatments exhibited extremely low inflorescence production and did not differ among treatments in year-one (Fig. 5). In year-two, inflorescence production was generally much higher, with inflorescence production differing by date and peaked between 30-60% of tillers for most treatments. Fall year-one defoliation increased inflorescence production within adult removal as compared to the respective no defoliation treatments in year-two, while spring year-two defoliation decreased inflorescence production within no and seedling removal treatments (Fig. 5). In year-three, inflorescence production was lower as compared to year-two, most likely due to lower spring precipitation (Fig. 1). Fall year-one defoliation with no neighbor removal had higher inflorescence production compared to no defoliation with no neighbor removal in the third year (Fig. 5).

Seedling survival only differed by year (Table 3). More seedlings survived from year-one to year-two (91.8%) than from year-two to three (86.2%). However, there was no significant difference in seedling survival as a function of neighbor removal or defoliation (Table 3).

Community Foliar Cover and Plant Density

Bunchgrass foliar cover at the subplot level differed by neighbor removal, defoliation, age class, and year (Table 4). Seedling removal (mean = 3.54 %) had lower

overall foliar cover compared to no removal (5.63 %); spring year-two (4.02 %) and fall year-two (4.37 %) had lower cover compared to no defoliation (5.06 %) (Fig. 6A). Seedling cover (5.09 %) exceeded adult bunchgrass cover (3.86 %), and year-two displayed highest total bunchgrass cover (5.53 %) with year-three (4.56 %) and year-one (3.32 %) following (Fig. 6A). Foliar cover displayed significant two-way interactions with neighbor by age and neighbor by year, and three-way interactions with neighbor by defoliation by age and neighbor by age by year (Table 4). Seedling removal decreased seedling-aged cover within no defoliation and spring year-two defoliation, and fall year-one defoliation reduced seedling-aged cover within no removal (Fig. 6A). Adult removal decreased adult-aged cover in year-one only, while seedling removal decreased seedling-aged cover in year-two only (Fig 6A). Additionally, seedling-aged cover exceeded adult-aged cover across all adult removal treatments in years one and two and in no removal treatments in year-three (Fig. 6A). Adult-aged cover in adult removal was highest in year-two, and seedling-aged was lowest in year-one for both no and adult removal (Fig 6A). Lastly, none of the treatments reached the recommended management benchmark of 20% bunchgrass foliar cover by the end of the third growing-season after fire.

Bunchgrass density differed by neighbor and age class but not by defoliation treatment or year (Table 6B). Seedling removal (mean = 5.33 plants/m²) had lower plant density compared to no removal (8.65 plants/m²) but not adult removal (7.01 plants/m²), and overall seedling density (9.39 plants/m²) exceeded overall adult density (4.06 plants/m²). Plant density displayed significant two-way interactions with neighbor

by defoliation and neighbor by age, and three-way interactions with neighbor by defoliation by age and neighbor by age by year (Table 4). Adult removal decreased adult-aged density within no defoliation in years one and two, and seedling removal decreased seedling-aged density within no and spring year-two defoliation treatments in year-one (Fig. 6B). Seedling-aged density exceeded adult-aged density in both no and adult removal treatments in both years one and three (Fig. 6B).

Discussion

We found that altering plant community structure through neighbor removal treatments affected within-season senescence for seedlings and overall perennial bunchgrass foliar cover and plant density. Seedling removal lengthened the growing-season as compared to no removal. Adult removal decreased adult-aged cover and density; however, adult-aged cover and density recovered compared to no removal by the second or third year after fire. The positive effect of removing seedling neighbors on senescence may be due to remaining seedling bunchgrasses having fewer close neighbors competing for resources. Seedlings are often tightly clustered within drill furrows and face intense competition with neighbors for light, water, and soil nutrients; therefore, having a lower density of seedlings may allow them to better utilize soil resources and extend their growing-season. In contrast to the negative effects of seedling neighbors on senescence, seedling removal reduced total bunchgrass foliar cover and density of both seedlings and adults. This suggests that if the initial seedling

emergence is low, the potential for perennial bunchgrass recovery as a functional group is low. Therefore, if seedling density and overall perennial bunchgrass foliar cover are low in the first and second year after fire, an additional seeding treatment may be warranted to increase this functional groups' presence. Neighbor removal treatments also altered the relative density of seedling and adult perennial bunchgrasses, thereby effectively simulating potential post-fire restoration scenarios. These varying competitive scenarios occur regularly on post-fire restoration sites in the Great Basin and testing defoliation across the range of potential scenarios may aid restoration specialists in forecasting potential restoration outcomes.

We found that the timing of defoliation affected senescence, inflorescence and leaf production, stem length, and total bunchgrass foliar cover. Defoliation decreased the length of the growing-season only within seedling removal treatments; fall year-one and spring year-two defoliation accelerated senescence in year-two and spring and fall year-two defoliation accelerated senescence in year-three. This finding partially supports our second hypothesis that growing-season defoliation accelerates senescence but only when relative seedling density is low. Seedling removal treatments had lower overall foliar cover, which may be a result of lower soil moisture during the growing-season and subsequently earlier senescence after plants are defoliated. Surprisingly, fall defoliation also shortened the following growing-season. Fall defoliation removes residual dry matter from plant canopies, which may compound the effects of soil water evaporation the following growing-season.

