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Of Fire, Mammals, and Rain: Mechanisms of Plant Invasions

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Of Fire, Mammals, and Rain: Mechanisms of Plant Invasions

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A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

Of Fire, Mammals, and Rain: Mechanisms Driving Plant Invasions

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Doctor of Philosophy

Biological invasions are driving environmental state changes on a global scale. Exotic plant species must be successful at passing several abiotic and biotic filters to establish and disrupt the native plant community assembly. Understanding where exotic plants are on a regional scale and being able to characterize how exotic plants are generally interacting with their environment is crucial information for exotic species management (chapter 1). In the western United States human-related activities are augmenting the spread of exotic plant species by increasing the ignitions of wildfire. Wildfire can lead to nutrient pulses through the removal of intact native communities and returning some mineral content into the soil. Exotic plant species that have traits that efficiently acquire nutrients accompanied by rapid growth rates may outcompete native plants. In chapters 2, 3, and 4 experimental fires demonstrated that the direct effect of fire may not be as critical as the potential indirect effects of fire such as altering the behavior of consumers (chapter 2) and reducing competition (chapters 3 and 4). In the Mojave desert, rodent consumers can have strong top-down effects on plant community assembly through foraging selection preferences. Life history traits such as seedling and seed size can lead to differential herbivory and positively benefit some plant species while inhibiting others (chapter 1) which could indirectly alter plant-plant interactions. Plant competition is a biotic filter than can determine establishment success or failure. Species that with rapid growth rates and plastic growth responses are likely to be able to capitalize on fluctuations in available resources. In the Great Basin, forecasts in climate change models predict that precipitation timing will lead to heavier fall rains and more rain than snow in the winter. Water availability is one of the main limiting factors in semi-arid and arid ecosystems where native plants have adaptive traits to maximize resource use. The interaction of wildfire and changes in climate, specifically timing of precipitation is critical to understand to be able to predict and protect against increasing wildfire frequency and severity. In chapter three, the responses by a key exotic annual grass, *Bromus tectorum*, and keystone native perennial shrub *Artemisia tridentata* subsp. *wyomingensis,* were positive for increased early fall precipitation but much more pronounced for *B. tectorum*. Exotic annual plants are able to respond to changes in timing of fall precipitation and have extreme growth which leads to superior competitive abilities through interference and priority effects (chapter 4). Native plants can compete with exotics but the magnitude of the effects are diminished compared to the negative interaction from exotics. Together these findings demonstrate that across several regions exotic annual grasses are capable of passing through abiotic filters and disrupting biotic interactions of the native plant community. This is likely to lead to increased spread of exotic annual species and may indicate potential and availability of fine fuel production supporting increases in size and frequency of wildfires in the western United States.

Keywords: invasion, community assembly, climate change, fire, exotic plants, competition, cheatgrass, *Bromus*, remote sensing, GIS, precipitation timing

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CHAPTER 1

Spatiotemporal Patterns of Cheatgrass Invasion in Colorado Plateau National Parks

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ABSTRACT

Exotic annual grasses are transforming native arid and semi-arid ecosystems globally by promoting invasive grass-fire cycles that drive vegetation state changes. Cheatgrass (*Bromus tectorum*), a particularly widespread and aggressive exotic annual grass, is a key management target in national parks of the western United States due to its impacts on wildfire and biodiversity loss. Cheatgrass is known for its high interannual variability and can grow in a wide range of conditions. The objectives were to 1) map the presence and persistence of cheatgrass in national park units across a 11-year period using remote sensing, and 2) identify the biophysical parameters that correlate with cheatgrass persistence. We used remote sensing and GIS tools to develop a systematic model to characterize the status and environmental correlates of cheatgrass invasions in seven national park units in the western United States. On average cheatgrass covered 4% of park areas, each park ranging from 1-25% coverage. Where cheatgrass was detected, persistent populations across time (hot spots) made up on average 13% of cheatgrass areas. Hot spots were found in areas with deeper plant-available water, lower elevations, colder mean winter temperatures, flatter slopes, higher soil clay content, and lower mean fall precipitation. Study results identified spatiotemporal patterns of plant invasions and key

environmental drivers that influence those patterns. GIS tool development and analysis from this study were used to generate invasion maps which will aid identification of impacts on key management objectives related to wildfire and biodiversity loss so the impacts can be mitigated efficiently.

INTRODUCTION

Invasive grasses are transforming ecosystems, incurring great socioeconomic and environmental costs (Pimentel et al. 2005; Vitousek et al. 1996). These costs accumulate due to reductions in biodiversity, productivity, nutrient cycling, and altered fire regimes (Brooks et al. 2004; D'Antonio and Vitousek 1992). The rapid spread and success of invasive annual grasses can be explained by their short life cycles, large investment in reproduction, and opportunistic response to favorable climate conditions (Chambers et al. 2007). Future replacement of native plant communities by exotic annual grass species is likely to be fueled by increases in land use intensification and climate change (Dukes and Mooney 1999). While exotic grass invasions are occurring globally, dryland ecosystems of western North America are being converted to non-native grass communities at a particularly rapid pace (Bradley et al. 2018).

Understanding the spread of invasive grasses is challenging because of their high spatial and temporal variability. The interaction of landscape position and microenvironment create large spatial heterogeneity, in both the presence and productivity of invasive grasses, and their persistence through time (Bradley and Mustard 2006; Horn and St Clair 2017). Explaining temporal and spatial patterns of invasion is a critical dimension of developing a comprehensive invasive species management strategy (Ashton et al. 2016). There is substantial inter-annual variability in the abundance and density of invasive annuals that is driven by weather (Ashton et al. 2016; Horn et al. 2015), population structure (Mack and Pyke 1983), and community

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processes (Germino et al. 2015; St. Clair et al. 2016). This temporal variability can amplify responses to environmental change relative to native plant communities (Elmore et al. 2003), making it difficult to detect and explain patterns of invasion and the underlying mechanisms at landscape scales. To capture both temporal and spatial dynamics associated with plant invasions has required either modeling or using spectral signals unique to invasive species in certain climate conditions and analyzing long-term remote sensing imagery (Balch et al. 2013; Biganzoli et al. 2013).

Cheatgrass (*Bromus tectorum*), an invasive annual grass from Eurasia, is one of the most insidious exotic plants in western North America (Balch et al. 2013; Reisner et al. 2013) where it has spread across 22.7 million ha. (Duncan et al. 2004) and is expected to establish into new areas given future climate predictions (Bradley 2009b). Cheatgrass is phenotypically plastic and genetically diverse, allowing it to occupy a diversity of habitats (Concilio et al. 2013; Meyer et al. 2016; Reisner et al. 2013). It is highly competitive with a great deal of native vegetation, often altering plant community structure by promoting recurrent wildfire and altering nutrient dynamics (Booth et al. 2003; Urza et al. 2017). Because of its widespread impacts, cheatgrass is a critical species to understand, and its unique phenology makes it an ideal species to study using remote sensing techniques (Bradley et al. 2018). In the Colorado Plateau, cheatgrass mainly germinates in the fall, develops an extensive root system during the winter and reaches maximum biomass in mid-spring, compared to early summer for native plants (Mack and Pyke 1983; Munson et al. 2011). This temporal difference in greenness allows for the identification of landscape locations dominated by cheatgrass. The distribution of cheatgrass on the Colorado Plateau, a physiographic region bounded by the Rocky Mountains and deserts areas in western

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North America, is particularly alarming because it spans even into well-protected national parks who's primary focus is conservation (Munson et al. 2015).

Remote sensing can be an ideal tool to detect and monitor invasive grasses, because it can reveal abundance and spread at high resolution, across large spatiotemporal scales, at relatively low cost (Bradley et al. 2018; Bradley and Marvin 2011). Combining remote sensing, geographic modelling, and statistical modelling allows for the quantification of the spatial extent of grass invasion and how it changes with variation in biophysical conditions. We took the approach of combining a novel remote sensing technique, known as Detection of Early Season Invasives software (henceforth DESI) (Kokaly 2011), with Hotspot analysis, a spatial analysis tool (ESRI 2011), to characterize patterns of cheatgrass invasion. Hotspot analysis has been previously used for analysis of road incidents, urban crime analysis, and epidemiologic studies (Craglia et al. 2000; Maciel et al. 2010; Songchitruksa and Zeng 2010), but to our knowledge has not been applied to track the establishment and spread of invasive species and identify the biophysical correlates underlying plant invasions.

The objectives of this study were to develop an innovative method to systematically model and identify the spatial extent and temporal patterns of cheatgrass, and characterize the environmental associates of cheatgrass invasions in seven national parks in the Colorado Plateau region of western North America. We specifically examined cheatgrass invasion in national parks because of its direct and negative impacts on key management objectives of the National Park Service related to invasive grass-fire cycles and biodiversity conservation. Our study objectives were to:

1) Map the presence and persistence of cheatgrass in seven national park units across a 11-year period on the Colorado Plateau.

2) Identify the important biophysical factors that associate with the presence and persistence of cheatgrass across space and time.

MATERIALS AND METHODS

Site Description

Seven national park units were selected across the Colorado Plateau region: Arches, Bryce Canyon, Canyonlands, and Capitol Reef National Parks (NP), Dinosaur and Natural Bridges National Monuments (NM), and Glen Canyon National Recreation Area (NRA). These national park units are extremely popular tourist destinations visited by millions of people each year (Utah Office of Tourism 2017). The study areas span from the low elevation (930 m) southern unit of Glen Canyon NRA, with a mean annual precipitation of 181 mm yr^{-1} and mean annual temperature of 15.6 °C, to the higher elevation (2700 m) unit of Bryce Canyon NP with a mean annual precipitation of 370 mm yr^{-1} and mean annual temperature of 5.7 °C (Table 1). These park units have large elevational ranges within and among them (930m-2700m) (Table 1). The low elevation areas are arid to semi-arid and composed of shrublands and grasslands. Woodlands dominated by pinyon pine (Pinus edulis), juniper (Juniperus osteosperma), and various shrubs occupy middle elevation areas. At high elevation, mixed conifer forests are the primary plant community. Cheatgrass was introduced to Washington, Utah and British Columbia, during the mid 19th century, originating from populations in Europe {Mack and Pyke 1983. By 1930 its range expanded to include plant communities ranging from salt desert shrub, perennial grassland and shrublands throughout western North America (Morrow and Stahlman 1984). The greatest cheatgrass abundance occurs within the Great Basin and Columbia Basin regions where it is adapted to a variety of soil types and moisture conditions. It is an increasing concern in the Colorado Plateau where disturbances are decreasing native plant communities and biological soil

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crusts increasing invasion potential (Schwinning et al. 2008). Cheatgrass has been mapped extensively across the Great Basin (Balch et al. 2013; Bradley et al. 2018) but little has been done in the Colorado Plateau on large scales.

Experimental Design and Analysis

Landsat imagery, DESI software (Kokaly 2011), and Hotspot spatial analysis (ESRI 2011) were used to identify cheatgrass abundance and persistence and correlate it to environmental variables. Landsat satellite imagery was obtained from 1999-2009 and converted to DESI maps for individual years using the methods of Kokaly (2011) outlined here. The DESI software is comprised of programs written in Interactive Data Language that run with ENvironment for Visualizing Images (Harris Geospatial Solutions, Boulder, CO) and uses Landsat 5 TM and Landsat 7 ETM images to calculate a seasonal normalized difference vegetation index (NDVI) values using surface reflectance. In contrast to native vegetation, cheatgrass has a distinct peak greenness in the early spring, and no greenness in mid-summer, associated with senescence. Therefore, we calculated a difference NDVI (dNDVI) at a pixel-level to create a map of cheatgrass presence/absence using the following equation:

$$dNDVI = NDVI_{early\text{-}season} - NDVI_{mid\text{-}summer}$$

The optimal window for the early-season satellite image in our study area was previously found to be between March 30 and April 23 and the mid-summer image between June 18 and July 12 (Kokaly 2011). Cloud cover can distort the radiance and reflectance of vegetation so images with high cloud cover were not used for analysis. Cloud-free images in the optimal time window were used to produce dNDVI values at a pixel-level within park boundaries. We used previously established dNDVI thresholds for our study region to designate a high or low probability of a pixel containing cheatgrass (Kokaly 2011). The threshold for a high probability

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of a pixel containing cheatgrass was dNDVI > 0.1, and the threshold for low probability of a

pixel containing cheatgrass was 0.075 < dNDVI < 0.1. Pixels with dNDVI < 0.075 were

designated as a pixel absent of cheatgrass and assigned a value of 0 for subsequent analysis.

Maps were produced for all seven parks showing presence (low and high probability combined)

and absence of cheatgrass.

We extracted cheatgrass cover estimates from 4,121 unique site x year combinations from

1999 – 2009 at permanent monitoring plot (30 x 30 m) and transect (100 m) locations within the

study area (Miller 2018; Munson et al. 2011) to perform an accuracy assessment and ground

truth the maps. Cheatgrass was considered present if it occurred at > 10% canopy cover inside

monitoring plots (Miller 2018; Munson et al. 2011). We randomly selected 1,200 monitoring

locations and compared cheatgrass presence to the DESI maps. Overall accuracy was found to be

85 – 92% across all years of the study period. Maps accuracy was confirmed by park staff with

expertise on cheatgrass locations.

Kokaly (2011) identified confidence levels for whether individual pixels were dominated by

cheatgrass. The highest confidence pixels, given a value of 2, had a high probability of

cheatgrass (dNDVI > 0.1) and more than 1 of the 8 neighboring pixels with a dNDVI > 0.075

(low probability threshold). Moderate confidence pixels, given a value of 1, had a lower

probability of cheatgrass (0.1 > dNDVI > 0.075) and 1 or more of the 8 neighboring pixels with

a dNDVI > 0.075. All DESI cheatgrass maps for each study site were combined using the GIS

software, ArcMap 10x (ESRI 2011). Each pixel in this integrated map is a summed cheatgrass

value of all years ranging between 0 and 22. A value of zero corresponded to no annual pixels

over the period of record having any probability of cheatgrass. If each year had a high

confidence value across all years, a pixel value of 22 was assigned. The end result was one raster

layer where each pixel represented all DESI images from each year added together (the final DESI layer) (Figure 1-1). Higher pixel values suggest greater cheatgrass persistence across years in that specific pixel location.

Hotspot analysis (ESRI 2011) provided a means to statistically evaluate cheatgrass persistence across space and time in the DESI maps. The final DESI layer was converted from raster to vector data, in which the centroid of each pixel became a point with the associated cumulative value of cheatgrass detection probability from all years. Hotspot Analysis calculates the Getis-Ord Gi*statistic (Ord and Getis 1995), which evaluates the sum of an individual point and all surrounding points proportionally to the sum of all points in an individual DESI layer. Z-scores and associated p-values from the Gi* statistic were then calculated for each point. If a point and its neighboring points had a large positive z-score and p>0.05, there is significant spatial clustering called a hotspot. In this study, hot spots represent greater persistence of cheatgrass due to spatial clustering of populations with detection that occurred most years throughout the study. If the z-scores were close to zero and resulted in an insignificant p-value, the point had no spatial clustering and thus cheatgrass presence was considered ephemeral. Coldspots were populations with low or infrequent presence (detection did not occur most years) that had a significant spatial clustering.

Elevation, slope, and aspect, were calculated from a digital elevation model (DEM) (State of Utah Division of Technology and Information Services 2003). Slope and aspect were calculated using the ArcMap v.10x Slope and Aspect Tool with each of the DEM layers. Soil texture (percent sand and clay at 0 – 20 cm depth) were obtained from the NRCS Web Soil Survey (Soil Survey Staff 2015). Depth of plant available water, at a 25 cm profile depth, downloaded from the NRCS Web Soil Survey (Soil Survey Staff, 2015) is a measurement that aggregates available

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water supply at field capacity with corrections for salinity, and rooting depth. Climate data for this study included the mean Standardized Precipitation and Evapotranspiration Index (mean SPEI) (https://wrcc.dri.edu/wwdt/time) from the previous September through May of a DESI image, and antecedent mean summer, fall, winter, and spring precipitation and summer, fall, winter and spring temperature for each year of a DESI image (e.g., 1999 fall precipitation was used for the 2000 DESI image). Precipitation and temperature data were collected from PRISM climate datasets (Daly et al. 2002). All PRISM data were resampled using a cubic convolution to match the 30m x 30m pixel size of the DESI output image.

Because national parks in our study area experience a large number of visitors that can affect cheatgrass distributions, we compiled spatial layers of park boundaries, visitor centers, campgrounds, roads, and trails from the National Park Service GIS data portal (https://irma.nps.gov/DataStore/). We digitized the most current park and trail maps to include published trails and other points of interest from the National Park Service. We created a 200 m buffer around these high human use areas using ArcMap (ESRI 2011) to include invasive annual plant growth that may occur near human impacted locations. For instance, cheatgrass does not grow on paved roads, but likely occurs on the road shoulder or land adjacent to a road (Gelbard and Belnap 2003).

Statistical Analysis

We used a Principal Components Analysis (PCA) to identify whether parks could be grouped together to increase the spatial scale of analysis. We expected cheatgrass dynamics to vary depending on general physical attributes such as common climate and topographic variables (e.g. elevation distributions); therefore, analyzing grouped parks with shared attributes increases spatial scale compared to analyzing each park individually. We used a correlation matrix to

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determine whether the biophysical factors including precipitation, temperature, elevation, slope, and soil characteristics could be pooled for use in a Principal Components Analysis (PCA). Mean summer, fall, and spring temperature and winter precipitation were left out of the PCA (Pearson's correlation > 0.85) due to uneven loading potential (Smith 2002). Using a benchmark cumulative Eigenvalue of 70%, the parks were categorized into like groups (see results below). PCA was performed using JMP 13pro (JMP Pro 1989-2012).

To test which biophysical factors were significant in explaining cheatgrass occurrence and persistence using the Hotspot analysis, a stepwise discriminant analysis was performed using SAS© software (SAS Institute 1990). However, due to the very low proportion of coldspots (Table 1) that caused a violation of the general 9:1 hotspot:coldspot ratios assumption (Zuur et al. 2007), the coldspots were dropped from the analysis. Because of high correlations between temperature and precipitation data, all temperature data except for mean winter temperature was left out of the discriminant analysis. Our decision to keep precipitation data over temperature is due to the evidence that fall temperatures are likely to be favorable for cheatgrass growth as long as there is sufficient water (Germino et al. 2015). Mean SPEI was also a way to incorporate temperature as a biophysical component. To avoid violating the assumption of spatial independence, we performed a repeated simulation of randomly selecting 1000 points from each Hotspot analysis category and ran the stepwise discriminant analysis 1000 times with no repeated samples. The order in which variables were used for the discriminant functions were recorded in summary tables to identify which biophysical attributes best discriminated against hotspot categories in a weighted frequency table (Table 2). Weighted frequency was calculated by taking into account the order in the discriminant function (1st, 2nd, 3rd, etc) and how frequent the variable was used at that order. This was done for all parks combined and then for each group

of parks categorized by the PCA. Once those biophysical variables were identified in the weighted frequency table, a discriminant function was made for each grouping.

To test whether the mean values of the biophysical characteristics were statistically significant across hot spots, ephemeral, and no cheatgrass points, we performed a pairwise comparison using Wilcoxon rank sum test with a Bonferroni correction method using the stats package in R (Hollander et al. 2013; R Development Core Team 2016). A random sample with minimum distance set by the inverse distance weighting measurement used in the hotspot analysis was used to ensure spatial independence of the samples because points outside of that distance range were not used to assess hotspot categorization during the hotspot analysis phase.

Kernel density estimation plots were used to visually characterize the most important biophysical variables in explaining cheatgrass presence of each park group. Kernel density estimation, approximates the probability of the distribution for the population of a particular measured biophysical variable based on the sample population for that biophysical variable. These estimates are then used to visualize differences in distributions of the characterizing biophysical attributes between each hotspot analysis category for each park group when displayed on the same plot. Kernel density estimation plots were created using ggplot2 package in R (R Development Core Team 2016; Wickham 2016).

<div align="center">RESULTS</div>

PCA

Two principal components were found to be important in categorizing park groups (Figure 1-2). Component One (Eigenvalue= 51.3%) was largely driven by mean fall and mean spring precipitation, mean winter temperature and elevation, with relatively equal contributions from each variable. The second component (Eigenvalue=19.8%) largely consisted of clay and sand

content with equal contributions from each of these three variables. Component One clustered the parks into two main groups: hot, dry parks (AN group: Arches, Canyonlands, Capitol Reef, Glen Canyon, and Natural Bridges) and the cold, wet parks (BD group: Bryce Canyon and Dinosaur).

Hot Spots

Cheatgrass had a value of at least 1 in the final composite layer (all years combined) in 3.8% of the area across all parks (Table 1-1, Figure 1-3). Within the 3.8% area where cheatgrass was detected, hot spots, ephemeral, and coldspots populations covered 12.9%, 85.9%, and 1.2% respectively (Table 1-1). The AN park group had twice as much cheatgrass cover as the BD park group but the BD park group had slightly more hot spots (Table 1-1). The two smallest parks, Dinosaur NM and Natural Bridges NM, had the highest cheatgrass detection where 24.8% and 14.8% of the parks were covered in cheatgrass in addition to the highest proportion of hot spots (Table 1-1).