Defoliation interacted with neighbor removal to both increase and decrease within-season inflorescence production. Fall year-one defoliation increased inflorescence production within adult removal in year-two and no removal in year-three, suggesting a positive effect of removing prior year's foliage or causing plants to allocate more to reproduction because of the initial stress of defoliation. Spring defoliation decreased inflorescence production in year-two with all neighbors present and virtually eliminated inflorescence production with seedling removal, suggesting that growing-season defoliation can have profound negative effects on both senescence and reproduction. Fall year-one defoliation increased leaf production within no removal in year-two, and spring year-two defoliation decreased leaf production within seedling and adult removal in year-three. This suggests potential positive effects of fall defoliation and negative effects of spring defoliation on the following year's leaf growth. Spring year-two defoliation decreased stem length across all neighbor treatments in year-two and within seedling removal in year-three, suggesting that seedlings cannot readily regrow tillers after spring defoliation. Fall year-two defoliation decreased stem length within seedling removal in year-three, suggesting some detrimental effects of fall defoliation on tiller growth the following season.

In addition to accelerating senescence and decreasing stem length, leaf and inflorescence production, spring defoliation reduced total bunchgrass foliar cover. These combined effects further suggest that spring defoliation within the first few years after fire may be detrimental to achieving the goal of reestablishing bunchgrasses. Our

finding corroborates prior research suggesting that post-fire spring grazing has negative effects on adult perennial bunchgrasses after fire (Bates and Davies 2014).

We predicted that the presence of neighbors and spring defoliation would decrease seedling survival; however, seedling survival was not affected by neighbors or defoliation but only by year. Low initial seedling emergence is often attributed to a lack of suitable winter precipitation (James et al. 2012); however, suitable growing-season precipitation may determine seedling survival over the first several years after fire. Decreased growing-season (summer) precipitation can decrease bunchgrass growth in semi-arid systems (Busso and Richards 1995), which may have led to decreased seedling survival from year-two to three. Additionally, drought stress combined with livestock grazing can lead to rapid population declines for bunchgrasses in arid systems (Busso and Richards 1995). Therefore, when restoration treatments display good initial seedling establishment but subsequent post-fire precipitation is below normal, this suggests a conservative approach to reintroducing livestock.

Our plots were compared against the recommended management benchmark of achieving 20% perennial bunchgrass foliar cover prior to reintroducing livestock. None of our treatments reached this benchmark within three years after fire, which would mean that livestock grazing should still be delayed. However, plant community structure at both sites consisted of a high percentage of grass and forb restoration species with generally low non-native plant cover. Perennial bunchgrass foliar cover peaked at approximately 17% for our no removal, no defoliation treatment and ranged from approximately 6-15% across all other treatments. These sites displayed significant

seedling emergence and minimal seedling mortality yet still have not reached the 20% benchmark by the third growing-season, suggesting that variability in community structure across sites may not lead to achieving this benchmark. We suggest assessing ecological potential of each site based on plant community structure and presence of preferred native and restoration species to determine suitability for livestock reintroduction, rather than using a universal bunchgrass foliar cover benchmark.

The decision as to when to reintroduce livestock after fire is critical to promoting restoration success. Post-fire plant community structure will vary broadly across *A. tridentata* ssp. *wyoming* communities and this decision must take that variability into account. Spring grazing should be avoided especially when seedling and overall bunchgrass densities are low. Fall grazing may increase inflorescence production in the year following; however, it may also shorten the following growing-season. Defoliation did not significantly affect seedling mortality, and the majority of seedlings in our study survived to end of the third growing-season after fire. Other restoration treatments may experience low initial seedling emergence or high seedling mortality due to lack of suitable precipitation or high invasive species pressure. If either of these situations occur, implementing additional restoration actions may be appropriate. Delaying livestock grazing until after the second growing-season after fire may be appropriate; however, if initial seedling establishment is high, grazing within the first two years after fire may have fewer negative effects on seedlings. If suitable seedling establishment and growth is not observed within the first two growing-seasons, further delay of livestock grazing is warranted to allow for community recovery.

Managing disturbance after restoration in arid systems can improve the potential success of those treatments. Improper timing or excessive defoliation can detrimentally affect growth and survival of planted restoration species, which may in turn lead to the subsequent failure of that treatment. If treatment failure becomes a concern, additional restoration actions should be considered to limit stressors to restoration species. These actions may range from applying herbicide to reduce non-native species or additional seeding treatments to increase restoration species density. Successful restoration of natural ecosystems in the first few years can increase overall ecosystem resistance and resilience in the face of potential future disturbances and uncertain climate.

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Tables

Table 1. Log-rank comparison significance values for treatment-level Kaplan-Meier curves. Column and row headings denote vegetation treatment combinations, with the upper row denoting neighbor removal and the lower row denoting defoliation treatments. Bolded p-values are significantly different at $P < 0.05$, and italicized p-values are significantly different at $P < 0.10$.