Biophysical Attributes by Park Group

All Parks

For all parks combined, the best discriminant function combined the following six variables in decreasing order of importance: depth of plant-available water, elevation (m), mean winter temperature (C), mean winter precipitation (mm), slope (degree), and percent clay (Λ= 0.8836213, F= 7349, P ≤ 0.0001) (Table 1-2). Percent weight for each variable decreased nearly 2-fold in descending order (Table 1-2). Because the top four variables for each park group comprised >80% of the discrimination, we report only them (though results for all variables can be viewed in Table 1-4). Hot spots had a higher probability of occurring in areas with deeper

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plant-available water (P ≤ 0.05) and a lower elevation by 90-100 m (P ≤ 0.05) compared to ephemeral populations and no cheatgrass areas. Hot spots also had 1 °C colder mean winter temperatures (P ≤ 0.05) than ephemeral but no difference in mean winter temperatures compared to no cheatgrass (P > 0.05). Hot spots had fairly similar mean winter precipitation values of 43.6 mm/winter (P > 0.05) (Table 1-3, Figure 1-3). Ephemeral populations had a higher probability of being found in areas with: deeper plant-available water (P ≤ 0.05), a 60 m lower average elevation (P ≤ 0.05) and warmer mean winter temperatures (P ≤ 0.05), but similar mean winter precipitation (P > .05) when compared to no cheatgrass areas (Table 1-3, Figure 1-3).

Arches, Canyonlands, Capitol Reef, Glen Canyon, Natural Bridges Park Group

The best discriminant function for the hot, dry parks (AN group) used five variables in decreasing order of importance: percent clay, elevation, mean winter precipitation, depth of plant-available water, and distance to human infrastructure (km) (Λ= 0.88265, F= 4808.2, P ≤ 0.0001) (Table 1-2). Clay content was 4 ± 0.02 % in hot spots compared to ephemeral or no cheatgrass locations (Table 1-3, Figure 1-4) (P ≤ 0.05). Hot spots were 100-160 m lower elevation (P ≤ 0.05) and was on average a 0.5 km closer to human infrastructure (P ≤ 0.05) compared with ephemeral populations and no cheatgrass areas (Table 1-3, Fig 1-3). Hot spots had 1 mm more mean winter precipitation and deeper plant-available water (P ≤ 0.05) than no cheatgrass areas (P ≤ 0.05). There was no difference in mean winter temperature and plant available water between hot spots and ephemeral populations (P > 0.05). Ephemeral populations had higher probability of being found in 3% higher percent clay (P ≤ 0.05) than no cheatgrass areas. Ephemeral populations had lower elevations by 62 m on average (P ≤ 0.05), and deeper plant-available water depths (P ≤ 0.05) compared to no cheatgrass areas. There were no

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differences in ephemeral and no cheatgrass areas mean winter precipitation (P > 0.05) (Table 1-3, Figure 1-2:1-6).

Bryce Canyon and Dinosaur Park Group

The best discriminant function for the BD group used seven variables in decreasing order of importance: slope, mean winter temperature, depth of plant available water, mean fall precipitation, elevation, and mean SPEI, and distance to human infrastructure (Λ= 0.7164597, F= 6996.7, $P \le 0.0001$) (Table 1-2). Hot spots had a 2.4- and 4-fold decrease in slope ($P \le 0.05$) compared to ephemeral and no cheatgrass areas (Table 1-3, Fig 1-6). Hot spots had a 0.35 °C drop in mean winter temperature ($P \le 0.05$), deeper plant-available water ($P \le 0.05$), and nearly 9 mm less mean fall precipitation ($P \le 0.05$) than ephemeral populations and no cheatgrass areas (Table 3, Figure 1-6). Ephemeral populations had a 1.7-fold decrease in slope ($P \le 0.05$), a similar mean winter temperature ($P > 0.05$), deeper plant-available water ($P \le 0.05$), and similar mean fall precipitation when compared with no cheatgrass areas ($P > 0.05$) (Table 1-3, Figure 1-1:1-6).

DISCUSSION

The systematic model that we developed as part of our first objective demonstrated that there are strong spatial and temporal factors associated with the distribution of cheatgrass in the Colorado Plateau national parks. By combining the insights and results derived from remote sensing, detection algorithms, and hotspot analysis, the data indicate that cheatgrass can be mapped on large landscape scales with high accuracy and efficiency (Figure 1-3) allowing an examination of the biophysical correlates driving its distribution (Table 1-2 and 1-3, Figure 1-4:1-6). Our findings indicate that *hot spots,* areas with persistent cheatgrass, are found across the

Colorado Plateau and appear to be most strongly correlated with deeper plant available water, lower elevations, colder mean winter temperatures, flatter slopes, and lower mean fall precipitation compared to *ephemeral* populations and *no cheatgrass* areas (Table 1-3). However, there are notable landscape differences between the two park groups, and their separation creates a more tailored suite of biophysical characteristics with which to examine cheatgrass distribution. This is important information in understanding where future invasions and possible expansions are likely with projected climate change (Bradley et al. 2018).

Presence and Persistence of Cheatgrass

Cheatgrass dominates nearly 4% of the total area of Colorado Plateau's national parks (Table 1-1, Figure 1-3). This is likely an underestimate of cover, given the required detection thresholds (Bradley et al. 2018; Kokaly 2011) and the more robust alpha level cutoffs we used (see methods). Of particular concern is Dinosaur NM, where hot spots covered nearly 25% of the park area (Table 1-1). In this park, grazing and fires have created widespread disturbance in the past 150 years (Sherrill and Romme 2012) that promote cheatgrass establishment and spread (St. Clair et al. 2016). Cheatgrass is considered one of the most aggressive invasive plant species and its successful establishment increases the likelihood of more frequent and larger fires (Bradley et al. 2018). This suggests that parks which have a high percentage of cheatgrass hot spots, like Dinosaur NM, are at increased risk of shorter fire intervals (Sherrill and Romme 2012). Increases in fire occurrence will substantially degrade visitor experiences (Bowman et al. 2011), reduce ecosystem services and biodiversity (St. Clair et al. 2016), and diminish the ability of the National Park Service to meet its mandate to conserve native species (National Park System Advisory Board 2001; Thompson et al. 2011).

Spatial patterns of cheatgrass invasion may have a foundation in the historical and current land use of the parks. Patterns seen in Glen Canyon NRA show ephemeral populations are spatially spread along the Lake Powell reservoir and Colorado river's edge (Figure 1-3). Receding water levels in response to drought and increased water demand in Glen Canyon NRA exposes more land every year, causing concern that cheatgrass may colonize in those locations (Bureau of Reclamation 2016). High numbers of recreationists in those areas in Glen Canyon compound the problem, as cheatgrass is an opportunistic invader that responds well to disturbance (Bradford and Lauenroth 2009; Gelbard and Belnap 2003). Other land uses, such as historical agricultural use, have led to a degraded native state previous to park establishment (Knapp 1996; Munson et al. 2016). In Canyonlands, where hot spots are found mostly in the south and southeastern parts of the park (Figure 1-3), continuous and heavy grazing from the mid-1800's until park establishment in 1964 has facilitated heavy invasions and as a result native plants have struggled to re-establish and rebound even after >40 years of no grazing (Fick et al. 2016). Grazing in semi-arid and arid ecosystems can lead to an increase in invasibility by removing biotic resistance from the perennial herbaceous vegetation (Knapp 1996; Walker et al. 1981).

Biophysical Correlates

   Hot spots and *ephemeral* populations had a higher probability of being located in areas with deeper plant available water (Table 1-3; Figure 1-4:1-6). Soil moisture is a strong regulator of seed germination and a strong determinant of plant establishment success (Horn et al. 2015; Prevéy and Seastedt 2014; Roundy et al. 2007). Cheatgrass is a good competitor for soil water because of fast growing roots and a long growing season particularly when it germinates in the fall (Mack and Pyke 1983; Melgoza et al. 1990). Soil moisture is typically recharged with late

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summer monsoons on the Colorado Plateau, which can favor winter annual plants like cheatgrass that germinate in the fall when there is adequate soil moisture (Munson et al. 2011). Soil moisture at the surface can be vulnerable to evaporation in warmer temperatures, therefore having deeper soil moisture available after summer precipitation will favor establishment after fall germination before transitioning to winter (Cline et al. 1977; Miller et al. 2006).

Precipitation timing influences plant productivity and germination but may not be as good of an indicator for discriminating between cheatgrass population groups (Table 1-3) (Horn et al. 2017; Prevéy and Seastedt 2015). Our results show that *hotspot* distributions were not strongly correlated with differences in the amount of precipitation in spring, summer, or winter periods and only slightly with fall precipitation compared to *ephemeral* or *no cheatgrass* (Table 1-3, Figure 1-4:1-6). *Hot spots* were found in areas with lower mean fall precipitation compared to *ephemeral* and *no cheatgrass* areas (Table 1-3, Figure 1-6d). We expected increased mean fall precipitation to play an important role in determining persistent populations of cheatgrass because of the positive effect of early precipitation on fall germination (Gill et al. 2018; Horn et al. 2017; Prevéy and Seastedt 2014). However, as the data show this is not the case (Table 1-3; Figure 1-6d). Potentially the reason why there are increased probability of hot spots with lower fall precipitation is when soils have water at depths greater than 0.5 m, niche partitioning between natives and cheatgrass increases (Bradford and Lauenroth 2009; Schwinning and Ehleringer 2001). Lower fall precipitation may not wet the soil deep enough, negatively affecting natives with deeper roots, in which they are not able to persist and/or compete with cheatgrass for limited water resources higher in the soil profile increasing cheatgrass' potential persistence (Chambers et al. 2007; Cline et al. 1977). Our findings also show that ephemeral populations and no cheatgrass areas have near identical mean fall precipitation (Table 1-3, Figure 1-6d). This

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may imply that ephemeral populations are growing in well-established native woody communities in which the natives are not as susceptible to cheatgrass' competitive effects (Booth et al. 2003). Climate scenarios predict changes to fall precipitation that could favor the increase of ephemeral populations (Christensen et al. 2007; Horn and St Clair 2017). More ephemeral populations could eventually mean more hot spots by increasing propagule availability (Horn et al. 2017; Mazzola et al. 2011).

Persistent populations of cheatgrass were found in areas with lower mean winter temperature (Table 1-3; Figure 1-4 and 1-5). Temperature influences soil-water relations and long-term survival of cheatgrass seedlings (Chambers et al. 2007; Davis et al. 2000). Cheatgrass can germinate at cold temperatures and harden off before winter temperatures drop too low or grow throughout the winter (Chambers et al. 2007; Meyer et al. 1997). Cooler temperatures result in less evapotranspiration which would increase favorable soil-water conditions (Chambers et al. 2007; Davis et al. 2000; Meyer et al. 1997). Even at higher elevations, slower accumulation of degree-days favors cheatgrass density and population growth due to a lower risk of detrimental winter germination (Griffith and Loik 2010). Ephemeral populations are more likely found in warmer mean winter temperatures than areas of no cheatgrass and persistent populations (Table 1-3, Figure 1-4 and 1-5). Without sufficient precipitation, a warmer winter could prevent persistence in cheatgrass growth through the lack of suitable soil moisture (McMichael and Quisenberry 1993).

Cheatgrass establishment can vary strongly across elevation gradients (Abella et al. 2012; Prevéy and Seastedt 2014). *Hot spots* and *ephemeral* populations had a higher probability of being found below elevations of 1300 m (Table 1-3, Figure 1-4b), similar to the results of Chambers et al. (2007), and may be limited by long term soil freezing and increased snow cover

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at higher elevations (Griffith and Loik 2010). Higher elevations typically have later snow pack melt which delays cheatgrass growth and emergence (Concilio et al. 2013). Lower elevations that still have some snow cover have warmer soils and earlier spring melt which is conducive to cheatgrass germination and growth (Chambers et al. 2007; Roundy et al. 2007). Climate variability also increases with lower elevations which increases susceptibility to invasion in an arid or semi-arid environment (Chambers et al. 2007; Dukes and Mooney 1999).

Hot spots were more likely in areas with higher percent clay (Table 1-2, Figure 1-5). Soil characteristics greatly affect the germination and establishment of plants through their influence on water relations and nutrient holding capacity (Marschner 1983). Higher clay content has higher water and nutrient holding capacity (Hillel 1998). Cheatgrass showed higher germination and establishment in areas with greater clay content in wet years (Miller et al. 2006) likely due to better water availability in the upper profile of the soil where cheatgrass typically can outcompete native plants (Bradford and Lauenroth 2009).

We found more hot spots in flatter landscape settings (Table 1-3, Figure 1-6a), possibly because of greater soil stability and increased land use compared with places with steep slopes. Flatter slopes typically experience less water induced soil erosion and increased soil depths which favor water retention (Morgan 2009). Studies have also shown downslope patterns in clay and silt content which would create more suitable conditions for cheatgrass persistence (Neff et al. 2005; Reynolds et al. 2006). Flatter landscapes also experience and are more easily accessible for animal and human use (Morgan 2009). Cheatgrass has a well-documented positive interaction to disturbance and increased land use (Bradley et al. 2018; Gelbard and Belnap 2003; West et al. 2017) which could be intensified in areas that have easier access. Soil erosion, removal of native vegetation, and decreased biological soil crusts have adverse impacts that

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increase susceptibility and success of invasion by cheatgrass (Belnap et al. 2001; Cline et al. 1977; Levine et al. 2003).

Our results did not show that human infrastructure such as trails, roads, and visitor centers played a key role in discriminating between *hot spots, ephemeral,* and *no cheatgrass* areas (Table 1-2). However, *hot spots* were on average closer to human infrastructure compared to *ephemeral* and *no cheatgrass* (Table 1-4). Legacy effects of historic land uses could lead to the persistence of cheatgrass in certain areas of these parks and historical disturbance is likely to play a key role in how the biophysical correlates interact (D'Antonio and Thomsen 2004; Mack et al. 2000; Neff et al. 2005). For example, as parks like Canyonlands experienced heavy and continuous grazing before park establishment, biological soil crusts that are known to be able to resist and prevent cheatgrass establishment by creating physical barriers for germination and growth are disrupted creating an opportunity for invasion (Deines et al. 2007; Serpe et al. 2008). Areas of the park that meet the landscape criteria for *hot spots* in the AN park group (low elevation, higher clay, flatter slopes, and deeper soils) (Table 1-3, Figure 1-3 and 1-5) are also areas that have had these historical land disturbances that have shown long term legacy effects in other studies (Figure 1-2) (Fick et al. 2016; Munson et al. 2016).

GIS Remote Sensing

The results of this study have broadened our understanding of landscape level biophysical factors that are associated with cheatgrass establishment and persistence. The combination of remote sensing and GIS technology we used was both cost- and time- effective, unlike many previous efforts (Mack 2010). Previous GIS remote sensing studies of cheatgrass distribution had to be highly selective in what years were used (Balch et al. 2013; Bradley 2009a; Bradley and Mustard 2006), were restricted by the coarse resolution of MODIS (250m and 1km) (Balch et al.

2013; Bradley et al. 2018; Stohlgren et al. 2010), and required >40% plant cover for accurate detection (West et al. 2017). Although our DESI analysis used commercial software (*ENVI version 4.8* (*Exelis Visual Information Solutions,* Boulder, Colorado)), comparing NDVI images from different seasons can be more widely adopted on publicly available cloud-computing platforms to detect cheatgrass and other invasive species with distinct phenologies. This approach can lead to highly accurate detection, across different landscapes, with relatively low invasive cover, an increased number of years, and at greater spatial resolution.

Conclusion

The expansion of cheatgrass is a major concern for the national park service and land managers because of its ability to alter fire cycles and create vegetation state changes (D'Antonio and Vitousek 1992). The hot spots we identified provide an ideal target for high priority management, as these areas are likely seed sources for the future expansion of cheatgrass populations (Mazzola et al. 2011). By reducing hot spots, expansion may be halted or slowed. *Ephemeral* populations are problematic in certain years, especially those with above-average precipitation, and can perpetuate habitat degradation potentially creating more *hot spots* (Bradley et al. 2018; Pilliod et al. 2017). As the understanding of what causes big fire years and the biophysical traits associated with invasive species-fire cycles improves (Balch et al. 2018), knowing the geographic locations of potential *hot spots* and *ephemeral* populations based on predictive modelling would enable more preventative management measures. In addition, these areas need to be analyzed and assessed under future climate conditions or expected changes in land use, as invasion potential may change (Bradley 2009b; Prevéy and Seastedt 2015). Using our data combined with future climate models might provide preliminary predictions about future establishment and spread of cheatgrass across the Colorado Plateau. Preventing unnatural

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wildfire damage would decrease economic, ecologic, and human health hardships associated with wildfire (Bowman et al. 2011; Thompson et al. 2011). Areas with no cheatgrass are important to identify so that limited management resources can be applied elsewhere. This hierarchical management approach allows more effective utilization of resources and likely better outcomes in these changing landscapes.

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Media.
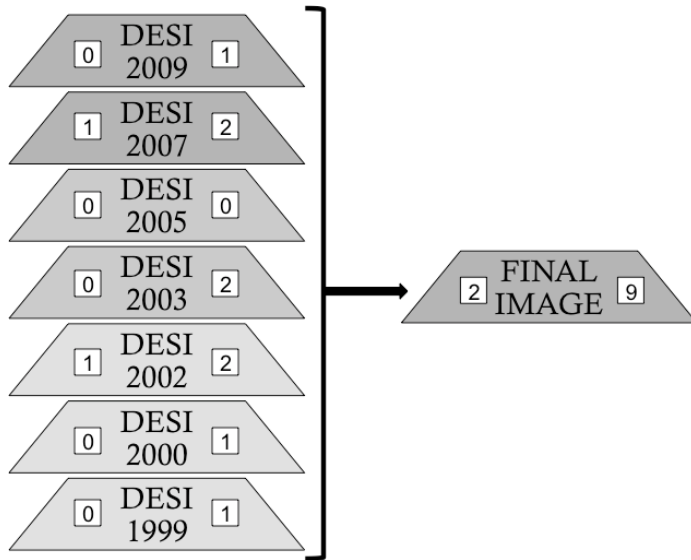
Figure 1-1 Conceptual model showing how the final DESI image was produced by combining all available DESI images for each park.
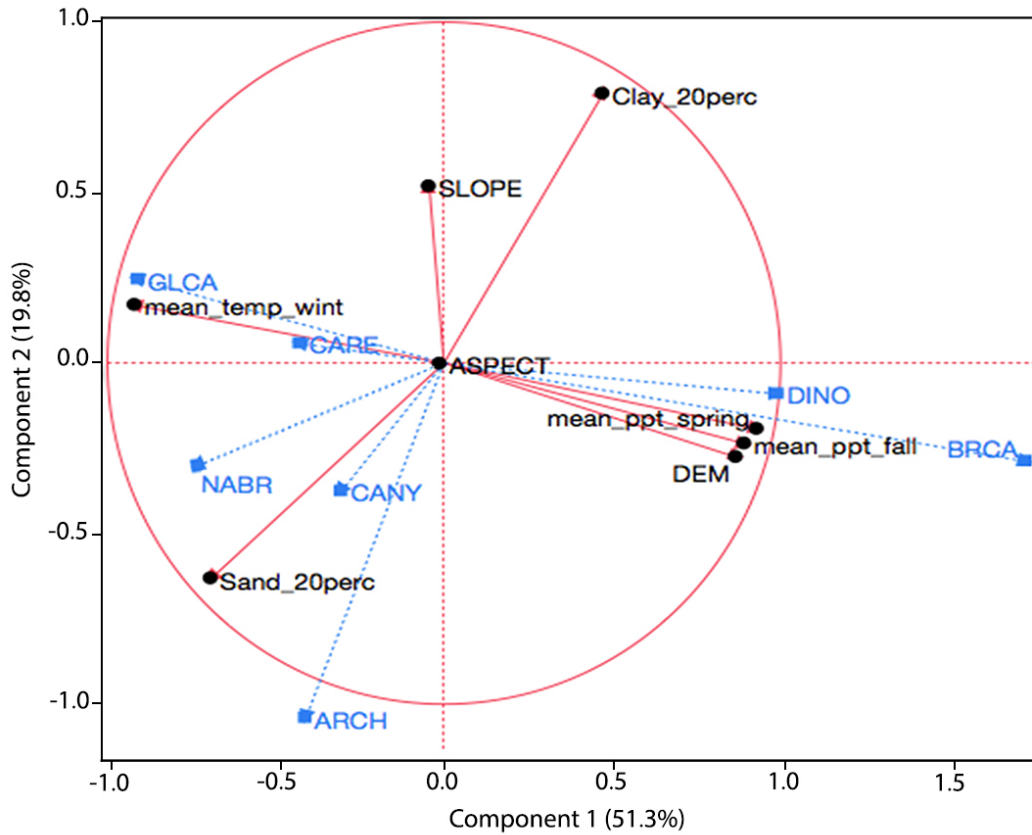
Figure 1-2 PCA biplot showing the loading for each variable. Park groupings were determined mainly by the clustering along Component 1 axis. Bryce Canyon NP (BRCA) and Dinosaur NM (DINO) became BD park group. Glen Canyon NRA (GLCA), Capitol Reef NP (CARE), Natural Bridges NM (NABR), Canyonlands NP (CANY), and Arches NP (ARCH) were grouped into the AN park group. Eigenvalues for each component given in each axis title.
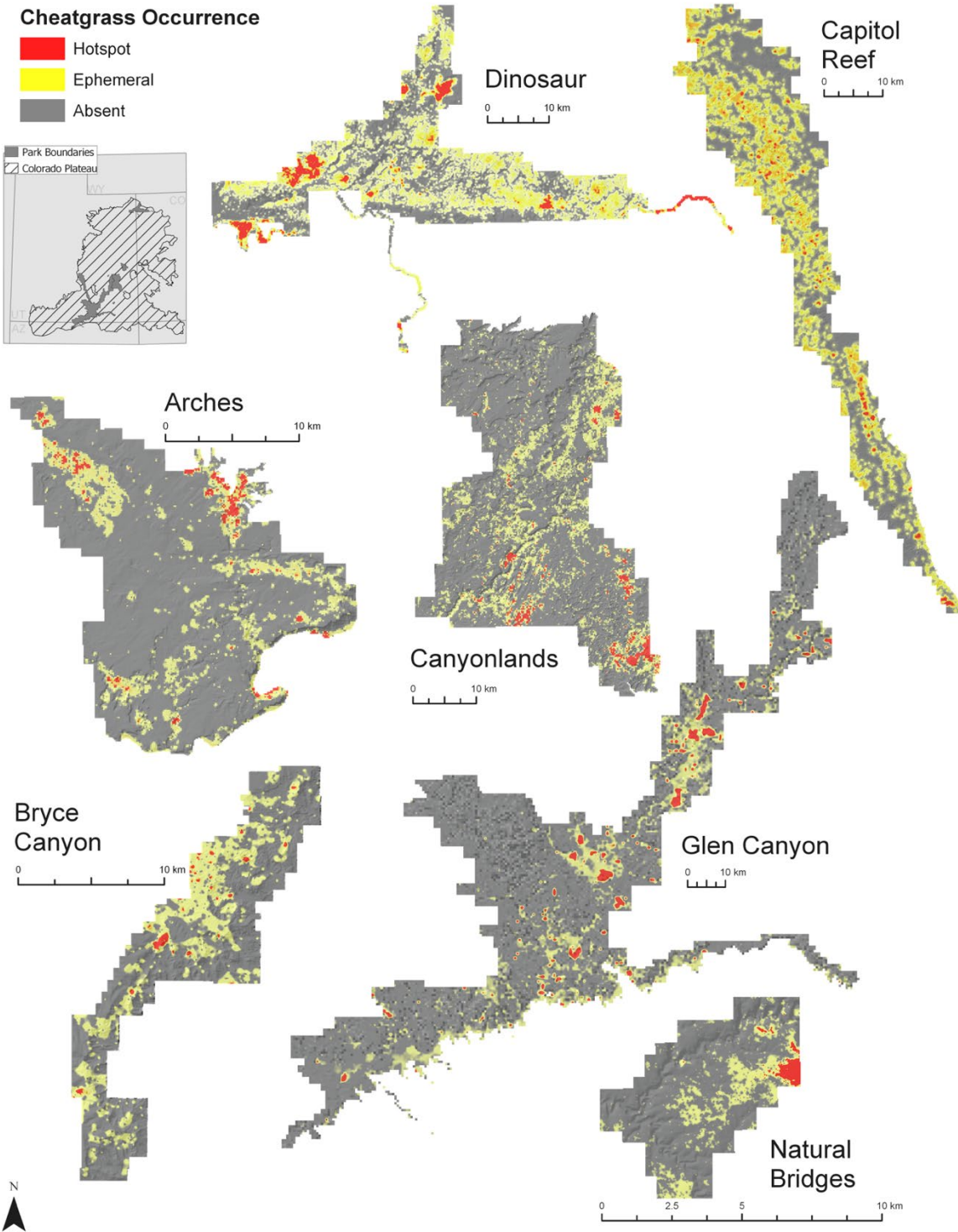
Figure 1-3 Hotspot maps visualizing each park and the locations of hotspots, ephemeral populations, and areas of no detectable cheatgrass growth. Each park base layer is an elevation relief.
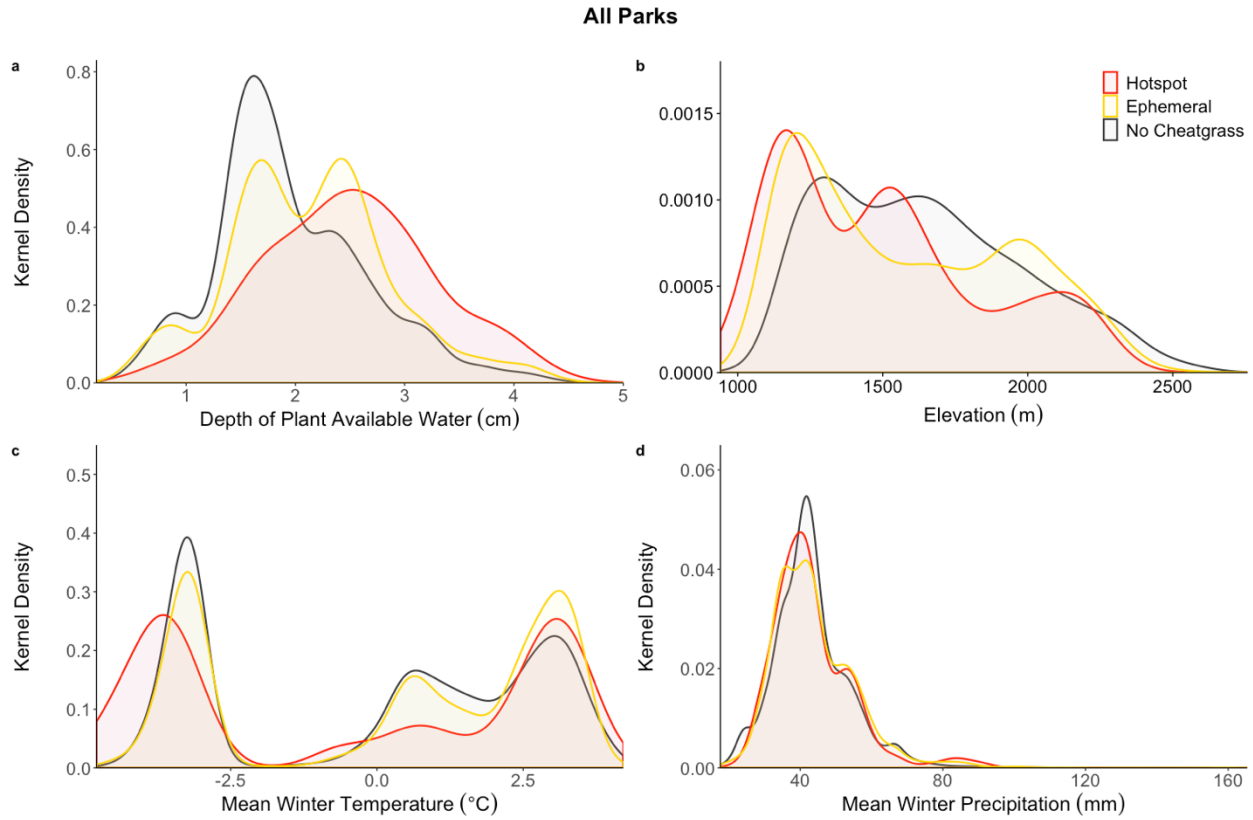
All Parks

Figure 1-4 Kernel density plots of the top four weighted variables when all parks are combined: (a) Plant available water depth (38.1%), (b) Elevation (20.6%) (c) Mean winter temperature (13.0%), and (d) Mean winter precipitation (7.4%)
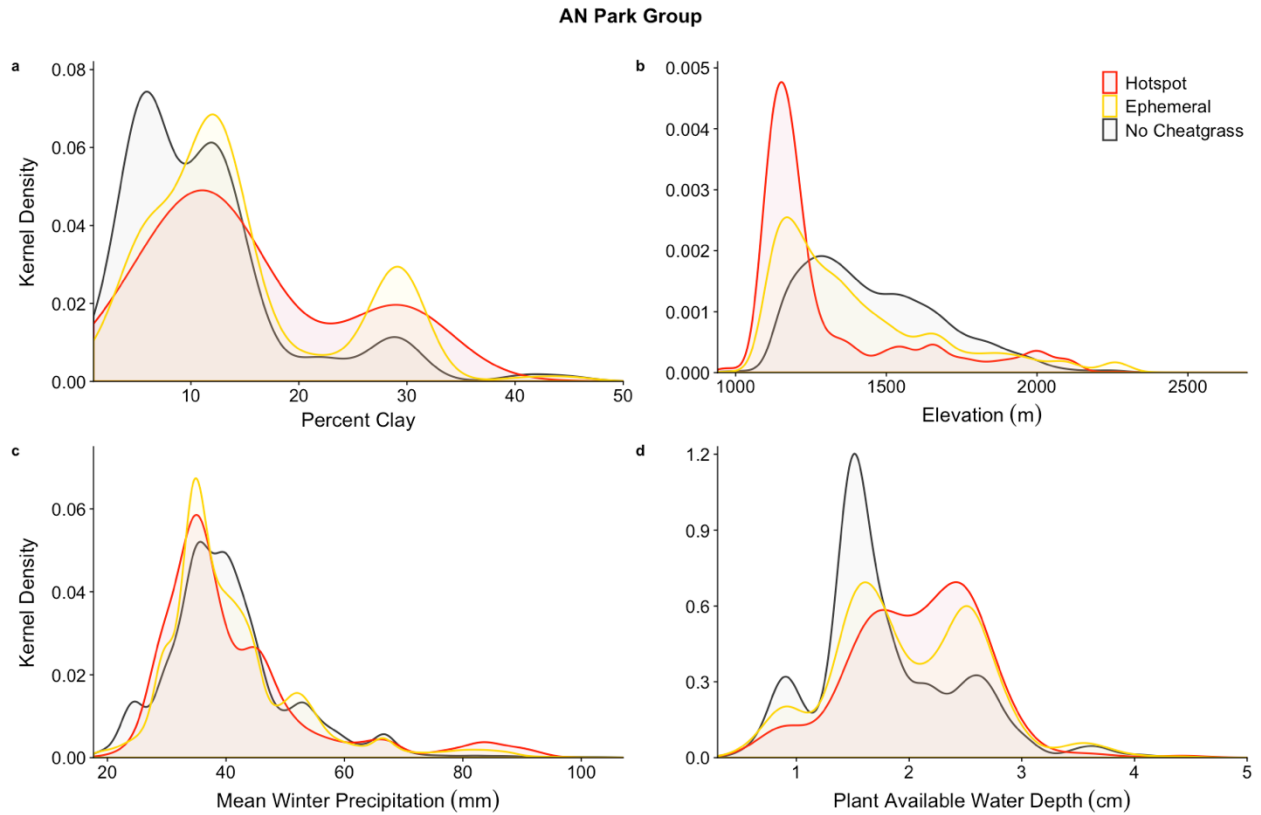
Figure 1-5 Kernel density plots of the top four weighted variables for the AN Park Group (Arches, Canyonlands, Capitol Reef, Glen Canyon, and Natural Bridges): (a) Percent Clay (33.5%), (b) Elevation (22.5%), (c) Mean winter precipitation (12.6%) and (d) Plant available water depth (6.3%)
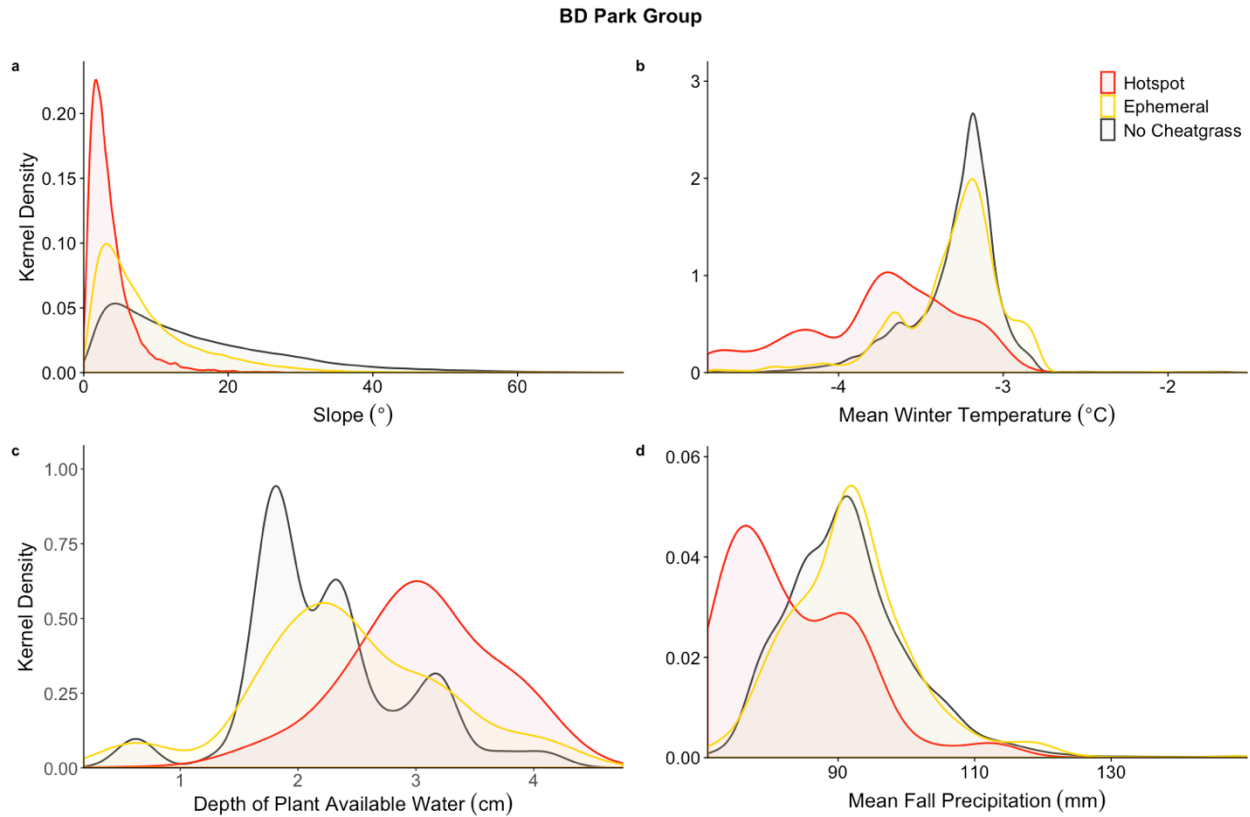
Figure 1-6 Kernel density plots of the top four weighted variables in the discriminant function for the BD Park Group (Bryce Canyon and Dinosaur): (a) Slope (38.3%), (b) Mean winter temperature (23.8%) (c) Plant available water depth (12.0%), and (d) Mean fall precipitation (7.4%)

Table 1-1 Climate, elevation, cheatgrass cover, and cheatgrass persistence (hotspot – spatially significant persistent populations of cheatgrass, ephemeral – spatially insignificant temporally variable populations of cheatgrass) in each park unit and park group (AN-Arches, Canyonlands, Capitol Reef, Glen Canyon, and Natural Bridges; BD park group- Bryce Canyon and Dinosaur)

| National Park Unit | Park Characteristics | | | | | Cheatgrass % of Total Park Area | Hotspot Analysis of Total Cheatgrass | |
	Average annual precipitation (mm)	Average Tmax C	Average Tmin C	Elevation Range (m)	Area (km2)		Hotspot	Ephemeral
Arches National Park	209.6	22.2	6.3	1245-1723	310	2.6%	10.3%	89.7%
Bryce Canyon National Park	369.5	13.3	-1.9	2400-2700	145	1.5%	2.6%	97.4%
Canyonlands National Park	212.5	19.0	5.5	1128-2170	1365	5.9%	12.1%	87.9%
Captiol Reef National Park	189.0	18.6	5.5	1800-2700	979	0.8%	2.7%	97.3%
Dinosaur National Monument	227.8	16.3	2.7	1432-2700	853	24.8%	16.8%	82.9%
Glen Canyon National Recreation Area	181.7	21.8	9.5	930-2319	5075	5.7%	11.3%	86.6%
Natural Bridges National Monument	299.6	17.2	3.7	1600-2000	31	14.8%	13.0%	86.9%
All Parks	241.4	18.3	4.5	930-2700	8758	3.8%	12.9%	85.9%
AN Park Group	218.5	19.8	6.1	930-2700	7760	5.0%	11.3%	87.2%
BD Park Group	298.6	14.8	0.4	1432-2700	998	2.5%	16.6%	83.1%

Table 1-2 Biophysical attributes weighted frequency in discriminating among hotspots, ephemeral, and no cheatgrass. * denotes attributes included in the best discriminant function for each park group.

	Weighted frequency percent		
	All Parks	AN Group	BD group
Aspect	0.6%	1.9%	0.2%
Depth of plant available water (cm)	38.1% *	6.3% *	12.0% *
Distance to human infrastructure	0.3%	6.0% *	2.9% *
Distance to park boundary	0.5%	1.2%	0.3%
Elevation (m)	20.6% *	22.5% *	5.5% *
Mean fall precipitation (mm)	3.4%	4.9%	7.4% *
Mean spring precipitation (mm)	2.9%	4.0%	0.1%
Mean SPEI	0.3%	0.9%	3.9% *
Mean summer precipitation (mm)	2.7%	3.5%	2.7%
Mean winter precipitation (mm)	7.4% *	12.6% *	2.8%
Mean winter temperature (C)	13.0% *	0.4%	23.8% *
Percent clay in top 20 cm of soil	3.9% *	33.5% *	1.5%
Percent sand in top 20 cm of soil	0.8%	1.5%	2.6%
Slope	5.5% *	0.8%	38.3% *

Table 1-3 Top four biophysical attributes in order for best discriminant function. Means ± SE presented for each cheatgrass population type: No cheatgrass (NC), Ephemeral, Hotspots, in the top three rows of each park group. Pairwise comparisons were done using Wilcoxon rank sum test. W-values and significance indicated by asterisks: *P ≤ .05, **P ≤ .01, ***P ≤ .001 in the bottom three rows of each park group.