Treatment Combination		No Removal				Adult Removal				Seedling Removal			
		No Defoliation	Fall Year 1	Spring Year 2	Fall Year 2	No Defoliation	Fall Year 1	Spring Year 2	Fall Year 2	No Defoliation	Fall Year 1	Spring Year 2	Fall Year 2
No Removal	No Defoliation	< 0.01											
	Fall Year 1	0.54 0.45	< 0.01										
	Spring Year 2	0.26 0.56		< 0.01									
	Fall Year 2	0.21 0.94			< 0.01								
Adult Removal	No Defoliation	0.35 0.97				< 0.01							
	Fall Year 1		0.52 0.88			0.89 0.58	< 0.01						
	Spring Year 2			0.33 0.47		0.32 0.21		< 0.01					
	Fall Year 2				0.65 0.37	0.90 0.34			< 0.01				
Seedling Removal	No Defoliation	0.04 0.14				0.24 0.13				< 0.01			
	Fall Year 1		0.78 0.02				0.34 0.02			0.06 0.95	< 0.01		
	Spring Year 2			0.32 0.64				0.97 0.24		0.03 0.10		< 0.01	
	Fall Year 2				0.87 0.91				0.69 0.43	0.39 0.10			< 0.01

Year Two	Within neighbor /	Year Two	Within defoliation /		Within treatment
Year Three	across defoliation	Year Three	across neighbor		/ across years

Table 2. ANOVA table for leaf production, stem length, and flower production by neighbor, defoliation, date, and year.

A	<i>Leaf Production</i>								
	Year One			Year Two			Year Three		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Neighbor	2	0.15	0.861	2	1.1	0.331	3	0.8	0.710
Defoliation	3	1.18	0.314	3	5.5	0.001	2	31.7	< 0.001
Date	2	2.8	<i>0.059</i>	5	117.6	< 0.001	4	31.2	< 0.001
Neighbor x Defoliation	6	8.4	< 0.001	6	17.2	< 0.001	6	3.3	0.003
B	<i>Stem Length</i>								
	Year One			Year Two			Year Three		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Neighbor	2	0.7	0.514	2	0.1	0.906	3	0.1	0.710
Defoliation	3	2.4	<i>0.067</i>	3	128.4	< 0.001	2	21.5	< 0.001
Date	2	0.6	0.560	5	12.8	< 0.001	4	288.8	< 0.001
Neighbor x Defoliation	6	8.7	< 0.001	6	7.4	< 0.001	6	4.6	< 0.001
C	<i>Flower Production</i>								
	Year One			Year Two			Year Three		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Neighbor	2	0.9	0.324	2	0.6	0.368	3	0.2	0.710
Defoliation	3	2.1	<i>0.078</i>	3	61.2	< 0.001	2	5.3	< 0.001
Date	2	4.0	0.011	5	7.1	< 0.001	4	34.6	< 0.001
Neighbor x Defoliation	6	2.9	0.005	6	13.5	< 0.001	6	2.6	0.013

Bold values denote significance at $P < 0.05$ and italicized values denote significance at $P < 0.10$.

Table 3. ANOVA table for across-season seedling survival by neighbor, defoliation, and year.

Effect	Seedling Survival		
	df	<i>F</i>	<i>P</i>
Neighbor	2	0.6	0.473
Defoliation	3	0.6	0.655
Year	1	7.2	0.008
Neighbor x Defoliation	6	1.5	0.159
Neighbor x Year	2	0.1	0.939
Defoliation x Year	3	0.2	0.859
Neighbor x Defoliation x Year	6	1.1	0.322

Bold values denote significance at $P < 0.05$ and italicized values denote significance at $P < 0.10$.

Table 4. ANOVA table for foliar cover and plant density by neighbor, defoliation, plant age class, and year.

Effect	df	Foliar Cover		Plant Density	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Neighbor	2	7.7	0.002	5.2	0.010
Defoliation	3	3.6	0.013	0.4	0.768
Age	1	28.9	< 0.001	197.8	< 0.001
Year	2	31.4	< 0.001	1.7	0.189
Neighbor x Defoliation	6	1.5	0.174	2.1	0.048
Neighbor x Age	2	28.1	< 0.001	67.9	< 0.001
Defoliation x Age	3	0.2	0.896	0.6	0.646
Neighbor x Year	4	14.6	< 0.001	1.0	0.391
Defoliation x Year	6	0.9	0.488	0.2	0.987
Age x Year	2	7.3	0.001	2.8	<i>0.060</i>
Neighbor x Defoliation x Age	6	3.2	0.003	4.1	< 0.001
Neighbor x Defoliation x Year	12	0.6	0.818	0.3	0.995
Neighbor x Age x Year	4	2.5	0.044	4.5	0.001
Defoliation x Age x Year	6	0.9	0.463	0.1	0.993
Neighbor x Defoliation x Age x Year	12	0.6	0.816	0.3	0.987

Bold values denote significance at $P < 0.05$ and italicized values denote significance at $P < 0.10$.