Top Four Weighted Biophysical Attributes

		Depth of plant available water (cm)	Elevation (m)	Mean winter temperature (C)	Mean winter precipitation (mm)
All Parks					
	No cheatgrass	1.96 ±0.001	1645 ±1	0.02 ±0.004	43.4 ±0.02
	Ephemeral	2.14 ±0.001	1585 ±1	0.30 ±0.005	44.04 ±0.02
	Hotspots	2.5 ±0.003	1497 ±1.5	-0.35 ±0.01	43.48 ±0.05
Pairwise comparisons	NC x Hotspots	144447 ***	302590 ***	2556078	1486500
	NC x Ephemeral	1302367 ***	1706133 ***	1377300 **	93324
	Ephemeral x Hotspots	120327 ***	81642 *	80655 *	237137

		Percent clay in top 20 cm of soil	Elevation (m)	Mean winter precipitation (mm)	Depth of plant available water (cm)
AN Group- *Hot, dry*					
	No cheatgrass	11.17 ±0.02	1460 ±0.5	40.4 ±0.02	1.79 ±0.001
	Ephemeral	14.6 ±0.02	1398 ±0.6	41.05 ±0.02	1.99 ±0.001
	Hotspots	15.15 ±0.05	1302 ±1.6	41.44 ±0.08	2.07 ±0.003
Pairwise comparisons	NC x Hotspots	112343 ***	361217 ***	249627 *	148160 *
	NC x Ephemeral	1108367 ***	1864667 ***	1472367	1202567 ***
	Ephemeral x Hotspots	106437 *	63422 ***	85469	109227 ***

		Slope	Mean winter temperature (C)	Depth of plant available water (cm)	Mean fall precipitation (mm)
BD Group- *Cold, wet*					
	No cheatgrass	14.98 ±0.03	-3.51 ±0.00	2.25 ±0.01	91.98 ±0.03
	Ephemeral	8.8 ±0.02	-3.31 ±0.00	2.42 ±0.002	92.03 ±0.03
	Hotspots	3.7 ±0.02	-3.75 ±0.003	3.04 ±0.004	83.33 ±0.06
Pairwise comparisons	NC x Hotspots	403463 ***	36797 ***	101121 ***	353160 ***
	NC x Ephemeral	2021367 ***	1487967	1280467 ***	461900
	Ephemeral x Hotspots	46890 ***	41653 ***	136557 ***	43954 ***

Table 1-4 All biophysical attributes in order of importance in best discriminant function. Means ± SE presented for each cheatgrass population type: No cheatgrass, Ephemeral, Hotspots. Pairwise comparisons using Wilcoxon rank sum test W values significance indicated by asterisks: *P ≤ .05, **P ≤ .01, ***P ≤ .001. Note: NC = No cheatgrass. Dotted line indicates break point where attributes to the left were included in the best discriminant function and attributes to the right were not

All Biophysical Attributes

		Depth of plant available water (cm)	Elevation (m)	Mean winter temperature (C)	Mean winter precipitation (mm)	Slope	Percent clay in top 20 cm of soil	Mean fall precipitation (mm)	Mean spring precipitation (mm)	Mean summer precipitation (mm)	Percent sand in top 20 cm of soil	Aspect	Distance to park boundary (km)	Mean SPEI	Distance to human Infrastructure (km
All Parks															
	No cheatgrass	1.96 ±0.001	1645 ±1	0.02 ±0.004	43.4 ±0.02	15.37 ±0.02	13.45 ±0.01	75.34 ±0.03	53.02 ±0.04	21.31 ±0.004	65.43 ±0.03	184.91	3.02 ±0.004	-0.42 ±0.001	2.85 ±0.005
	Ephemeral	2.14 ±0.001	1585 ±1	0.30 ±0.005	44.04 ±0.02	13.82 ±0.02	15.17 ±0.01	73.9 ±0.03	52.48 ±0.04	21.7 ±0.005	63.61 ±0.03	191.69	3.05 ±0.005	-0.42 ±0.001	2.7 ±0.004
	Hotspots	2.5 ±0.003	1497 ±1.5	-0.35 ±0.01	43.48 ±0.05	9.34 ±0.05	16 ±0.04	72.2 ±0.06	52.33 ±0.1	21.37 ±0.01	61.99 ±0.07	193.13	2.98 ±0.012	-0.45 ±0.0001	1.93 ±0.01
Pairwise comparisons	NC x Hotspots	144447 ***	302590 ***	2556078	1486500	1658300 ***	1328500	1567200 *	246630	1558300	1581300	1445300	1559200	1527100 ***	1545600 ***
	NC x Ephemeral	1302367 ***	1706133 ***	1377300 **	93324	64248 ***	98031 ***	90850 **	1566067	86072 *	92920	89646	95635	86750	74702
	Ephemeral x Hotspots	120327 ***	81642 ***	80655 *	237137	331740 ***	198890	253900	95199	267570	146500	237840	240545	261970 *	290095 ***

		Percent clay in top 20 cm of soil	Elevation (m)	Mean winter precipitation (mm)	Depth of plant available water (cm)	Distance to human infrastructure (km)	Mean fall precipitation (mm)	Mean spring precipitation (mm)	Mean summer precipitation (mm)	Aspect	Percent sand in top 20 cm of soil	Distance to park boundary (km)	Slope	Mean SPEI	Mean winter temperature (C)
AN Group- Hot, dry															
	No cheatgrass	11.17 ±0.02	1460 ±0.5	40.4 ±0.02	1.79 ±0.001	3.22 ±0.007	65.8 ±0.02	38.7 ±0.02	61.6 ±0.02	185 (S-SW)	74.5 ±0.04	3.6 ±.006	15.6 ±0.03	-0.4 ±0.0002	1.9 ±0.02
	Ephemeral	14.6 ±0.02	1398 ±0.6	41.05 ±0.02	1.99 ±0.001	2.88 ±0.006	64.9 ±0.03	38.9 ±0.02	60.7 ±0.03	194 (S-SW)	69.03 ±0.03	3.5 ±0.006	16.3 ±0.03	-0.42 ±0.0002	2.1 ±0.003
	Hotspots	15.15 ±0.05	1302 ±1.6	41.44 ±0.08	2.07 ±0.003	2.64 ±0.02	63.5 ±0.07	37.3 ±0.06	58.1 ±0.06	192 (S-SW)	67.9 ±0.08	4.2 ±0.02	13.7 ±0.09	-0.43 ±0.0007	2.3 ±0.007
Pairwise comparisons	NC x Hotspots	112343 ***	361217 ***	1490050	148160 *	1581600 ***	1591950 **	249627 *	1659800	1474750	1864600 ***	1498900	1534250	1609250 **	1415650 *
	NC x Ephemeral	1108367 ***	1864667 ***	88607	1202567 ***	83211 *	80182	1472367	80960 ***	101367 *	88251 ***	109190	8852	90555 *	110720 ***
	Ephemeral x Hotspots	106437 *	63422 ***	247350	109227 ***	274230 **	284635 **	85469	291960 ***	215090	306115	199945	254375	261625	183330

		Slope	Mean winter temperature (C)	Depth of plant available water (cm)	Mean fall precipitation (mm)	Elevation (m)	Mean SPEI	Distance to human Infrastructure (km	Mean winter precipitation (mm)	Mean summer precipitation (mm)	Percent sand in top 20 cm of soil	Percent clay in top 20 cm of soil	Distance to park boundary (km)	Aspect	Mean spring precipitation (mm)
BD Group- Cold, wet															
	No cheatgrass	14.98 ±0.03	-3.51 ±0.00	2.25 ±0.01	91.98 ±0.03	1966 ±0.7	-0.44 ±0.0002	2.2 ±0.005	48.6 ±0.03	73.2 ±0.04	49.7 ±0.03	17.4 ±0.01	2.1 ±0.004	185 (S-SW)	78 ±0.04
	Ephemeral	8.8 ±0.02	-3.31 ±0.00	2.42 ±0.002	92.03 ±0.03	1962 ±0.6	-0.42 ±0.002	2.3 ±0.006	50.1 ±0.03	73.9 ±0.04	52.6 ±0.04	16.3 ±0.02	2.03 ±0.004	187 (S-SW)	79.8 ±0.04
	Hotspots	3.7 ±0.02	-3.75 ±0.003	3.04 ±0.004	83.33 ±0.06	1747 ±1.9	-0.46 ±0.0007	1.01 ±0.008	46.1 ±0.05	65.7 ±0.09	54.5 ±0.11	17.1 ±0.05	1.5 ±0.008	194 (S-SW)	71.6 ±0.1
Pairwise comparisons	NC x Hotspots	403463 ***	36797 ***	101121 ***	353160 ***	1506250 ***	1324800 **	1511900 ***	1343000 *	1441300 ***	1374700	1810950	830700 **	1512750	1379300 **
	NC x Ephemeral	2021367 ***	1487967	1280467 ***	461900	54814	71871	56235	72848	59735	111545 **	94332 ***	38285	105745	62836
	Ephemeral x Hotspots	46890 ***	41653 ***	136557 ***	43954 ***	337380 ***	274830	337395 ***	266745 ***	318645	158145 *	273600	289715 **	8245	155015 ***

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CHAPTER 2

Fire, Rodent Herbivory, and Plant Competition: Implications for Invasive Grass-Fire Cycle in the Mojave Desert

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Doctor of Philosophy

ABSTRACT

Biological invasions are a primary driver of state changes in Earth's ecosystems. Anthropogenic alterations to disturbance regimes, such as fire, and loss of biotic resistance may contribute to invasion driven state changes in arid ecosystems. Our objective was to experimentally investigate how fire and changes in rodent presence modifies herbaceous plant community structure and invasions in an arid system. We imposed experimental fires and reduced rodent density using fencing in a full factorial design in the Mojave Desert. Vegetation surveys were conducted to determine plant density, cover, and biomass of herbaceous plants over a five year period. Rodent exclusion increased the density, cover, and biomass of *Bromus rubens,* an invasive annual grass, and density of native and exotic forb species. In contrast, rodent exclusion decreased the density, cover and biomass of *Schismus* spp. another dominant annual invader. Fire increased *Schismus* spp. and forb species density, cover, and biomass but decreased *B. rubens* density. Negative spatial correlation between *B. rubens* and *Schismus* spp. and forbs indicate strong local competition. Fire reduced rodent diversity 2.5-fold. Increases in the rodent community diversity were negatively correlated with *B. rubens* cover and biomass, and native plant diversity. In our study, rodent exclusion and plant competition introduced variability in the composition of the herbaceous plant community thereby altering the fine fuel and flammability characteristics of the vegetation. Our results suggest that higher rodent activity and diversity and

competition from *Schismus* spp. and the forb community reduced the density and biomass of *B. rubens*, which because of its taller growth form and flammability characteristics would decrease fire potential. However, the results also suggest that fire may be self-reinforcing by reducing rodent community diversity, which was positively correlated with higher density and biomass of *B. rubens*.

INTRODUCTION

The introduction and spread of exotic species are among the most widespread and damaging human impacts on earth's ecosystems (Vitousek et al. 1997, Pimentel et al. 2005, Vilà et al. 2010). Plant invasions can trigger state changes in vegetation that result in reductions of biodiversity and loss of ecosystem services (Pimentel et al. 2005). Patterns of plant invasions are influenced by biotic interactions between plant invaders and native organisms via competition and herbivory that create biotic resistance to invasion. Disturbance can increase the invasibility of an ecosystem by impacting native biological community structure leading to reduced biotic resistance to invaders (Davis et al. 2000). For example, disturbance-driven decreases in native plant cover increases space, light, and soil resource availability and therefore, promotes the success of plant invaders (Esque et al. 2010a, Steers and Allen 2012). Disturbance can also modify the composition of native consumer communities that control plant invader establishment through seed predation and seedling herbivory (St. Clair et al. 2016).

Human-related activities are altering wildfire regimes at a global scale with broad implications for the invasibility of earth's ecosystem (Vitousek et al. 1997, Brooks 1999a, Germino et al. 2015 and references therein). In dryland ecosystems, which cover as much as 40% of the Earth's terrestrial surface (Sarukhán et al. 2005), there is a close association with human activities, increased exotic annual grass presence, and increased potential for fire ignition (Mack

1981, Gelbard and Belnap 2003). In deserts of North America, wildfires promote invasion success by decreasing biotic resistance through removal of native vegetation (Steers and Allen 2012, St. Clair et al. 2016). Removal of intact native plant communities by fire provides resource opportunities and competition release from native plants that promotes invasive annual grass establishment (Levine et al. 2004, Germino et al. 2015, Horn et al. 2015). Dominance of invasive grasses after fire can decrease the re-establishment success of native plant communities (Brooks et al. 2004, Germino et al. 2015). Fire can also indirectly affect the plant community by modifying the behavior and composition of consumer communities that regulate plant community assembly (Elton 2000, Levine et al. 2004, Horn et al. 2012). Shifts in plant community composition and structure in response to these interactions can alter the fuel characteristics of the plant community that influence the probability and spread of wildfires that promote invasive grass-fire cycles (D'Antonio and Vitousek 1992, Brooks et al. 2004, St. Clair and Bishop 2019).

Rodent herbivory creates top-down control on plant community assembly (Beatley 1976, Inouye et al. 1980, Pearson et al. 2014) and biotic resistance against the establishment of invasive species through seed predation and seedling herbivory (Pearson et al. 2014, St. Clair et al. 2016). Rodents structure plant communities partly by seed caching under shrub canopies and aiding in seed dispersal (Beatley 1969, Price and Joyner 1997). Rodents may therefore facilitate the spread of invasion by increasing dispersal of invasive seeds (Beatley 1976, Price and Joyner 1997, Horn et al. 2017). However, previous studies have documented establishment suppression of weak plant invaders by rodents (Pearson et al. 2012) and there is emerging evidence that they may also create biotic resistance against aggressive plant invaders (St. Clair et al. 2016). Because rodent abundance, richness, and diversity can drastically decrease in response to wildfire (Ostoja

and Schupp 2009, Horn et al. 2012) post-fire conditions may create windows of opportunity for plant invaders to be released from rodent suppression (Allington et al. 2013).

Competition is a key driver of plant community structure and provides a mechanism for biotic resistance against plant invasions (Levine et al. 2004). Intact native plant communities have been shown to reduce the establishment and spread of exotic plant species (Pearson et al. 2012, St. Clair et al. 2016). However, competition within plant communities typically decreases following fire resulting in increased availability of soil resources (Shea and Chesson 2002, Allen et al. 2011, Horn et al. 2017). The niche opportunity hypothesis posits that when resources or a previously occupied niche becomes available, a plant invader that is equipped to capitalize on that opportunity can establish (Davis et al. 2000, Allen et al. 2011, Horn and St. Clair 2017, Gill et al. 2018). In arid and semi-arid environments, native annual plants commonly have positive spatial associations with shrubs due to better microhabitat growing conditions (Brooks and Chambers 2011) leaving a resource and niche opportunity in the open spaces between shrubs (Brooks and Chambers 2011, Schafer et al. 2012). This niche opportunity could allow an exotic plant to move away from a direct competitor and exploit a neighboring but relatively uninhabited area by native plants, filling in inter-shrub spaces with plant biomass and contributing to the invasive grass-fire cycle (D'Antonio and Vitousek 1992, Shea and Chesson 2002).

The Mojave Desert is an ideal study system to examine the interplay of disturbance, herbivory, and competition on ecosystem invasibility because fires are becoming more frequent (Brooks and Matchett 2006), rodents are abundant as a primary consumer and there are multiple plant invaders influencing fire ecology in the system (Brooks and Chambers 2011). The two dominant plant invaders in the Mojave Desert are *Bromus madritensis* L. ssp. *rubens* (hereafter *B. rubens*) and *Schismus* spp. (*Schismus barbatus* or *Schismus arabicus*), and several studies

have examined their role in and response to fire (Brooks and Matchett 2003, 2006, DeFalco et al. 2007, Germino et al. 2015 and references therein). Fewer studies have examined competitive effects between invasives and natives in the Mojave Desert as a function of fire and little research exists examining the influence of consumers on invasibility of the Mojave Desert through experimental treatments (but see Brooks 1995). In high precipitation years *B. rubens* and *Schismus spp.* can fill in intershrub spaces that typically are left void of enough vegetation to carry fire (Brooks and Matchett 2003). However, when both are present on the landscape, *B. rubens* is found more commonly under shrub canopies, particularly the fire susceptible shrub *Coleogyne rasmosissima* Torr. (Beatley 1966) and dominant shrub *Larrea tridentata,* while *Schismus spp.* fills the intershrub spaces (Brooks and Matchett 2003, Allen et al. 2011). However, there is a lack of understanding of how these spatial relationships may be modified by fire or rodent activity and impact competitive relationships and fire potential.

The objective of this study was to experimentally investigate the effects of fire and changes in the rodent community on plant community structure and invasion outcomes in the Mojave Desert. We asked the following questions: 1) What are the effects of fire and rodent exclusion on the establishment and growth of invasive annual grasses and herbaceous forbs, including exotic and native species? 2) Are changes in rodent diversity, richness, and abundance correlated with post-fire plant community characteristics? 3) Is there evidence of competitive interactions between invasive grass species or between exotic grasses and forb species and are they modified by fire or rodent exclusion across space?

MATERIALS AND METHODS

Study Site

The study was conducted at Lytle Research Preserve, Washington Co., UT, USA, in the northeast region of the Mojave Desert (37°08′54″N, 114°00′51″W). No known fires have occurred at the study site in recent decades based on a well-developed perennial shrub community. Cattle grazing has not occurred at the site since 1985. The soil is a semidesert shallow hardpan (blackbrush) classified as very gravelly sandy loam (Soil Survey Staff 2015). It is located at 915 m elevation and mean annual precipitation is 272 mm and mean annual temperature is 16 °C (Western Regional Climate Center 2000). Vegetation is dominated by *Larrea tridentata, Coleogyne rasmosissima* Torr., *Ambrosia dumosa,* and *Yucca brevifolia.* The inter-shrub space contained a dominant establishment of the non-native annuals *Bromus madritensis* L. ssp. *rubens* and *Erodium cicutarium.*

Plot Design

The study tests the main effects of fire and rodent exclusion in a full factorial block design replicated five times (St. Clair et al. 2016). Each 60 m x 60 m experimental block was split into four randomly assigned 30 m x 30 m treatment sub-plots with the following treatment combinations: burned-rodents present, burned-rodents excluded, unburned-rodents present, unburned-rodent excluded. The burn treatment was conducted in June 2011 using a drip torch as an ignition source. The study site was already invaded when the study began with average red brome densities of 1319 stems m^{-2} in the inter-shrub spaces which carried fire across the plots. The experimental fire decreased native shrub density by 59%. Wire mesh fencing was installed around the perimeter of each treatment plot with 30 cm buried below ground and 70 cm above ground. Rodent exclusion plots had a 20 cm strip of aluminum flashing placed at the top to keep

rodents from climbing over the fences. Rodent access plots were achieved by cutting 12 cm x 10 cm opening every 4 m around the fence perimeter to allow rodent entry. The study area was enclosed by barbed wire fencing to exclude livestock but had an 80 cm gap at the bottom to allow the entry of mammals and reptiles in and out of the study area.

Vegetation Surveys

Plant Density

Plant density surveys were conducted annually in April-May for years 2013-2016. Density counts were done using four parallel randomized transect lines, spaced at least 2 m apart with a modified Daubenmire frame (25 cm x 50 cm) placed every 2 m for a total of 12 quadrats per transect line. Frame placement on each transect line started at least 2 m from the fence to avoid edge effects. Because they were so abundant, invasive annual grasses *B. rubens* and *Schismus* spp. were counted in a subframe of 10cm x 25cm.

Plant Cover

Plant cover measurements were done in 2016 using the step-point intercept method (Helm et al. 2004) along the same four transect lines used for density measurements. A pin was dropped starting at least 2 m from the fence, every 0.5 m for a total of 48 pin drops per transect line. For each pin drop, the topmost plant intersecting the pin was recorded as a canopy layer.

Biomass

Herbaceous plant biomass was collected in April 2016. All living above ground herbaceous biomass rooted within the 25 cm x 50 cm modified Daubenmire frame used for vegetation density counts was removed. Biomass was collected along the same four randomized transects used for vegetation density measurements starting at the 2 m mark and sampled every 4 m for a

total of 6 sampling frames per transect. All biomass was taken back to the laboratory and dried at 80 °C for 48 hours then weighed to the nearest gram.

Rodent Surveys

Rodent surveys were conducted every spring, summer, and fall period for 3 consecutive nights per trapping session. Eight large Sherman traps were placed in a 1.5 m diameter circle at the center of each treatment plot with two control trap circles for each block located at randomized locations outside the treatment plots. Each morning rodents were collected and assessed for species, gender, age, reproductive status and weight (to the closest 0.5 g). New individuals were given an ear tag with a unique identifier to track for subsequent nights and trapping sessions. Rodent abundance was calculated as the number of unique individuals per species trapped within a trapping session. Rodent species in order of abundance, were *Dipodomys merriami, Peromyscus crinitus, Chaetodipus formosus, Neotoma lepida, Ammospermophilus leucurus, Peromyscus boylii , Peromyscus maniculatus, Peromyscus truei,* and *Onychomys torridus.* The Brigham Young University Animal Care and Use Committee approved the small mammal survey protocols (IACUC#120202).

Statistical Analysis

Plant density, plant community diversity, cover, and biomass were modelled using linear mixed effects models (Pinheiro et al. 2017) with main and interactive effects of fire, rodent, and year with experimental blocks designated as the random effect. To meet homogeneity of variance assumptions a varIdent covariance structure for fire, rodent and/or year was used when needed. A simple linear regression was used to analyze the effects of rodent diversity, abundance, and richness on native and total plant diversity and density averaged across treatment blocks. Piecewise structural equation modelling was used to model the type (positive or negative) and

strength (statistical significance and critical values) our treatments had on plant density between plant species using 'psem' package in R (Lefcheck 2016). To analyze the competitive spatial correlation a simulated permutation Spearman's correlation test (n=2000) was used to test the strength of the correlation of between *B. rubens* and *Schismus* spp. as measured by densities in each quadrat used for density sampling. This was done for all years combined as well as each year individually across all treatment possibilities and combinations.

RESULTS

Plant Community Responses to Rodent Exclusion

Rodent exclusion increased *B. rubens* density (216 m^2 to 294 m^2), cover (11% to 17%), and biomass (1.8 gm^{-2} to 3 gm^{-2}) when averaged across years ($P<0.001$, $P<0.001$ and $P=0.07$) (Figure 2-1, Tables 2-1 and 2-2). Rodent exclusion increased forb density 7% from 156 m^2 to 214 m^2 ($P<0.0001$) but did not significantly affect forb cover or biomass compared to plots with rodent access (Figure 2-1, Tables 2-1 and 2-2). In contrast, rodent exclusion reduced *Schismus* spp. density (993 m^2 to 751 m^2), cover (30% to 22%), and biomass (2.5 gm^{-2} to 1.4 gm^{-2}) 1.2-, 1.5-, and 1.7-fold compared to rodent present plots ($P<0.0001$, $P<0.0001$ and $P<0.05$) (Figure 2-1, Tables 2-1 and 2-2). Excluding rodents also slightly decreased total herbaceous density ($P=0.07$) but did not affect cover or biomass (Tables 2-1 and 2-2). There was a significant interaction between fire and rodent exclusion on forb density in which the effects of fire were greater in rodent exclusion plots ($P=0.02$) (Figure 2-1, Table 2-1). Rodent exclusion increased diversity of the plant community 1.4-fold ($P<0.05$) but had no significant effect on richness of the plant community (Figure 2-2).

Plant Community Responses to Fire

Native and invasive plant species had varying responses to fire in this study. Fire decreased *B. rubens* densities by 9% compared to unburned plots when averaged across the four-year study period (P=0.04) while fire had no significant effect on *B. rubens* cover and biomass (Figure 2-1, Tables 2-1 and 2-2). In contrast, *Schismus* spp. densities, cover, and biomass doubled in burned plots compared to unburned plots when averaged across the study period and in 2016 (P<0.0001) (Figure 2-1, Tables 2-1 and 2-2). Fire nearly doubled forb density and cover compared to unburned plots (P<0.0001 and P<0.01) (Figure 2-1, Tables 2-1 and 2-2). Similarly, forb biomass increased 2.3-fold in burned plots compared to unburned plots in 2016 (P< 0.001). Fire increased total herbaceous density, cover, and biomass 1.5-fold or higher (Figure 2-1, Tables 2-1 and 2-2). Plant community diversity decreased 1.4-fold in response to fire (P<0.05) while fire had no significant effect on plant species richness (Figure 2-2). Except where stated above, there were no other significant fire and rodent interactions for plant density, cover, biomass, richness or diversity (P>0.1, Figures 2-1 and 2-2, Tables 2-1 and 2-2).

Rodent Community Responses to Fire and Rodent Exclusion

Burned plots had a drastic reduction in rodent diversity (Shannon's diversity index, P<0.0001) 2.5-fold and slightly decreased rodent richness (P=0.064) compared to unburned plots averaged across the study period (Figure 2-3). Fire did not change rodent abundance (P=0.16) in comparison to unburned plots averaged across time (Figure 2-3). The rodent exclusion fences were successful and reduced the number of unique individuals per trapping session 3-fold over the study period (P<0.001).

Plant-Rodent Interactions

Rodent diversity was negatively correlated with forb diversity when measured in rodent access plots across all treatment plots during the four-year study period ($R^2= 0.68$, $P<0.01$) (Figure 2-4). In addition, decreasing rodent diversity increased *B. rubens* cover and biomass ($R^2=0.53$, $P<0.05$; $R^2=0.6$, $P<0.01$). Rodent diversity was not correlated with *Schismus* spp. density, cover, or biomass or rodent abundance ($R^2<0.1$).

Plant Competition

There was evidence of competitive interactions between *B. rubens, Schismus* spp., and forbs (Figures 2-5 and 2-6). The strength of the negative correlation between the two invasive grasses doubled from 2013 (rho=-0.24, $P<0.0001$), when *Schismus* spp. first started to appear, to 2016 when *Schismus* spp. attained higher densities and percent cover than *B. rubens* (rho=-0.43, $P<0.0001$) (Figures 2-1 and 2-5, Table 2-1). All treatment combinations had significant negative correlation between the two grasses (Figure 2-5).

The results from the piecewise structural equation model (pSEM) are displayed in a graphical synthesis of how the experimental treatments are affecting plant species and potential competitive interactions between plant species (Figure 2-6, Table 2-3). Rodent exclusion positively affected *B. rubens* and forb densities ($P<0.001$; $P=0.02$) but negatively affected *Schismus* spp. ($P<0.01$). The pSEM showed that fire benefitted *Schismus* spp. and forb densities ($P<0.0001$) but negatively affected *B. rubens* ($P=0.02$). *Schismus* spp. and forbs increased with time ($P<0.001$; $P=0.04$) and *B. rubens* decreased ($P=0.02$). Because pSEM is unidirectional with no testing of reciprocal relationships, *B. rubens, Schismus* spp. and forbs were each run in a model as the main predictor totaling in three pSEM models. In the first pSEM *B. rubens* negatively affected *Schismus* spp. ($P=0.08$) and both *B. rubens* and *Schismus* spp. negatively

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impacted forb densities (P=0.1; P<0.001) (Figure 2-6). The second pSEM model showed *Schismus* spp. negatively affected *B. rubens* (P=0.05) (Figure 2-6; Table 2-3). The third pSEM model forbs negatively impacted *B. rubens* and *Schismus* spp. (P=0.12, P=0.08) (Figure 2-6, Table 2-3).

DISCUSSION

This study provides evidence that fire, rodents, and competitive plant interactions had strong modifying influences on the assembly of the herbaceous plant community in our study system. Plants, particularly invasive species, often respond positively to post-fire conditions (Brooks et al. 2004, St. Clair and Bishop 2019) which is consistent with the 2-fold increase in *Schismus* spp. and forb species (which include exotic annuals) in this study (Figures 2-1 and 2-6, Table 2-2). Rodents have been shown to have both positive and negative effects on plant establishment (Orrock et al. 2008, Maron et al. 2012), which was consistent in our data as the two dominant invasive grasses had opposite responses to rodent treatments (Figure 2-6). This is likely due to variation in plant functional traits and competitive interactions (Cubera et al. 2009, Steers and Allen 2012, Bowman et al. 2017). Shifts in the rodent communities altered plant community structure and invasiveness of the study system (Figures 2-4 and 2-5), which is consistent with a comparable study in the Great Basin Desert (St. Clair et al. 2016). Our results also suggest that invasive grasses had strong competitive interactions in our study system (Figures 2-5 and 2-6), along with forbs, that may dictate fine fuel composition under shrub canopies and in intershrub spaces (Brooks 1999a, Shea and Chesson 2002). This study provides novel evidence that top down effects of consumers on plants, competition among plants, and their response to fire

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(Melgoza et al. 1990, Chambers et al. 2007, St. Clair et al. 2016) influence patterns of invasion and susceptibility to invasive grass-fire cycles in arid ecosystems (Brooks et al. 2004).

Effects of Rodents on Invasive and Herbaceous Plant Communities

Rodent exclusion positively affected both *B. rubens* and forb species in our study (Figures 2-1 and 2-6, Tables 2-1 and 2-2) (St. Clair et al. 2016). Seed predation is a primary mechanism by which rodents influence plant community assembly (Brown and Heske 1990). Rodent consumers have been shown to prefer larger seeds over small seeds (Brooks 1999b, Maron et al. 2012). The positive effect of rodent exclusion on *B. rubens* may be due it having a larger seed than most of the other species. The increase in forbs in rodent exclusion plots is consistent with other studies that suggest most native forbs, albeit small seeded species in our study, are most likely preferred by small mammals over exotic plant species (Maron et al. 2012, Bowman et al. 2017). Seedling herbivory is another mechanism by which rodents exert top-down control on plant community assembly (Bowman et al. 2017). Forb seedlings are typically preferred by rodents due to their increased forage quality compared to grasses (Cubera et al. 2009, Bowman et al. 2017) but seedling size is also a contributing factor (Pérez-Harguindeguy et al. 2003). Given that *B. rubens* seedlings may be larger or more abundant due to earlier germination than most natives, rodents may exert higher pressure on *B. rubens* seedlings at certain times of the year (Beatley 1969, Veech 2001). Excluding rodents increased total plant diversity (Figure 2-2) (Keane and Crawley 2002) but did not change plant species richness, suggesting that the rodent community may have more of a generalist strategy rather than targeting specific native plants (Keane and Crawley 2002).

Rodents had positive impacts on *Schismus* spp. (Figure 2-1, Tables 2-1 and 2-2). *Schismus* spp. has a miniscule seed that has been documented to fall into small soil cracks thereby

avoiding seed predation by rodents (Gutterman 1994). The positive affect of rodents on *Schismus* spp. are also likely indirectly driven by reduced competitive pressure by *B. rubens* and forbs as they experience greater top-down control by rodents (Figures 2-1 and 2-6) potentially due to greater seed predation (Shea and Chesson 2002, Orrock et al. 2008). Rodent consumers have been shown to influence invasions indirectly by reducing competition from native species (Veech 2001, Shea and Chesson 2002, Orrock et al. 2008, Allington et al. 2013).

Effects of Fire on Invasion and the Herbaceous Plant Community

Fire decreased *B. rubens* density with little to no effect on cover and biomass (Figure 2-1, Table 2-2). Shortly after fire, *B. rubens* has been known to decrease in abundance most likely due to high seed mortality because of lethal temperatures from fire (Brooks 2002, Esque et al. 2010b). Fire increased the density, cover, and biomass of *Schismus* spp. and forbs over time (Figure 2-1, Table 2-2) likely by reducing competition and increasing soil resource availability (Figures 2-1 and 2-6) (Melgoza et al. 1990, Shea and Chesson 2002, Chambers et al. 2007). Increased soil nutrients in post-fire environments (Allen et al. 2011, Horn et al. 2017) can lead to increased density, biomass, and cover in annual plants which is consistent with the responses of *Schismus* spp. and forbs in our study (Figures 2-1 and 2-6; Table 2-2) (Allen et al. 2011, Steers and Allen 2012). *Schismus* spp. positive response to fire (Figure 2-1) appears to have reduced the abundance (Figure 2-6) and diversity of forbs (Brooks 2000, Steers and Allen 2012). Due to its distinctive phenology, early season invaders such as *Schismus* spp. may be superior competitors in a burned environment by capitalizing on the post-fire nitrogen pulse and water earlier than most native plants (Figure 2-6) (Melgoza et al. 1990, Brooks et al. 2004, Esque et al. 2010a). This may explain why Shannon's diversity of herbaceous plants was lowest in burned plots (Figure 2-2) where *Schismus* densities were highest (Figure 2-1).

The Effects of Fire on Plant and Rodent Community Diversity

Fire decreased diversity of the herbaceous plant community but not plant species richness in our study (Figure 2-2). Disturbance initially can decrease diversity by removing individual plants and altering herbivore behavior (Grime 1973, Horn et al. 2012). As succession continues however, diversity can increase until competitive effects manifest (Shea et al. 2004, Catford et al. 2012). Increasing the frequency of disturbance likely favors the fast, early successional invasive grass species where niche pre-emption or environment transformation can decrease local diversity long-term (Catford et al. 2012). Species such as *Schismus* spp. or *B. rubens* have faster growth and higher propagule production which means that they can pre-empt native species inhabiting microsites and niche space (niche pre-emption) (Catford et al. 2012). Also, transforming native shrubland to invasive grassland will promote fire and establish an alternate transient state (Fukami and Nakajima 2011) preventing the community from attaining greater biodiversity in the future (Catford et al. 2012).

Fire decreased rodent diversity as observed by Horn et al. (2012) but not species richness or abundance (Figure 2-3). This was likely because *Dipodomys merriami,* a rodent species that spends more time in open spaces, compensated for the losses of quadrupedal species which prefer shrub cover that was lost in the fire (Ostoja and Schupp 2009, Horn et al. 2012). Exotic grasses like *Schismus* spp. and *B. rubens* re-establish plant cover after fire (Brooks et al. 2004, St. Clair et al. 2016) but do not provide the same cover structure as native shrubs (Freeman et al. 2014, St. Clair et al. 2016). Our data show decreased rodent diversity negatively correlates with forb diversity and *B. rubens* growth (Figure 2-4) both of which are closely associated with shrubs (Brooks 2000). The loss shrub cover after fire is likely the reason for the decrease in rodent diversity in our study (Figure 2-3) thereby losing rodent species that were foraging more often

near shrub cover (Horn et al. 2012) releasing herbaceous plant species from rodent herbivory through forage selection (Keane and Crawley 2002). This suggests that self-reinforcement of fire is augmented not only through decreasing plant competition providing opportunity for invasion, but also by triggering shifts in rodent community composition which could potentially induce greater plant invasion by the more flammable exotic grass *B. rubens* (Brooks 1999a, Brooks and Matchett 2006).

The Role of Competition in Structuring an Invasive Annual Grass Community

Competitive exclusion by exotic plant species modified native plant establishment in both unburned and burned environments (Brooks 2000). We also observed that *B. rubens* and *Schismus* spp. negatively affected the establishment of annual and perennial forbs (Figure 6) (Brooks 2000, DeFalco et al. 2007). When Brooks (2000) thinned *B. rubens* and *Schismus* spp. densities, exotic forbs became dominant and may maintain or promote an exotic plant community in post-fire environments. Maintenance of an exotic plant community would lead to a state change and a possible total loss of native plant species along with modified rodent community composition (Chambers 2007, St. Clair 2016).

There was evidence of strong competition between *Schismus* spp. and *B. rubens* in our study (Figures 2-5 and 2-6). Competition has previously been considered to be weak and difficult to assess between *Schismus* spp. and *B. rubens* because they occupy different microhabitats (Brooks 2000). This study gives a unique experimental insight into the competition between *Schismus* spp. and *B. rubens* because *Schismus* spp. was not present at the start of the experiment (Figure 2-1). Our results show that by the end of the experiment *B. rubens* and *Schismus* spp. were not occupying the same quadrat space at the same time but both were dominant in the plant community (Figures 2-1 and 2-6). One mechanism by which two strong competitors can

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maintain co-existence on the same landscape is through spatial niche differentiation (Davis et al. 2000, Shea and Chesson 2002). Native plant species typically don't inhabit the open inter-shrub space leaving open niche space. At the beginning of our experiment, *B. rubens* was commonly found throughout the plots and was one of the few species inhabiting this open space. When *Schismus* spp. appeared, possible direct plant-plant competition may have led *B. rubens* to occupy more space under shrub canopies and *Schismus* spp. maintained the intershrub space. An indication that *Schismus* spp. is driving niche differentiation is seen in the strengthening of the negative spatial correlation as *Schismus* spp. enters and increases in the system and in plots where *Schismus* spp. densities are highest (Figure 2-5). This spatial niche differentiation is commonly seen throughout invaded Mojave desert landscapes (Brooks 2000, Allen et al. 2011). These spatial associations may be caused by rodent seed-caching and/or increased suitability in the shrub microhabitat for *B. rubens* (Price and Joyner 1997, Horn et al. 2017), whereas *Schismus* spp. seed is too small for most rodent predation (Gutterman 1994) and can grow in less hospitable conditions in the inter-shrub space (Pucheta et al. 2011).

Conclusion

The activity of rodent communities may be a critical mitigating factor in establishment of invasive grass-fire cycle in the Mojave Desert (Figure 2-6). The loss of diversity in the rodent community due to fires (Figure 2-3) may provide a window of opportunity for *B. rubens* to increase propagule pressure (Figure 2-4) and overcome predation control from rodents and facilitate invasion providing flammable fine fuels to increase the size and frequency of wildfires in the Mojave Desert (Figure 2-4) (Brooks and Matchett 2006, Steers and Allen 2012, St. Clair and Bishop 2019). In the Great Basin, St. Clair and Bishop (2019) showed that reduction in rodent activity in a post-fire environment created areas with high *Bromus tectorum* (cheatgrass)

propagule pressure that led to more severe secondary fires. However, if *Schismus* spp. were to enter the system, and especially if rodent consumers were present at some capacity, then occupation of different microhabitats and differing responses to predator controls between *B. rubens* and *Schismus* spp. could potentially cause *Schismus* spp. to become the main fine fuel in the inter-shrub space. *Schismus* spp. has shorter stature and therefore does not carry fire as well as *B. rubens* (Brooks 1999a), therefore, an invasive grass-fire cycle may not be as likely or severe when *Schismus* spp abundance increases. If forb communities are favored (Brooks 2000, Schutzenhofer and Valone 2006), their high tissue water content, stature, and fuel properties are not favorable for spreading fire even though they respond positively to fire (Figure 2-6 and Table 2-2). However, human-driven changes in nitrogen deposition can lead to increases in annual plant cover and biomass possibly resulting in increased amounts of continuous fine fuel needed to carry fire (Steers and Allen 2012). As climate and anthropogenic ecosystem alterations affect invasive plant growth in the Mojave, further research in how consumer activities and competitive interactions may change in conjunction with climate and anthropogenic change will help better determine the potential for invasive grass-fire cycles in the Mojave Desert.