Figures

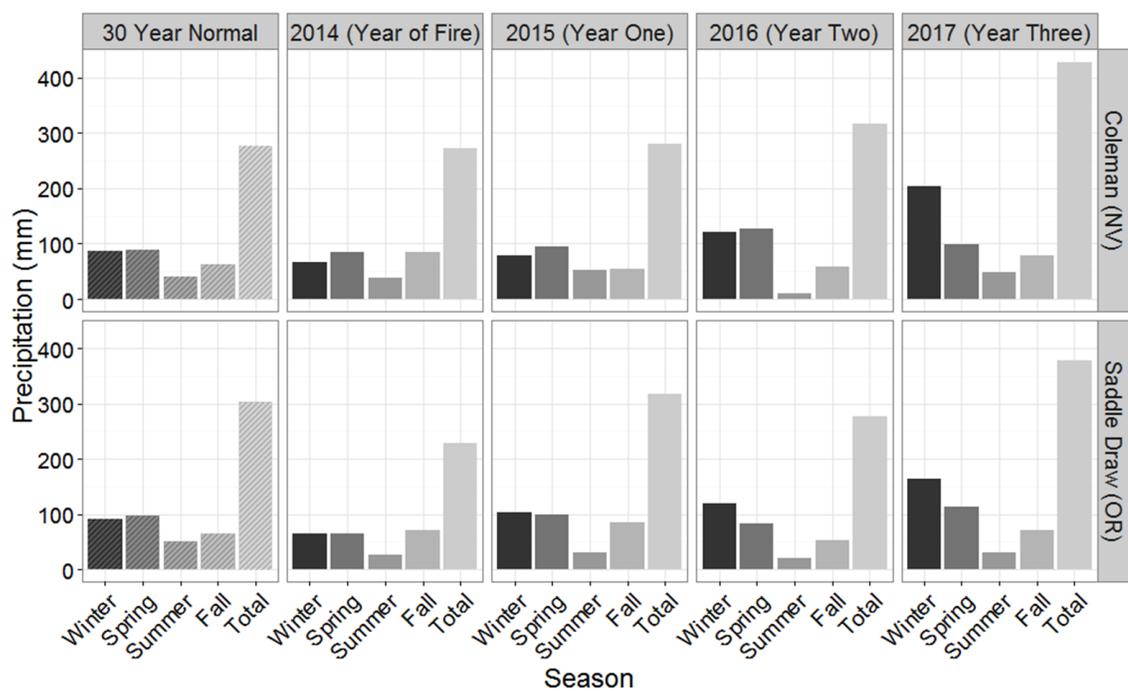
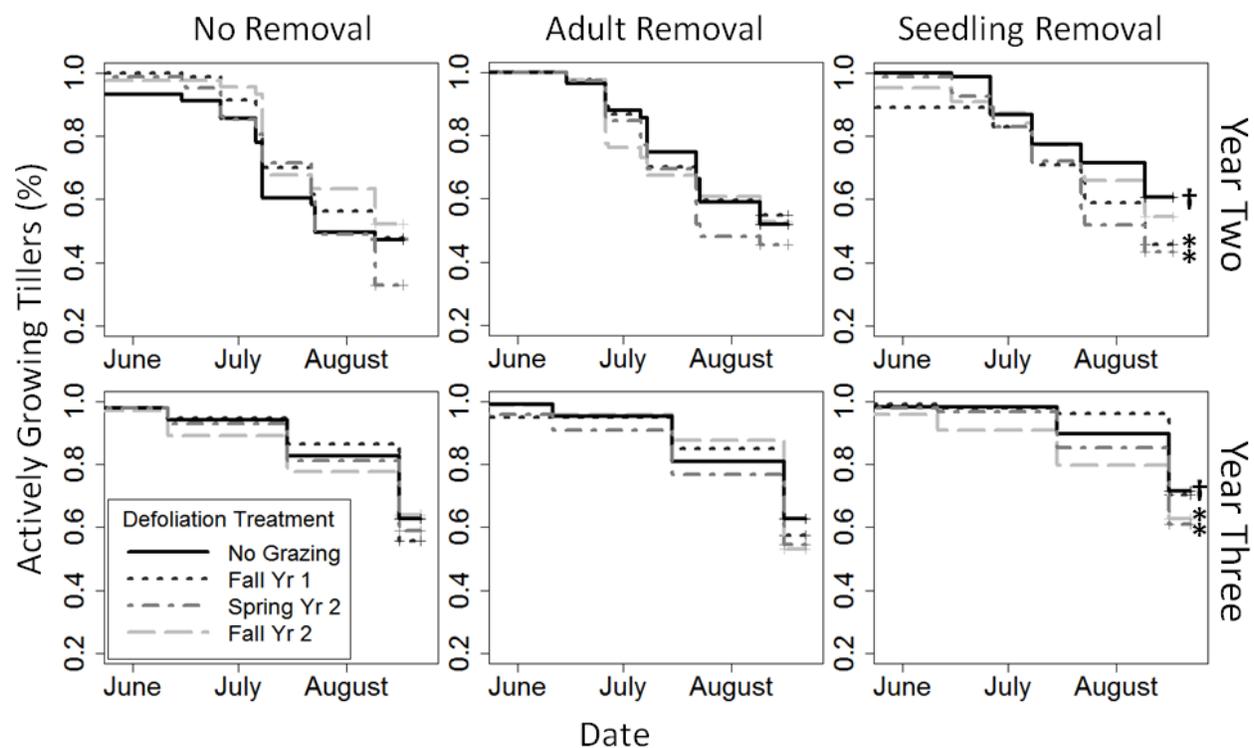


Figure 1. Precipitation for the Coleman (NV) and Saddle Draw (OR) fires (PRISM 2004). Seasons are winter (December of prior year – February), spring (March – May), summer (June – August), and fall (September – November).



1
 2 *Figure 2. Kaplan-Meier curves showing the percent of seedling tillers actively growing as a*
 3 *function of neighbor removal, defoliation, year, and date. * represent significant differences for*
 4 *defoliation treatments as compared to no defoliation within neighbor treatment, and †*
 5 *represent significant differences for defoliation treatments relative to no neighbor removal with*
 6 *the same defoliation treatment.*

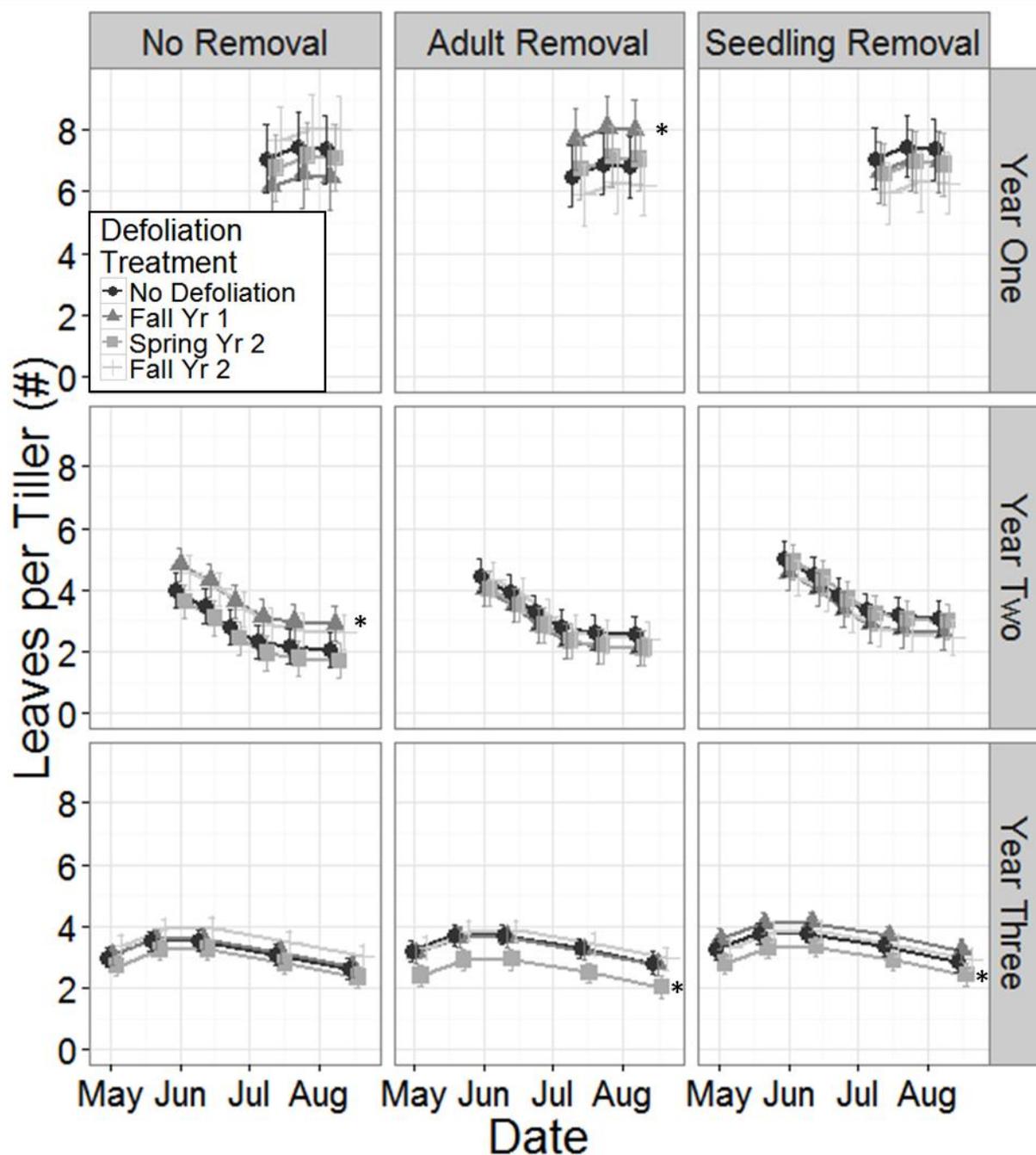


Figure 3. Number of actively growing leaves per tiller as a function of neighbor, defoliation, year, and date. Error bars represent 95% confidence intervals for each sample date. * represent significant differences for defoliation treatments as compared to no defoliation within the same neighbor treatment, and † represent significant differences for defoliation treatments relative to no neighbor removal with the same defoliation treatment.