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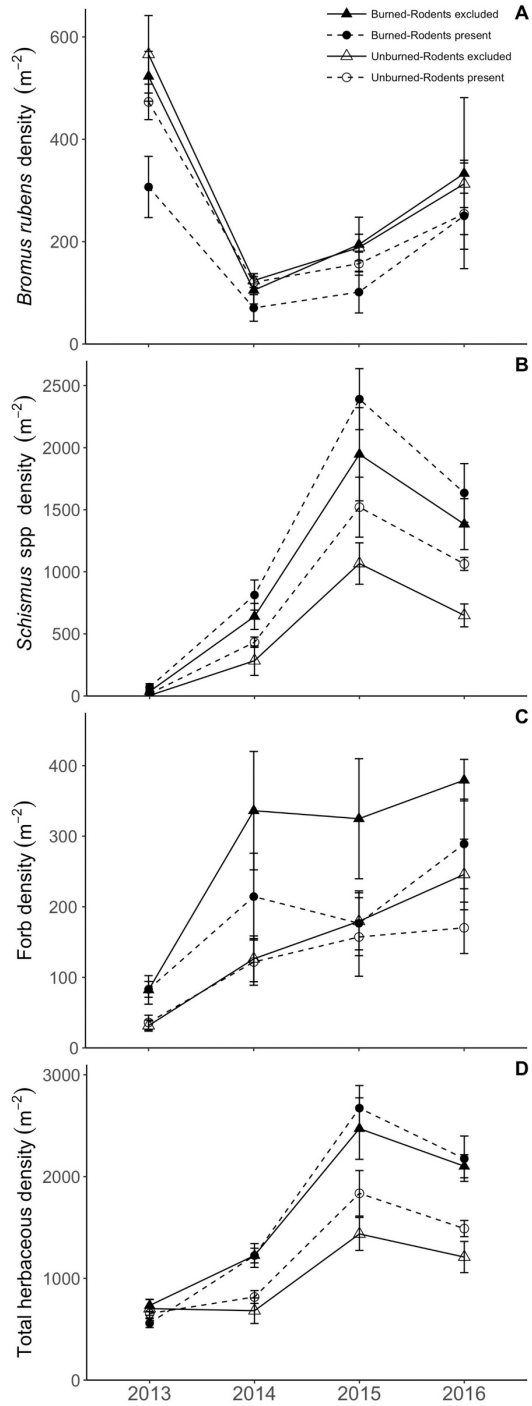
Figure 2-1 Effects of fire and rodent exclusion on (a) *Bromus rubens* (b) *Schismus* spp. (c) forb species and (d) total herbaceous plant density over time for the entire study period from 2013 to 2016. Mean values presented with ±SE. F-statistics and P-values are given in Table 2-1.
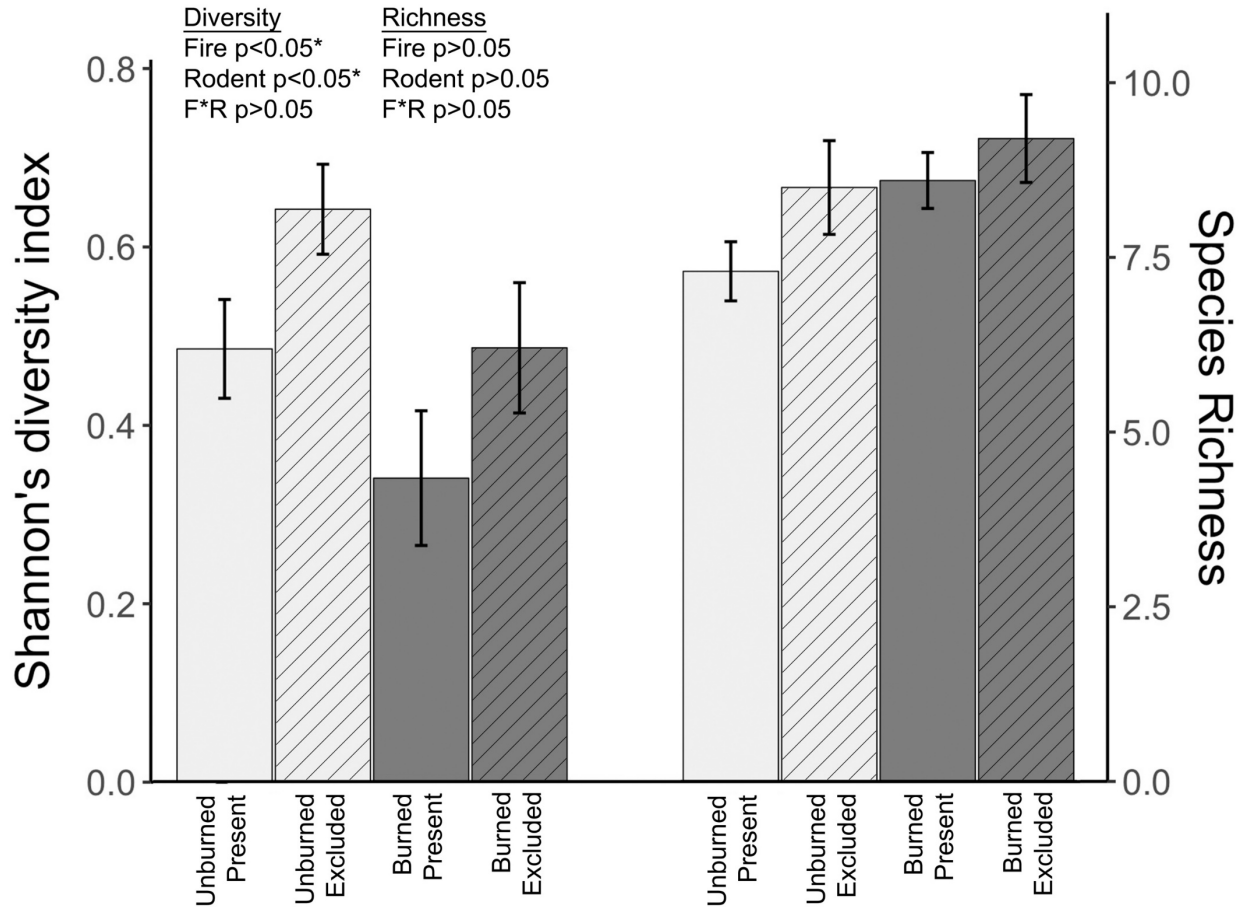
Figure 2-2 Effects of rodent exclusion and fire on Shannon's diversity index and species richness for the entire herbaceous plant community in 2016. Mean values presented with ±SE. Significance (p-value) for each treatment and treatment interaction indicated for diversity and richness top left of the figure.
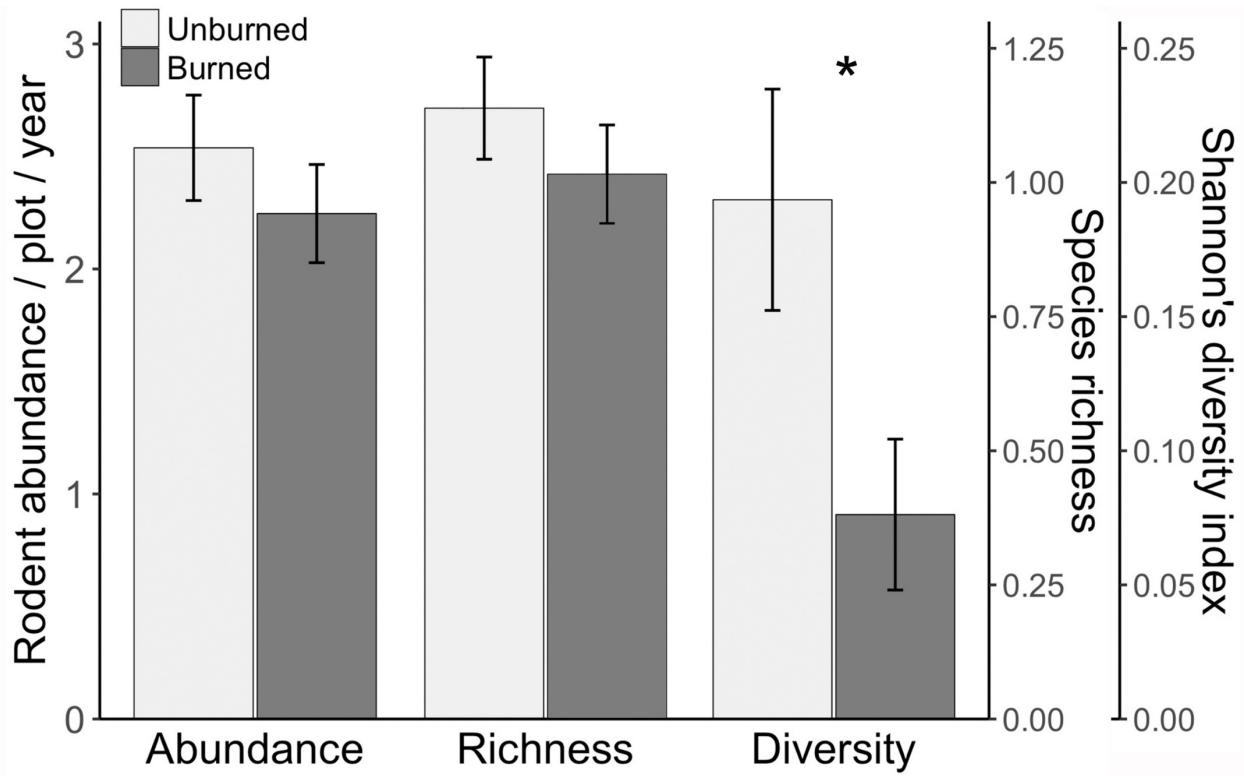
Figure 2-3 Effects of fire on rodent abundance, species richness, and Shannon's diversity index for the study period (2013-2016). Rodent diversity was the only rodent community measurement with significant differences (P<0.001) denoted with an asterisk (*). Mean values presented with ±SE.
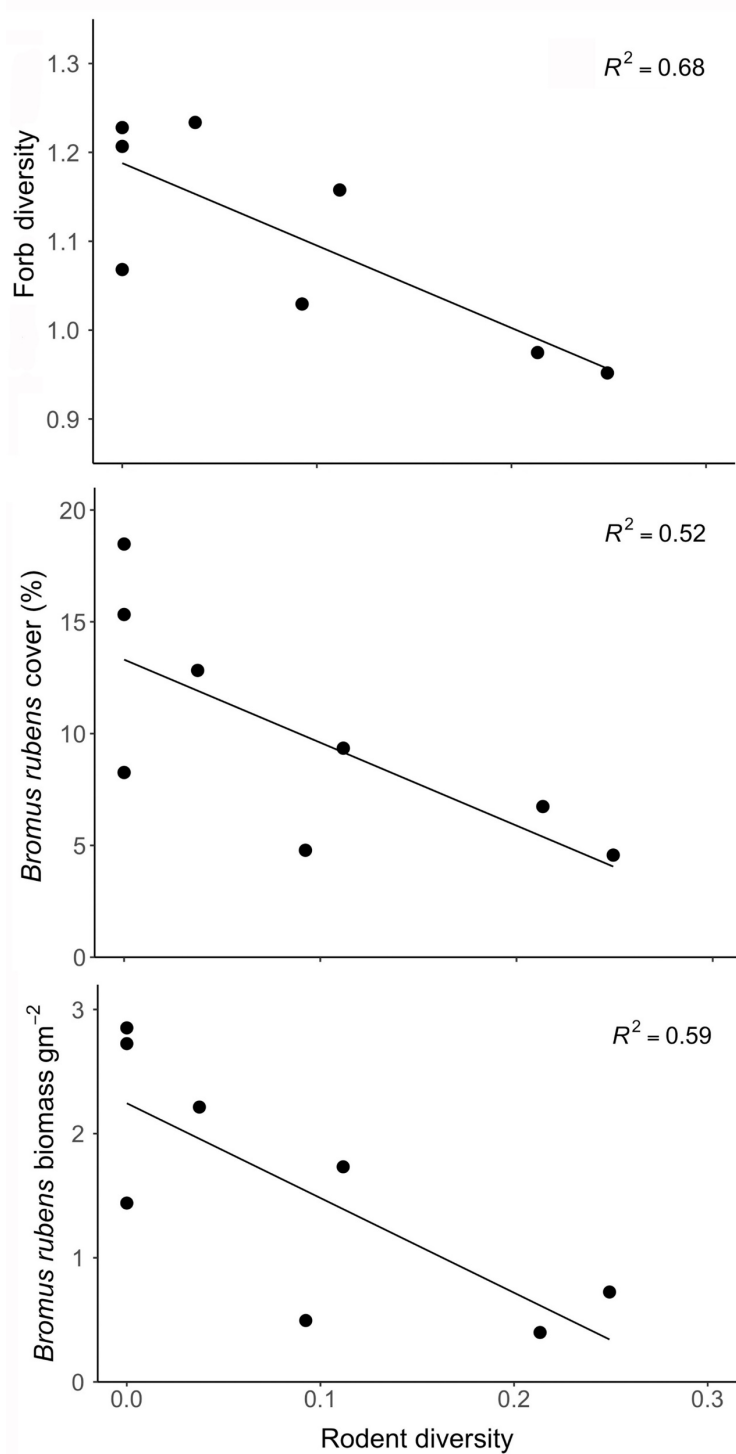
Figure 2-4 Negative linear relationship between rodent diversity in rodent present plots and herbaceous forbs (top), *B. rubens* cover (middle), and *B. rubens* biomass (bottom) from 2013-2016.

Treatment	rho
All combined	-0.48 ***
Burned	-0.49 ***
Unburned	-0.46 ***
Rodents Present	-0.50 ***
Rodents Excluded	-0.44 ***
Burned- Excluded	-0.51 ***
Burned- Present	-0.48 ***
Unburned- Excluded	-0.40 ***
Unburned- Present	-0.50 ***
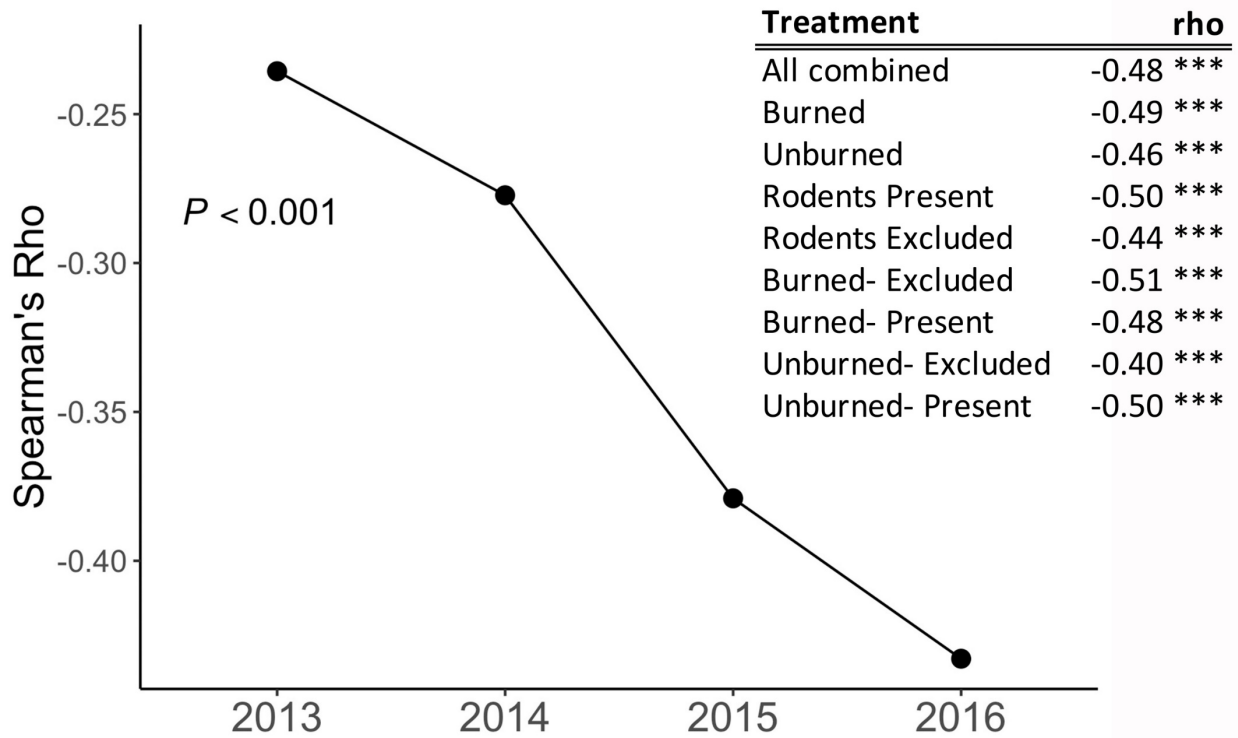
Figure 2-5 Correlation of *B. rubens* and *Schismus* spp. density over time when all treatments were combined. Spearman's rho presented from the simulated permutation correlation tests (n=2000) for all possible treatment combinations, asterisk (*) denotes p<0.05.

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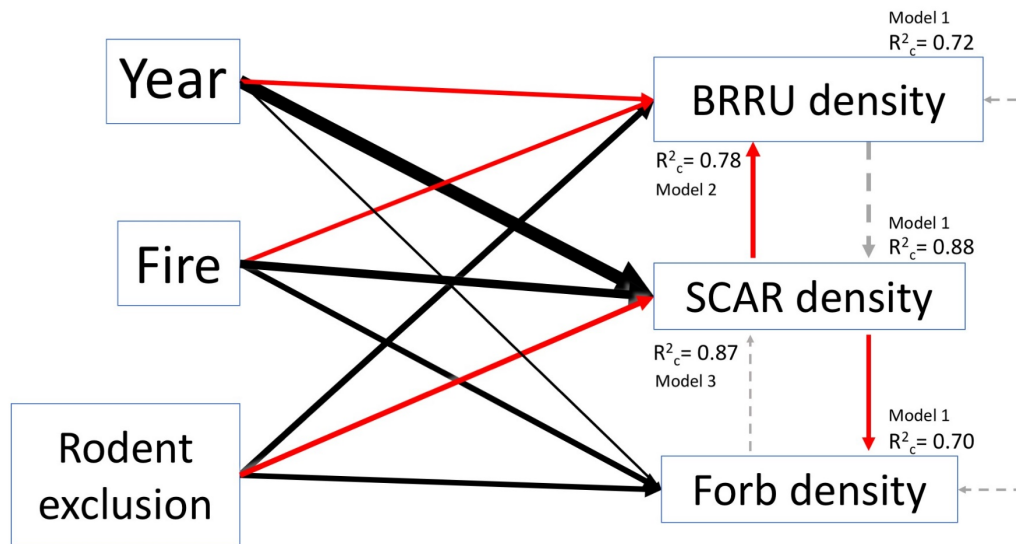
Figure 2-6 Direct and indirect effects of rodent exclusion, fire, and plant species on density of *Bromus rubens, Schismus* spp. and forb plant species. Black solid lines indicate positive significant (P<0.05) relationships, red solid lines indicate negative significant relationships, grey dashed lines indicate non-significant (0.15<P>0.05) negative relationship. Line widths indicate the strength of the relationship as determined by the critical value. R^2_c values are given for each unidirectional response for each model.

Table 2-1 Main and interactive effects of fire, rodent exclusion, and year on exotic grass density, forb density, and total herbaceous plant density. F-statistics presented with p-value significance denoted as follows: 0.08>P>0.05[+], P<0.05 *, P <0.01*, P<0.001**, P<0.0001***.

| Treatment | df | Exotic grass density | | Forb density | Total herbaceous density |
		Bromus rubens	Schismus arabicus		
Fire	1,48	3.53 [+]	54.87 ***	54.9 ***	86.96 ***
Rodent	1,48	11.67 ***	34.86 ***	18.6 ***	3.47 [+]
Fire * Rodent	1,48	1.95	0.06	6.09 *	2.04
Year	3,12	66.4 ***	44.13 ***	12.37 ***	35.46 ***
Fire * Year	3,48	0.77	7.54 ***	3.23 *	13.58 ***
Rodent * Year	3,48	2.5 [+]	2.82 *	2.4 [+]	2.24 [+]
F*R*Y	3,48	0.29	0.11	1.5	0.032
R^2_c		0.75	0.81	0.78	0.87

Table 2-2 Plant biomass and cover response to fire and rodent exclusion. Means presented ±SE. F-statistics presented for main and interactive effects of fire and rodent exclusion on exotic grass, frob, and total herbaceous plant cover and biomass for 2016 with p-value significance denoted as follows: $0.08 > P > 0.05^+$, $P < 0.05$ *, $P < 0.01$*, $P < 0.001$**, $P < 0.0001$***.

| Treatment | df | Exotic grass cover | | Forb cover | Total herbaceous cover |
		Bromus rubens	Schismus arabicus		
Unburned-present		9.3 ± 1.6	25.2 ± 2	4.5 ± 1.5	39 ± 4.7
Unburned-excluded		15.3 ± 3.2	13.4 ± 1	3.6 ± 0.9	32.3 ± 4.6
Burned-present		12.8 ± 4	35.1 ± 4.4	6.5 ± 1.6	54.5 ± 4.6
Burned-excluded		18.5 ± 5.6	31.3 ± 5.2	7.3 ± 1.1	57.9 ± 1.1
Fire	1,12	2	14.98 **	10.86 **	75.64 ***
Rodent	1,12	6.15 *	4.74 *	0.003	0.37
F * R	1,12	0.005	1.25	0.62	3.68 $^+$
R^2_c		0.69	0.53	0.59	0.87

| Treatment | df | Exotic grass biomass | | Forb biomass | Total herbaceous biomass |
		Bromus rubens	Schismus arabicus		
Unburned-present		18 ± 4	17 ± 2	5 ± 2	40 ± 8
Unburned-excluded		29 ± 8	9 ± 2	5 ± 1	42 ± 9
Burned-present		22 ± 8	34 ± 8	10 ± 2	66 ± 9
Burned-excluded		28 ± 10	20 ± 3	14 ± 3	61 ± 11
Fire	1,12	0.2	72.2 ***	15.7 **	25.6 ***
Rodent	1,12	4.1 $^+$	14.6 **	0.4	0.11
F * R	1,12	0.6	0.6	1.4	0.8
R^2_c		0.76	0.92	0.68	0.83

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Table 2-3 Path estimates, standard error, and P-value for piecewise structure equation models (pSEM). Predictors are rodent exclusion, the presence of fire, year, and each of the main plant species (*Bromus rubens, Schismus* spp., and forbs). The main differences between each pSEM model was the switch of plant species predictors and the plant species as a response. Fischer's goodness of fit with accompanying P-value is stated on the last row for each SEM model.

Predictor	Response	Estimate	SE	P-value
SEM model 1				
Rodent	*Bromus rubens*	41	14.2	<0.001
Rodent	*Schismus* spp	-210	72.7	<0.01
Rodent	forbs	10	4.1	0.02
Fire	*Bromus rubens*	-34	17.2	0.02
Fire	*Schismus* spp	461	78	<0.0001
Fire	forbs	36	5	<0.0001
Year	*Bromus rubens*	-47	14.2	0.02
Year	*Schismus* spp	377	82	<0.001
Year	forbs	9.3	1.9	0.04
Bromus rubens	*Schismus* spp	-0.6	0.35	0.08
Bromus rubens	forbs	-0.04	0.02	0.1
Schimus spp.	forbs	-0.1	0.004	<0.001
Fischer's goodness of fit = 0 with P-value =1, 0 df				
SEM model 2				
Schismus spp.	*Bromus rubens*	-1.4	0.02	0.05
Fischer's goodness of fit = 0 with P-value =1, 0 df				
SEM model 3				
Forbs	*Bromus rubens*	-0.05	0.003	0.12
Forbs	*Schismus* spp	-0.16	0.01	0.08
Fischer's goodness of fit = 0 with P-value =1, 0 df				

CHAPTER 3

Fire and Early Fall Precipitation Have Neutral to Positive Effects on Cheatgrass and Big
Sagebrush Establishment and Growth in the Great Basin

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ABSTRACT

Changes in wildfire regimes and fall precipitation timing related to climate change may
promote fluctuations in resource availability that reinforce invasion and state changes in deserts.
We investigate how earlier fall precipitation timing and fire affected a dominant native shrub
(sagebrush) and the most problematic invader (cheatgrass) in the Great Basin Desert. We
extracted soil cores from Rush Valley, UT and placed them in a common garden in Provo, UT
and planted seeds of sagebrush and cheatgrass independently. We imposed an experimental fire
and two fall precipitation timing pulses in a full factorial design. We measured seedling
emergence, plant height, biomass, density, seed production, and survival (sagebrush only). Early
fall precipitation did not significantly affect the amount of cheatgrass or sagebrush seedling
emergence. Early fall precipitation significantly increased cheatgrass density, height, biomass,
and seed production, and sagebrush height and biomass, but not density. Fire had no effect on
cheatgrass but increased sagebrush density, and survival. The data suggest that increasing fire
and earlier fall moisture in the Great Basin due to climate change can have neutral to positive
impacts on cheatgrass and sagebrush.

INTRODUCTION

Vulnerability to vegetation state change driven by climate change, biological invasions, and
changing disturbance regimes are a serious concern in conservation and management of Earth's

ecosystems (Chambers et al. 2014b; Scheffer et al. 2001; Vitousek et al. 1996). While all ecosystems experience natural change over time, human activities are accelerating changes in ecosystems that are pushing them beyond resilience thresholds (Chapin et al. 2000; Scheffer et al. 2001). These state changes can be irreversible, particularly when they occur in more sensitive arid and semi-arid ecosystems that cover more than 30% of the Earth's terrestrial surface (Sarukhán et al. 2005). Understanding plant community assembly and patterns of invasion in response to changing disturbance regimes and climate is vital in increasing ecosystem stability and resilience in a changing world (Chambers et al. 2014b).