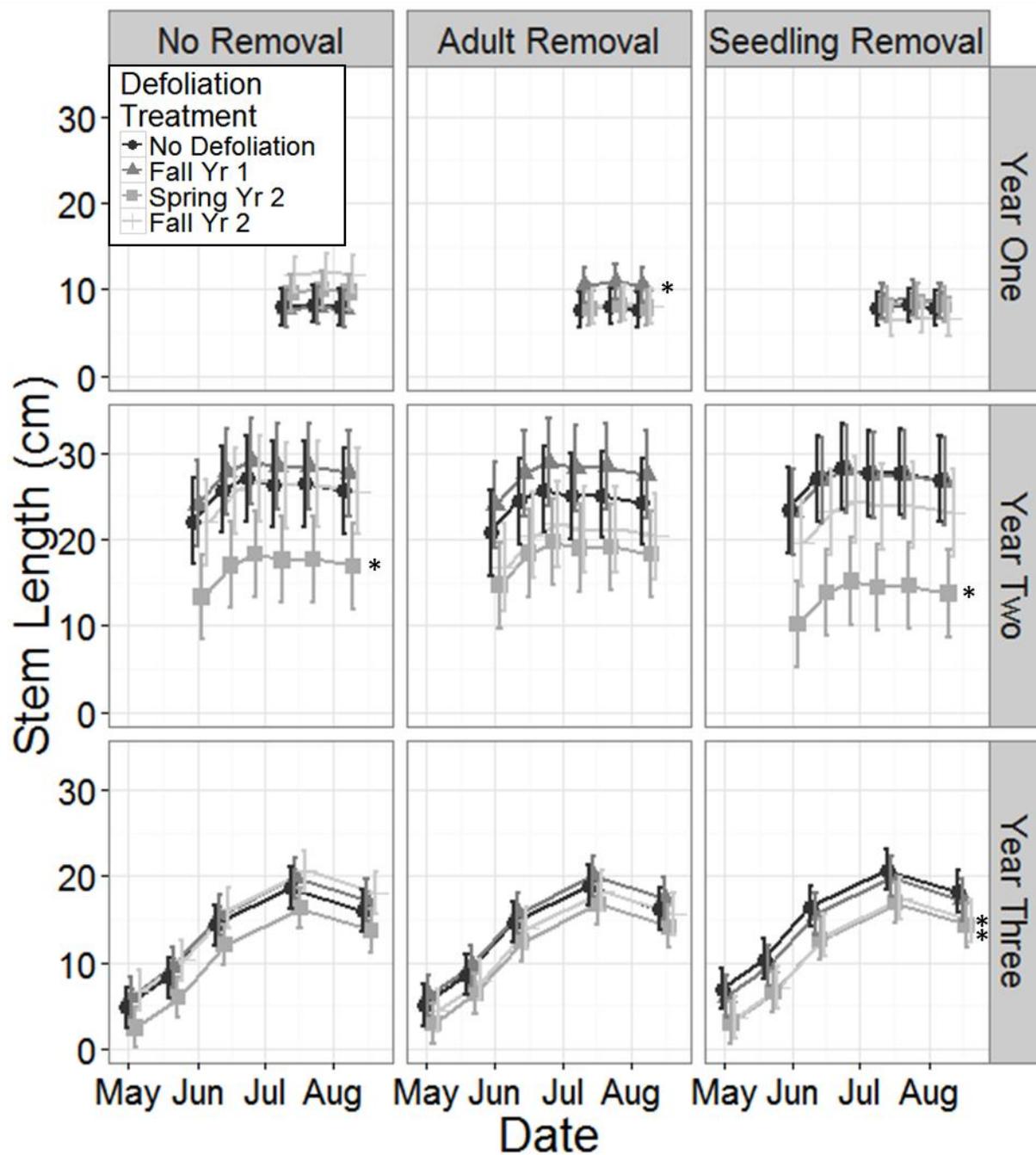


Figure 4. Tiller stem length as a function of neighbor, defoliation, year, and date. Error bars represent 95% confidence intervals for each sample date. * represent significant differences for defoliation treatments as compared to no defoliation within the same neighbor treatment, and † represent significant differences for defoliation treatments relative to no neighbor removal with the same defoliation treatment.

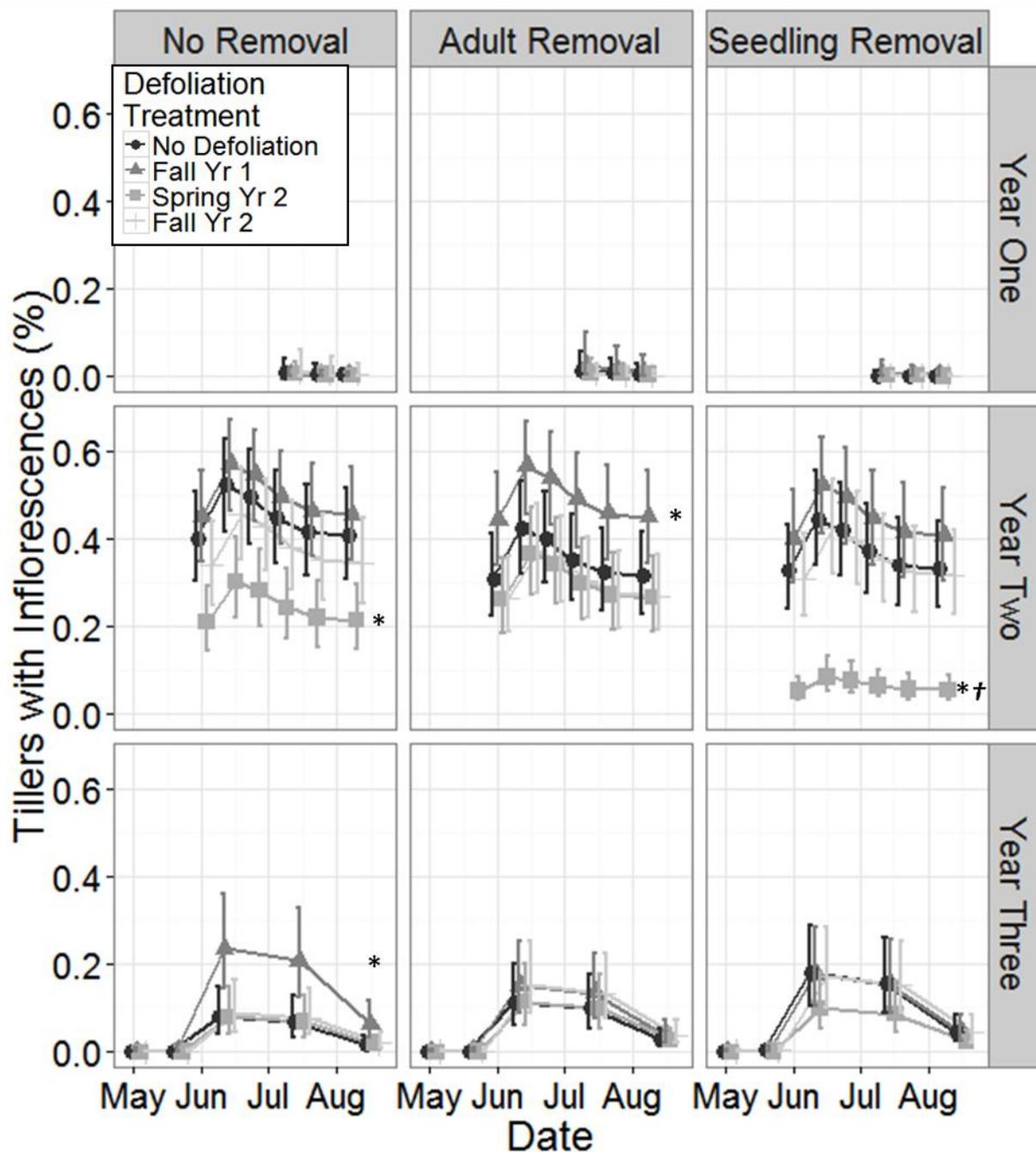


Figure 5. Percent of tillers with inflorescences as a function of neighbor, defoliation, year, and date. Error bars represent 95% confidence intervals for each sample date. * represent significant differences for defoliation treatments as compared to no defoliation within the same neighbor treatment, and † represent significant differences for defoliation treatments relative to no neighbor removal with the same defoliation treatment.