Variability in climate, resource availability, competition, and disturbance regimes can affect plant establishment in an ecosystem (Adair et al. 2008; Shea and Chesson 2002; Tilman 1997). Artemisia tridentata ssp. wyomingensis (hereafter sagebrush) is a native perennial shrub and a keystone shrub species of the Great Basin in western North America where it provides critical habitat for many imperiled native species (Chambers et al. 2014b). Seed for sagebrush is commonly mature and begins to disperse late fall and early winter (Schlaepfer et al. 2014). Sagebrush germination typically requires cold temperatures and light in combination with shallow contact with soil thereby limiting most germination to late winter-early spring (Meyer and Monsen 1992; Schlaepfer et al. 2014). Sagebrush long-term success can largely depend on having limited competition, limited disturbance, and sufficient cool-season precipitation recharging deeper soil layers (Booth et al. 2003; Chambers et al. 2014b; Schlaepfer et al. 2014). In contrast, the notorious invasive annual grass, Bromus tectorum (hereafter cheatgrass) can germinate and establish across a wide variety of environmental gradients (Bishop 2019; Chambers et al. 2007) from fall until spring with each precipitation event (Mack 1981; Meyer et al. 1997) and has successfully invaded over 210,000 km2 of the Great Basin in the western

United States (Bradley et al. 2018). Exotic annual grass invasion success, such as cheatgrass, has been attributed to an increased ability to capitalize on fluctuations in water and soil resources, particularly in high precipitation years, more rapidly than native plants (Balch et al. 2013; Germino et al. 2016; Horn and St Clair 2017; Pilliod et al. 2017). Cheatgrass invasion has serious ecological consequences including habitat degradation, loss of biodiversity, and altered disturbance cycles that promote stage changes (Germino et al. 2016). However, cheatgrass establishment is influenced by multiple biotic and abiotic interactions and can vary across space and time (Levine et al. 2003).

Precipitation is typically the limiting factor in the establishment and productivity of annual plants in arid and semi-arid environments (Horn and St. Clair 2017; Pilliod et al. 2017). Precipitation timing and intensity can largely affect plant productivity (Pilliod et al. 2017). Variation in precipitation timing can favor exotic annual grasses due to differences in life history traits where exotics can capitalize on changing availability of water resources (Horn et al. 2017; Prevéy and Seastedt 2015). The majority of precipitation in cold deserts of North America comes in early spring and winter when water has time to percolate into deeper soil profiles (Bates et al. 2006; Schwinning et al. 2003). Climate change forecasts suggest wetter winters and falls, and drier summers in cold deserts of North America with more precipitation falling as rain (Abatzoglou and Kolden 2011); fourth climate assessment}. Although trends of wetter fall and winters with warmer temperatures will likely favor plant growth it is not well understood how the redistribution of precipitation with climate change will impact native plant growth and invasive annual grasses that are leading to alternative states (Bradley et al. 2018; Pilliod et al. 2017).

Wildfires are becoming larger and more frequent in semi-arid and arid ecosystems as a result of invasive annual grasses and climate change including precipitation timing (Balch et al. 2018; Brooks et al. 2004). There is increasing evidence that changes in vegetation in response to wildfire may create state changes in desert vegetation (Brooks et al. 2004; Scheffer et al. 2001). Fire can provide opportunities for invasion by removing native plant community cover, altering behavior of consumers, and altering soil resource availability (Allen et al. 2011; Brooks et al. 2004; Horn et al. 2012). Invasion driven grass-fire cycles have developed in deserts of western North America due to the positive feedback between fire and exotic plant invasions (Pilliod et al. 2017). Invasive grass-fire cycles have shown to have detrimental effects on native sagebrush ecosystems (Booth et al. 2003; Chambers et al. 2014b; St. Clair et al. 2016).

The objective of this study was to determine how changes in precipitation timing and fire affect the establishment success of dominant native (sagebrush) and invasive (cheatgrass) plant species in the Great Basin. Based on projected timing shifts in fall precipitation and changing wildfire regimes, we hypothesized the following: 1) early timing of fall precipitation will have a stronger positive effect on cheatgrass than sagebrush due to its more responsive germination, and faster growth rates; 2) fire will increase the growth of cheatgrass and sagebrush by enriching soil N levels.

METHODS

Experimental Design

We extracted 32 soil cores in PVC cylinders that were 15 cm in diameter and 40 cm deep from intershrub spaces at Rush Valley in Tooele County, Utah, USA (40°05'26.17" N 112°18'18.01" W), a low-mid elevation (1650 m) sagebrush steppe ecosystem dominated by Wyoming big sagebrush (Artemesia tridentata subsp. wyomingensis; hereafter sagebrush) and

squirreltail (Elymus elymoides). Mesh screen was secured to the bottom of each core to allow water flow, root penetration, and to keep soils intact. Soils were classified as a silty, mixed mesic Haplic Natrargid Taylors Flat Loam (Soil Survey Staff 2015). There was no evidence of cheatgrass invasion specifically at the site of soil core extraction. Biological soil crusts were well-developed, and the native plants were comprised of a mature shrub/perennial grass community indicating no recent fires and/or grazing. The soil and surrounding areas were wetted to prevent dry cracking or breakage of biological soil crusts (biocrusts).

The cores were void of any vegetation and biological soil crusts remained intact. Cores were transplanted to an outdoor common garden at the Brigham Young University Life Sciences facility in Provo, Utah, USA (elevation 1450 m) 48 km east of Rush Valley where it is located on the eastern side of the Great Basin ecoregion. Provo's mean annual precipitation is 411 mm/year, mean annual temperature is 12.3 °C with 24.2 °C mean July and -1.1 °C mean January temperature. Cores experienced natural weather conditions from the beginning of the study in early September 2016 to mid-August of 2017. The soil seed bank was reduced by watering the cores after they were collected and carefully removing the few seedlings that emerged. A 2 m welded-wire fence surrounded the common garden and was buried 30 cm with 1.7 m above ground to prevent any major animal disturbance. The common garden was set up in randomized block design of four blocks with each of the following treatments: Burned- early precipitation, burned- late precipitation, unburned- early precipitation, unburned- late precipitation. Cores were buried in the soil leaving the top 1 cm above ground.

Fire, Precipitation, and Seeding Treatment

We collected seedless cheatgrass straw from Rush Valley, in an area with an of average 462 ± 20 g m-2 of cheatgrass fine fuel biomass. On September 5, 2016 sixteen of the cores

experienced a fire treatment by placing 526 g m-2 of cheatgrass straw within an aluminum cylinder on top of each soil core and burning it with ignition by a lighter. The fire combusted the straw completely to ash which was left on top of the soil surface resulting in an estimated N input of 9.9 g m-2 (St. Clair et al. 2016).

Twenty seeds of cheatgrass or sagebrush were placed on the soil core surface with no disturbance. Cheatgrass seeds were collected from Rush Valley and hand selected from individuals for large and robust florets. Sagebrush seeds were obtained from the Great Basin Research Center, Utah Division of Wildlife Resources (Ephraim, UT). Seed analysis verified by Wyoming Seed Analysis Laboratory, Powell, WY, as 70% viability and 66% germination success. Sagebrush seed was cleaned from all chaff and individual seeds hand selected for this experiment. Cheatgrass and sagebrush were sown separately with each treatment combination in each block for a total of sixteen cores seeded with cheatgrass and sixteen cores seeded with sagebrush. Seeding of cheatgrass and sagebrush happened on the first day of the precipitation treatment to ensure separation of germination between the two precipitation treatments and prevent seed loss due to wind or seed predation. Seeds were sown on top of each core with no disturbance or attempt to bury seeds

Precipitation treatments occurred from September 6-19, 2016 (early) and October 12-25, 2016 (late). These times were chosen to fit within the target seasonal range and within a window unlikely to receive heavy snowfall to interfere with watering (Sarukhán et al. 2005; Western Regional Climate Center 2000). Cores were given 1.5 mm of water once every morning and afternoon for a total of 3 mm water every day for the two-week period (Fig. 1). There were several natural rain events that occurred between the early treatment and the late treatment on September 14, September 23-24 and October 24-25. We did not water on natural rain event days

during the precipitation treatments. Natural rain events led to a difference of 18 mm between the two treatments (Fig. 1).

Plant Measurements

Seedling emergence was measured by counting seedlings one month after precipitation treatments began. Cheatgrass was destructively harvested for analysis in early June 2017 and sagebrush was collected in late August 2017. Harvested biomass was collected and dried at room temperature for six months. Cheatgrass plant measurements included counting individual tillers for density, above-ground biomass, stem height, and seed count. Seed count was calculated by using a random subsample to count seeds for individuals and an allometric equation was derived based on the number of seeds per unit mass of the seed head ($R^2 = 0.88$) to calculate the total seed per core. Sagebrush measurements included seedling emergence, density, above-ground biomass, and height. Survival was measured as the proportion of seedlings that emerged one month post-precipitation treatment to the number of individuals collected at the end of the experiment. As sagebrush typically doesn't produce seed until 2-3 years maturity (under ideal conditions) (Schlaepfer et al. 2014) our sagebrush did not produce flowers or fruits.

Soil Nitrogen Analyses

The entire volume of soil was removed from each core after collecting plant biomass (above and belowground) and dried at 50 °C for 72 hours and homogenized. A 30 g subsample from each soil sample was used to measure NO_3-N (nitrate) and NH_4-N (ammonium) concentrations (mg NO_3-N kg^{-1} and mg NH_4-N kg^{-1}). The nitrate and ammonium were extracted with 2 M KCL using rapid flow injection analysis (Quick Chem 8500; Lachat Instruments, Loveland, CO). The cadmium reduction method was used to determine nitrate concentrations (Keeney and Nelson 1982), and the salicylate-sodium nitroprusside method was used to determine the

ammonium concentration (Rowland 1983). Total nitrogen in soils was determined using a combustion nitrogen analyzer (TruSpec CN Determinator, LECO Instruments, St. Joseph, Mich., USA).

Statistical Analysis

Linear mixed effects analysis of variance models were used to test the main and interactive effects of fire and precipitation timing on emergence, establishment, and growth of cheatgrass and sagebrush and seed production of cheatgrass using the 'nlme' and 'stats' package in program R (Pinheiro et al. 2017). Linear mixed effects analysis of variance models were used to test the main and interactive effects of precipitation timing and fire on soil nitrogen for sagebrush and cheatgrass cores independently. Experimental block was used as the random effect for all modeling. All models met standard normality and homogeneity of variance assumptions. Pairwise comparisons were tested using a Tukey HSD.

RESULTS

Fire

Fire did not alter seedling emergence of cheatgrass or sagebrush (Figure 3-2) or affect cheatgrass establishment, growth, or seed production (Figure 3-3) ($P>0.1$). In contrast, fire significantly increased sagebrush density from 170 individuals m2 to 325 individuals m2 (2-fold, $P<0.01$), and seedling survival percent from 81% to 93% (Figure 3-4) ($P<0.01$). Fire did not affect sagebrush height or biomass ($P>0.1$) (Figure 3-4). There was a significant fire by precipitation timing interaction for sagebrush germination in which fire promoted germination with early precipitation but reduced it with late precipitation (Figure 3-2) ($P<0.05$). Fire did not

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affect the concentration of soil nitrate, ammonium, or total nitrogen for either cheatgrass or sagebrush at the end of the study (Table 3-1).

Fall Precipitation Timing

Earlier fall precipitation generally had positive effects on both plant species. Precipitation timing did not significantly affect cheatgrass or sagebrush seedling emergence (Figure 3-2) ($P>0.1$). Early precipitation increased cheatgrass seed production by 721433 seeds m-2 (2.7-fold), tiller density by 4528 tillers m2 (3.8-fold), average tiller height 12 cm (1.5-fold), and total biomass by 1874 g m-2 (4-fold) compared to late precipitation timing (Figure 3-3). Precipitation timing had no effect on concentrations of soil nitrate, ammonium, or total nitrogen in cheatgrass cores at the end of the study (Table 3-1). Early precipitation increased sagebrush height by 8 cm (3-fold) and biomass 548 gm-2 (7-fold) relative to the late precipitation treatment (Figure 3-4), but did not affect sagebrush density or survival ($P>0.1$) (Figure 3-4). Early precipitation timing significantly increased concentrations of soil nitrate 27% (3.6 mg NO_3-N kg-1 to 4.6 mg NO_3-N kg-1) and soil ammonium 57% (3.0 mg NH_4-N kg-1 to 4.7 mg NH_4-N kg-1) compared to late precipitation timing in sagebrush cores ($P<0.05$) (Table 3-1). Precipitation timing in sagebrush cores had no effect on total nitrogen concentrations (Table 3-1).

DISCUSSION

The importance of precipitation timing as opposed to total annual precipitation in determining plant productivity is increasingly recognized in arid systems (Bates et al. 2006; Horn et al. 2017; Pilliod et al. 2017; Prevéy and Seastedt 2014). How changes in precipitation timing may affect state changes in plant community structure within the context of changing fire regimes through empirical studies is still relatively unexplored though some support shows favor for exotic annual grasses (Horn et al. 2017; Knapp 1996; Prevéy and Seastedt 2014). Our study

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experimentally manipulated both precipitation and fire to ascertain responses of key species that are dominant vegetation types in the Great Basin Desert. Cheatgrass and sagebrush both showed positive responses to earlier fall precipitation which only partially supported our first hypothesis that cheatgrass would respond more positively than sagebrush (Figure 3-3 and 4). We expected to see neutral responses by sagebrush as local adaptations may pre-empt its ability to respond quickly to precipitation timing changes (Adler et al. 2009). In contrast, our second hypothesis was not strongly supported given that fire did not have a strong effect on cheatgrass as expected but doubled the density of sagebrush (Figure 3-4) suggesting that indirect effects (eg. removal of intact mature native plant communities) of fire on sage-steppe communities may facilitate cheatgrass invasion more than the direct effects (eg. nutrient pulses) of fire (McAdoo et al. 2013; Melgoza et al. 1990; St. Clair et al. 2016).

Effects of Fire on Invasive and Native Plant Establishment and Growth

Surprisingly, fire did not affect cheatgrass establishment or growth in our study (Figures 3-2 and 3-3) despite the fact that fire has been shown to promote cheatgrass invasion (Germino et al. 2016; St. Clair et al. 2016). Increases in soil resource availability and decreased plant competition due to native plant removal by fires, increases niche opportunities for invasive plant species (Shea and Chesson 2002; St. Clair et al. 2016). It is also well known that fire can disrupt biological soil crusts (biocrusts) which can physically and chemically alter the soil surface in ways that affect plant germination and growth (Allen et al. 2011; Chambers et al. 2007). The lack of positive responses of cheatgrass establishment, growth, and nitrogen concentrations to fire treatments in this study did not generally support the idea that post-fire nutrient pulses or chemical or physical modification of soil crusts facilitate cheatgrass success. These results initially seem in contrast to other studies that show biocrust's strong inhibition to cheatgrass

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growth that fire would then disrupt promoting cheatgrass establishment (Belnap et al. 2001; Deines et al. 2007; Serpe et al. 2006). However, studies have also shown biocrusts can enhance cheatgrass establishment and growth, which fire could disrupt (Ferrenberg et al. 2017; Zhang et al. 2016). Our results suggest that nutrient pulses or disruptions of soil crusts in response to fire do not explain positive responses of cheatgrass to fire. The major benefits of fire for cheatgrass may be when initial fires remove native shrubs and reduce competitive effects of native vegetation which result in more severe, recurrent fires (St. Clair and Bishop 2019). Severe and recurrent fires cause continuous biocrust damage and create stronger nutrient pulses, which may create promote cheatgrass invasion over time (Condon and Pyke 2018; Johansen 2003). It should also be recognized that our burn treatments were more typical of secondary fires driven by the fine fuels of invasive grasses rather than initial burns driven by woody fuels of native shrubs.

Post-fire conditions are typically thought to constrain sagebrush establishment (Chambers et al. 2014a; Davies 2011; Young and Evans 1978). However, a novel finding of this study is that fire can positively impact sagebrush establishment as evidenced by the 2-fold increase in density of sagebrush in burned cores (Figure 3-4). The lack of nutrient differences in the burned vs unburned sagebrush cores indicate that the physical seedbed characteristics, such as temperature and water availability, were more critical in sagebrush germination and establishment in this study. Native sagebrush seed germination and establishment can be highly variable based on soil moisture and temperature conditions and snowpack conditions (Knutson et al. 2014; Richardson et al. 2018) that can change in post-fire environments (Boyd et al. 2017). Sagebrush germinates better in warmer temperatures and has higher establishment success if seedlings are not exposed to freezing temperatures soon after germination (Boyd and Obradovich 2014; Richardson et al. 2018). Darker soils found after a fire increase soil temperature which may provide a better

microclimate for sagebrush establishment (Boyd et al. 2017; Boyd and Obradovich 2014). We planted in fall when germination can happen with more mild temperatures which has been predicted to increase sagebrush germination success (Richardson et al. 2018). Though well-developed biocrusts can inhibit sagebrush germination (Schlaepfer et al. 2014) low severity fires may create soil microsite conditions suiTable 3-for sagebrush germination (Germino et al. 2018).

Effects of Precipitation Timing on Invasive and Native Plant Establishment and Growth

Our experiment demonstrated how important timing of precipitation is in water-limited systems on both native and invasive plant establishment and growth (Figures 3-2:3-4). Even though both precipitation treatments had similar cumulative precipitation, earlier fall precipitation dramatically increased cheatgrass establishment, growth and seed production, and sagebrush growth. Climate change predictions show an increase in winter precipitation as rain and earlier precipitation in the fall period in the Great Basin ecoregion (Abatzoglou and Kolden 2011; Prevéy and Seastedt 2015). Increased precipitation during winter in the form of rain favors cheatgrass growth that can shift plant community composition (Prevéy and Seastedt 2014; Prevéy and Seastedt 2015). Phenological differences of cheatgrass compared to native grasses is a common mechanism in explaining cheatgrass increased competitive ability in acquisition of soil resources (Chambers et al. 2007; Melgoza et al. 1990; Prevéy and Seastedt 2015). Cheatgrass germination can occur from fall to spring and typically has higher germination success after long dry periods common in summer in the Great Basin after spring dispersal (Allen et al. 1995; Roundy et al. 2007). Wetter years tends to increase cheatgrass growth, which then can substantially increase the likelihood of recurrent wildfire during the summer period (Bradley et al. 2018; Pilliod et al. 2017). Our results indicate that earlier precipitation timing

increased cheatgrass fuel and propagule pressure (Figure 3-3) which when occurring in the field could shorten fire return intervals in deserts (Pilliod et al. 2017; St. Clair and Bishop 2019).

Early precipitation timing substantially increased the growth of sagebrush when grown independently (Figure 3-4). Native perennial shrubs in the Great Basin rely on winter recharge from fall rain and winter snow because it increases the time for deep percolation of soil water (Schwinning et al. 2003). Shifting precipitation timing from winter-early spring to earlier in the fall may positively affect soil recharge and lead to increased soil moisture where emerging seedlings and shrub taproots have access before winter conditions (Bates et al. 2006). This would also benefit deep rooted shrubs into the summer months when water is more limited (Bates et al. 2006; Cline et al. 1977). Earlier precipitation in the fall period also provides sagebrush and cheatgrass with a longer growing period during periods with optimal temperatures (Condon et al. 2011; Richardson et al. 2018). Warmer temperature with wetter soils can also increase nutrient uptake in sagebrush and nitrogen fixation by biocrusts (Belnap 2002; Pregitzer and King 2005; Schlaepfer et al. 2014). Earlier fall precipitation and fire positively affected sagebrush germination (Figure 3-2) which may be due to changes in soil temperature. Darker soils and ash in post-fire environments accompanied by increased precipitation and higher nutrient availability may partially explain sagebrush seedling emergence and establishment success (Boyd et al. 2017; Richardson et al. 2018). However, warmer soils without sufficient soil moisture can lead to seedling emergence failure (Bates et al. 2006; Boyd and Davies 2010) which is a possible mechanism for the decreased seedling emergence in burned-late precipitation cores (Figure 3-2).

Moisture levels is the primary limiting factor in nitrogen fixation of biocrusts in cold deserts (Belnap 2002). When moisture is available consistently to biocrusts in the optimal temperature range of 20-30C degree C maximum nitrogen fixation occurs (Belnap 2002). The

early fall precipitation treatment with regular soil wettings had a temperature range of 10-28° C increasing the likelihood that biocrusts were operating in optimal conditions for high levels of nitrogen fixation (Belnap 2002; Johnson 1982; Kershaw 1985). Whereas the late precipitation treatment dropped in temperature (6-19° C) and shortly after the watering treatment was imposed which would decrease the rate of nitrogen fixation. Most of the nitrogen that is released into the surrounding soil is nitrate followed by ammonium which is readily available for the uptake by vascular plants (Belnap 2002; Kershaw 1985). Cheatgrass has been shown to respond positively to increases in soil nitrogen and can readily deplete soil nitrogen stores (Belnap et al. 2016; Blank 2010; Rau et al. 2014) which could explain why there were no differences between precipitation treatments as well as lower soil nitrate concentrations in cheatgrass cores compared with sagebrush at the end of the study (Table 3-1). Nitrogen additions benefit sagebrush growth (Miller et al. 1991) but as sagebrush has a slower relative growth rate compared to cheatgrass (Germino et al. 2016; Schlaepfer et al. 2014), differences in the rate of nutrient uptake between the two species could account for why there were detectable differences of soil nitrogen in the sagebrush cores and not cheatgrass cores (Table 3-1).