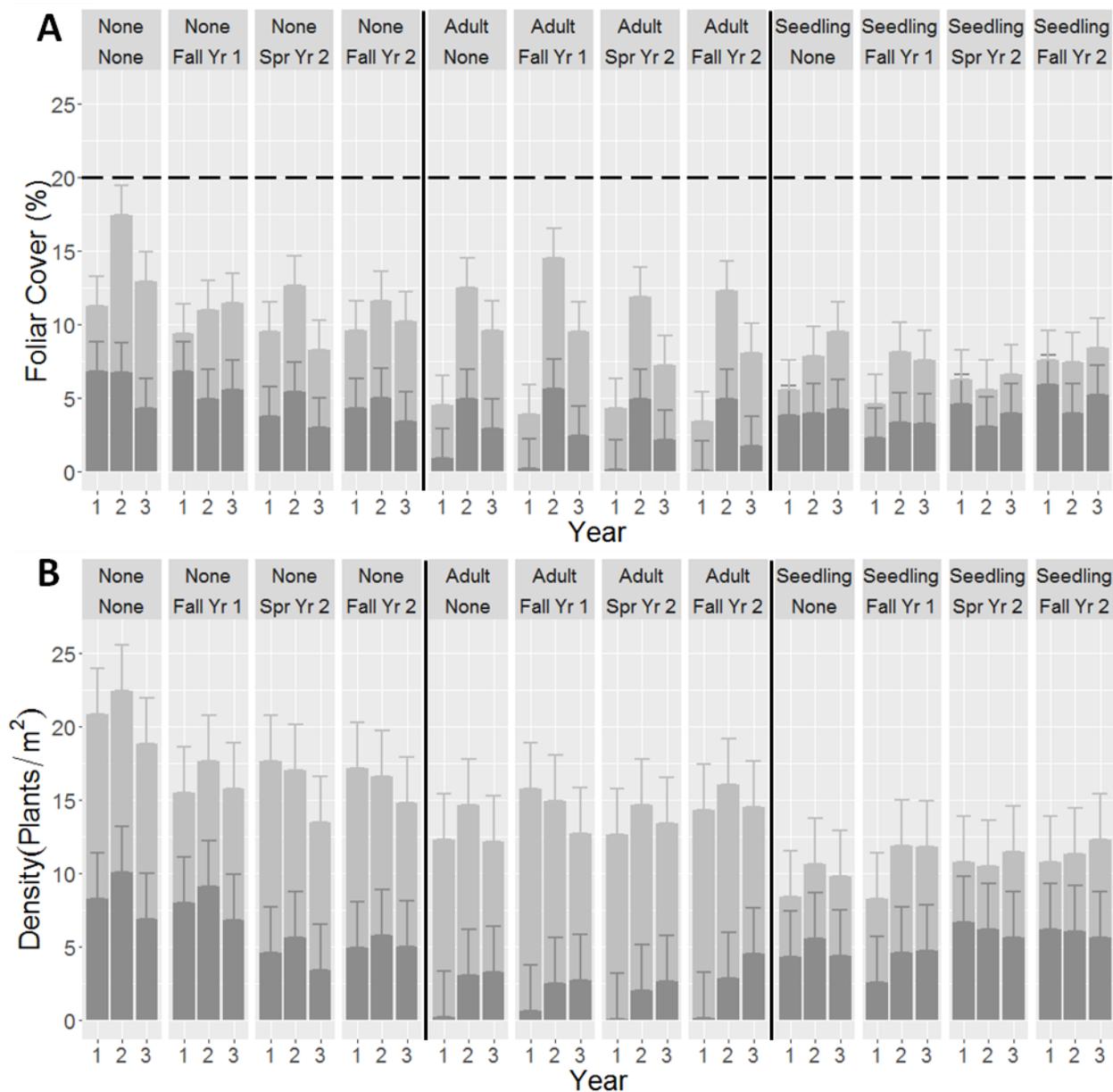


Figure 6. A) Percent foliar cover and B) plant density as a function of treatment type, age class, and year. Bars represent model perimeter estimates and error bars represent 95% confidence intervals. Column headings denote neighbor removal (upper row) and defoliation (lower row) treatments. Dark gray bars represent adult cover and light gray bars represent seedling cover. Fig. 6 A has a dashed line at 20% foliar cover to denote the suggested management benchmark for reintroduction of livestock grazing after fire.

OVERALL SUMMARY AND RECOMENDATIONS

This thesis asked and answered questions related to post-fire restoration and livestock grazing in Wyoming big sagebrush communities. I first assessed plant community dynamics in the absence of additional disturbance, and found that plant community composition changed as a function of time, with seeded functional groups increasing on both sites. This suggests that seeding treatments can be effective at structuring post-fire plant community structure and composition. Secondly, I found that bunchgrass spatial dynamics also changed as a function of time. Seedlings exhibited pronounced attractive patterns in year one, but less pronounced patterns with a shift in clustering distance by year two. Adults exhibited mixed spatial patterns on seedlings in year one, but more pronounced dispersive spatial patterns by year two. These shifting relationships will determine the eventual plant community structure of the dominant species on our sites. Lastly, we found seedling neighbor density was the dominant factor controlling seedling bunchgrass growth and survival in years one and two. Additionally, seedlings differed in their responses to neighbor density in year one, but not in year two. This suggests that maintaining lower neighbor densities during the first year may be essential for adequate seedling growth and survival, and that some species may be more suitable restoration options due to density independent survival.

Second, I examined the relationship between post-fire plant community structure and timing of initial post-fire defoliation. I found that altering plant community structure affected seedling senescence, bunchgrass foliar cover, and bunchgrass density. Removing seedlings led to delayed senescence and lower total bunchgrass foliar cover and density. Removing adults did not appear to have consistent effects on any metric, suggesting that this treatment was not

successful at altering plant community structure. Timing of defoliation affected bunchgrass seedling senescence, inflorescence and leaf production, stem length, and total bunchgrass foliar cover. Spring defoliation generally led to negative effects for bunchgrass growth, while fall defoliation exhibited fewer effects. Fall year-two defoliation exhibited fewer negative effects as compared to fall year-one, suggesting a slight positive benefit of delaying defoliation to the second year. Seedling removal and spring defoliation interacted to produce the most negative effects, including virtually eliminating inflorescence production in year two.

There are several general management recommendations from the results of these two experiments. Promoting bunchgrass seedling growing conditions the first year after fire by limiting immediate neighbors may promote seedling growth and survival. Avoiding spring defoliation all together and delaying fall defoliation until at least the second year after fire may also promote seedling growth. If initial seedling density is low, delaying livestock further or implementing additional restoration treatments may be warranted. Additionally, we will be tracking these experiments for years to come in the attempt to determine long-term effects of our initial experiments. Wildfires will continue to occur in these systems, and management decisions will need to be made about the appropriate restoration treatments and post-fire management strategy. We acknowledge intrinsic differences across sites, and the need for informed and broad management recommendations; however, a site-specific approach is recommended rather than a one-size-fits-all strategy. Lastly, a conservative approach to reintroducing livestock is appropriate when one is uncertain about possible negative effects on restored species.