Conclusion

Increased fire activity in the Great Basin (Bradley et al. 2018) and altered fall precipitation timing related to climate change is likely to have strong impacts on sagebrush-steppe plant community resilience to invasion and subsequent state changes (Pilliod et al. 2017; Prevéy and Seastedt 2014; Richardson et al. 2018). Based on our results, increased sagebrush establishment and growth can occur in post-fire conditions (Figure 3-4) and earlier precipitation in the early fall period providing better conditions for establishment success and growth (Richardson et al. 2018). However, while sagebrush germinated and established well in burned-early precipitation cores

(Figures 3-2 and 3-4), the positive response of cheatgrass to early precipitation grown in competition with sagebrush may be more likely to lead to state changes in native perennial shrublands to invasive annual grassland (Chambers et al. 2014a; Fukami and Nakajima 2011) especially if it drives recurrent fires (St. Clair and Bishop 2019). Cheatgrass' significantly higher densities than sagebrush in response to earlier fall precipitation suggests that differences in propagule pressure (Figures 3-3 and 3-4) and subsequent competition between sagebrush and cheatgrass is a foremost concern in restoration of sagebrush in post-fire environments (Brabec et al. 2015; Chambers et al. 2007). More empirical studies are needed to understand how co-occurrence and competition in burned environments will affect the balance between native plant establishment and invasion outcomes in response to climate change (Chambers et al. 2014a; Knapp 1996; Pilliod et al. 2017; Prevéy and Seastedt 2015).

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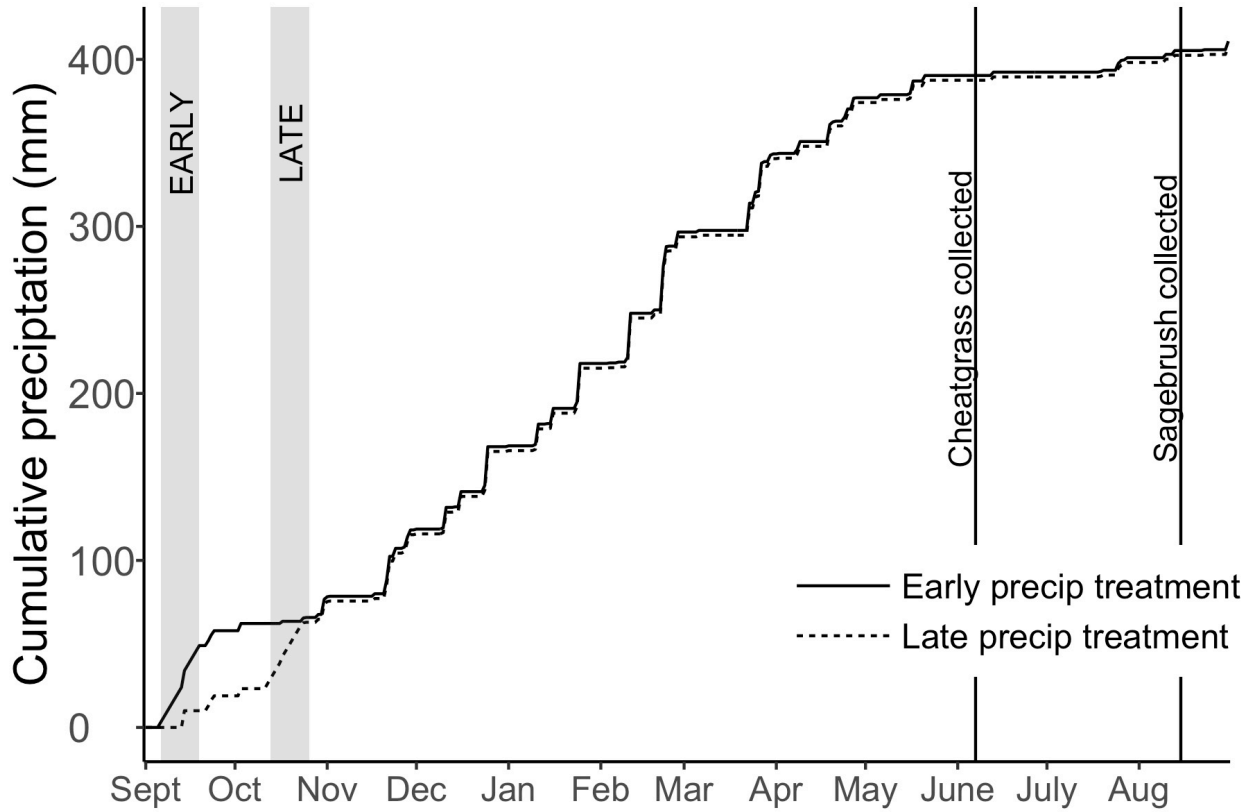
Figure 3-1 Comparisons of cumulative precipitation between early precipitation treatments (early September 2016) versus late precipitation treatments (mid-October 2016). Solid line represents the early precipitation treatment and the dashed lined represents the late precipitation treatment. Lines are shifted to reduce overlap. Precipitation timing closely mimicked each other barring a few native precipitation events seen between the two vertical grey bars. Grey vertical bars cover the time when watering treatments occurred. Solid vertical lines indicate when cheatgrass (BRTE) and Wyoming big sagebrush (ARTR) was collected from the soil cores

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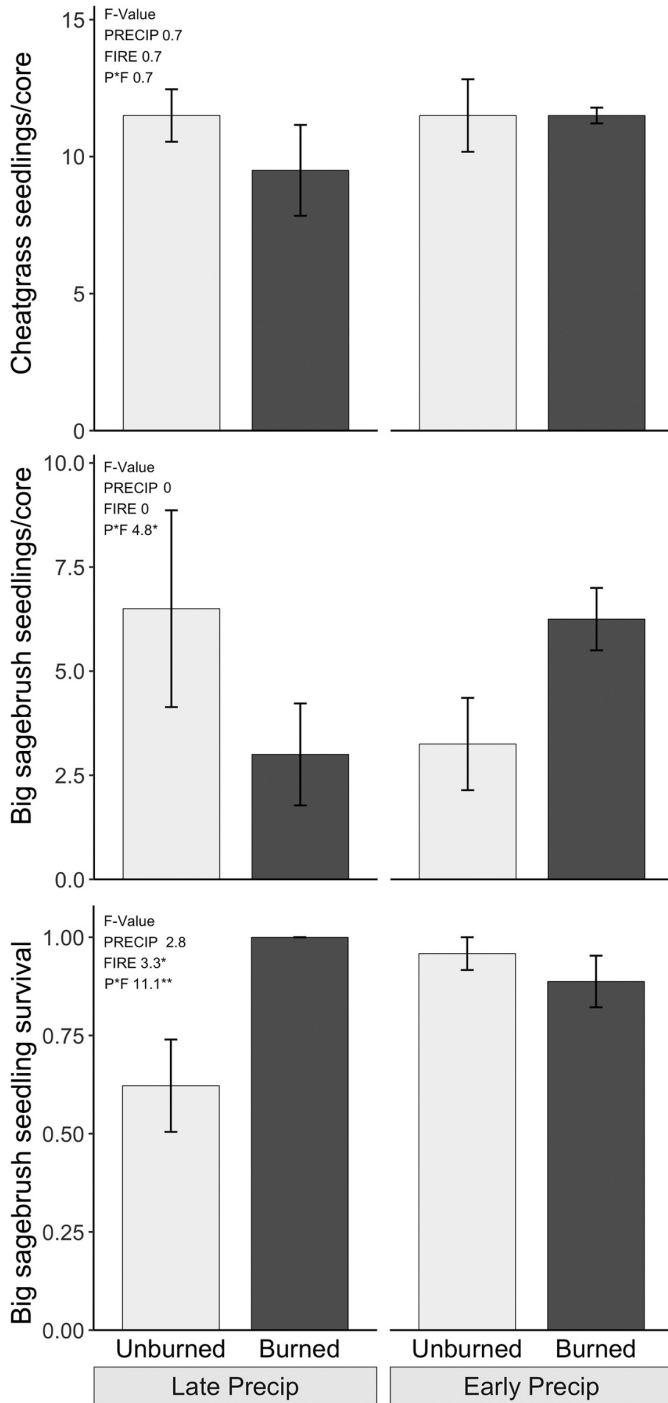
Figure 3-2 Precipitation timing and fire effects on cheatgrass and sagebrush emergence one-month post-precipitation treatment. Seedlings were counted one month after sowing. Means are presented ± SE. F-values presented with statistical significance (P<0.05) denoted with an asterisk (*)
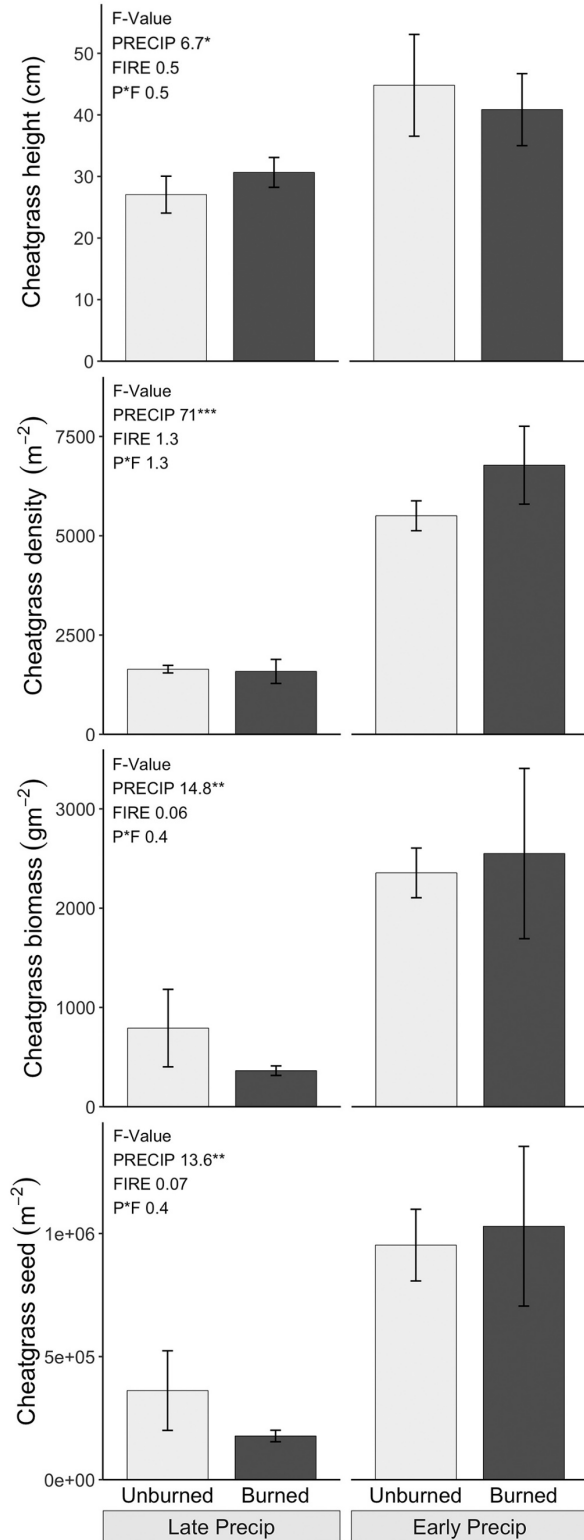
Figure 3-3 Precipitation timing and fire effects on cheatgrass height, tiller density, biomass, and seed production. Cheatgrass was destructively harvested in early June 2017. Means presented ± SE. F-values presented with statistical significance (P<0.05) denoted with an asterisk (*)

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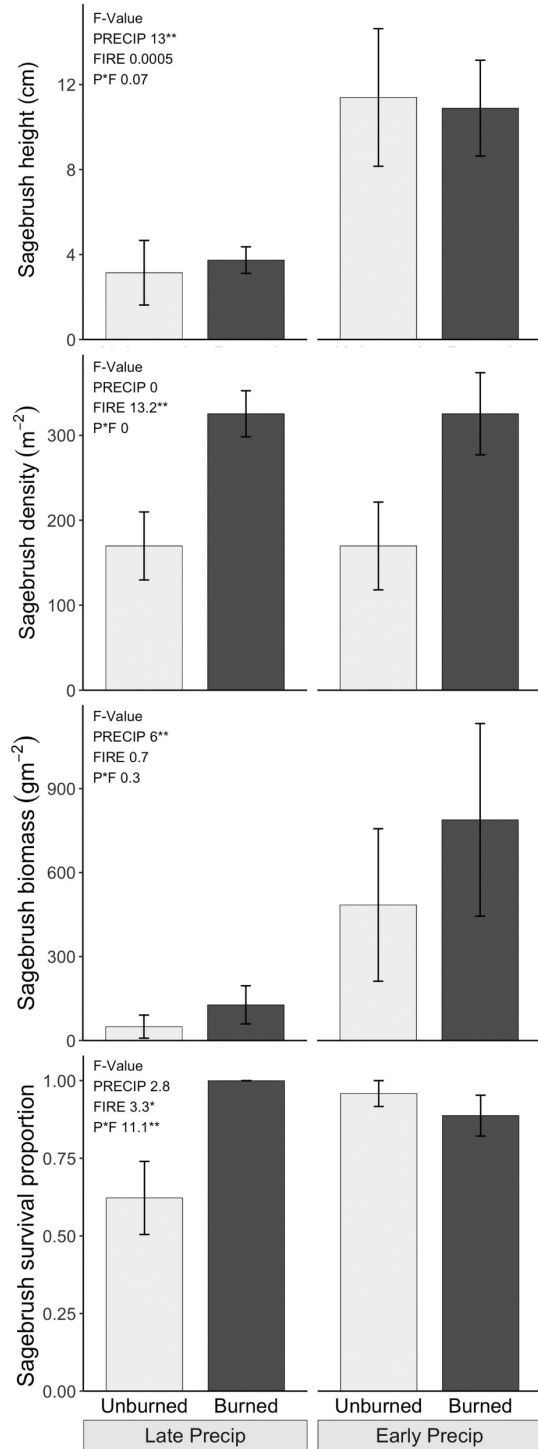
Figure 3-4 Precipitation timing and fire effects on sagebrush height, density, biomass, and seedling survival. Height, density, and biomass means presented ± SE. Seedling proportion is the number of seedlings (Figure 2) that survived until August when all sagebrush was harvested. F-values presented with statistical significance (P<0.05) denoted with an asterisk (*)

TABLES

Table 3-1 Soil nitrate, ammonium, and total nitrogen measured in cheatgrass and sagebrush soil cores. Soil was collected at the end of the study after plant biomass and roots were removed. Means presented ±SE. Letters denote pairwise differences. F-statistics presented for main effects of precipitation timing and fire on nitrate, ammonium, and total nitrogen concentrations with $P<0.05$*. R2c stated for total model with random effect of experimental block

Treatment	df	Nitrate (mg NO_3-N kg^{-1})	Ammonium (mg NH_4-N kg^{-1})	Total Nitrogen %
Cheatgrass				
Early-Burned		2.5 ± 0.8 [a]	4.4 ± 1 [a]	0.102 ± 0.01 [a]
Early-Unburned		2.7 ± 0.4 [a]	4.1 ± 0.8 [a]	0.09 ± 0.01 [a]
Late-Burned		3.8 ± 0.9 [a]	2.5 ± 0.5 [a]	0.07 ± 0.001 [a]
Late-Unburned		4.3 ± 1.2 [a]	4.4 ± 0.8 [a]	0.08 ± 0.007 [a]
Precip timing	1,9	2.8	1.4	2.9
Fire	1,9	0.4	0.3	3.5
R^2_c		0.45	0.53	0.59
Sagebrush				
Early-Burned		4.8 ± 0.7 [a]	5.0 ± 1.2 [a]	0.09 ± 0.01 [a]
Early-Unburned		4.4 ± 0.8 [a]	4.4 ± 0.4 [a]	0.09 ± 0.008 [a]
Late-Burned		3.8 ± 0.4 [b]	2.5 ± 0.5 [b]	0.09 ± 0.006 [a]
Late-Unburned		3.6 ± 0.6 [b]	3.5 ± 0.5 [b]	0.1 ± 0.006 [a]
Precip timing	1,9	5 *	5.6 *	0.5
Fire	1,9	0.6	1	1.4
R^2_c		0.6	0.51	0.3

CHAPTER 4

Competitive Exclusion of Native Plant Communities by Exotic Plant Species is Intensified by
Precipitation Timing but not Fire

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ABSTRACT

Climate change and wildfire may be shifting the competitive balance between native and

exotic plant species that could be driving state changes in vegetation in arid ecosystems. The

objective of this study was to determine competitive interactions between exotic and native plant

communities and how fire and shifts in fall precipitation timing due to climate change may

modify their competitive relationship. We selected key exotic annuals and native perennials from

the Great Basin Desert in western North America and grew them in different combination mixes.

We tested competitive responses of invasive and native plant communities in response to earlier

fall precipitation predicted future climate change and fire in a full factorial design. We found that

exotic plant communities were superior competitors and decreased native plant species height (2-

fold), density (2.3-fold), biomass (11-fold), seed production (200-fold), and C:N ratios (1.3-fold)

but not tissue N content. Native plant communities had little impact on the exotic plant

community but did decrease density, biomass, and seed production specifically of *Bromus

tectorum,* an exotic annual grass that is largely responsible for invasive grass-fire cycles in this

eco-region. Early precipitation timing intensified the competitive exclusion of natives by exotic

species, but fire was not found to be a strong modifier of competitive interactions. While all

species benefitted from earlier fall precipitation our data suggest that increases in fall

precipitation is likely to magnify the competitive exclusion of native vegetation by exotic annuals.

INTRODUCTION

Plant community assembly is influenced by abiotic and biotic interactions that vary across space and time (Kraft et al. 2015; McGill et al. 2006). Species can be excluded from a given habitat due to environmental filtering (the inability to persist solely due to abiotic conditions), biotic interactions (e.g. competitive exclusion) or the combination of both (Kraft et al. 2015). Successful invasion by exotic plant species depends on successfully passing through both of these ecological filters (Davis et al. 2000). Native plant communities are at risk of state changes when exotic plant species successfully establish, spread, and compete for resources (Catford et al. 2012; Chambers et al. 2016; Fargione et al. 2003).

Competition is a primary driver of plant invasion success (Chesson 2003; Davis et al. 2000; Vila and Weiner 2004). Native plant communities have been shown to inhibit plant invasions by limiting the establishment and spread of exotic plant species through competitive exclusion (biotic resistance) (Chambers et al. 2014a; Pearson et al. 2012; St. Clair and Bishop 2019). However, early successional exotics can exploit available resources when loss of native vegetation occurs after disturbance (Davis et al. 2000; Levine et al. 2003; Vila and Weiner 2004). In cases where resources are limited and competition is high (Davis et al. 2000) successful exotic annual species have been shown to competitively exclude native plants largely through earlier germination and faster growth that increases acquisition of soil resources (priority effects) (Booth et al. 2003a; Chambers et al. 2007; Germino et al. 2016b; Meyer et al. 1997; Vila and Weiner 2004; Wolkovich and Cleland 2011). Greater nitrogen acquisition and nitrogen use efficiency by exotics, can increase their competitive ability of exotics over natives (Funk and

Vitousek 2007). Climate change and shifting disturbance regimes due to human activities may affect resource acquisition strategies of exotic and native species that alters their competitive interactions (Blank 2010; Callaway and Aschehoug 2000; Herget et al. 2015; McGill et al. 2006; Vila and Weiner 2004) and others).

The magnitude and timing of precipitation is a strong determinant of plant establishment particularly in water limited systems (Sala and Lauenroth 1982; Schwinning and Sala 2004). In cold deserts of North America, precipitation typically comes in winter and early spring in the form of snow and rain (Miller et al. 2013). Forecasts of climate change for these regions include increased early fall precipitation and shifts from snow to more rain in the winter, accompanied by drier summers (Abatzoglou and Kolden 2011). Native species that can germinate during the fall period (temporal priority) and withstand harsh winter conditions may exhibit strong positive responses to earlier fall precipitation (Vaughn and Young 2015). However, exotics with strong priority effects are able to acquire resources earlier than most native species (Goodale and Wilsey 2018) and may also thrive with earlier fall precipitation (Gill et al. 2018; Horn et al. 2017; Young et al. 2015), which could intensify competitive interactions between the native and exotic plant communities. Recent work conducted in the Mojave Desert suggests that increases in fall precipitation may dramatically increase the competitive ability of exotic annual grasses (Horn et al. 2017, Horn and St. Clair 2017) but very little research has been done in this area of invasion biology. Dominance of exotic annuals in desert landscapes have been linked to larger and more frequent wildfires that are increasing in intensity with climate change (Chambers and Pellant 2008; Pilliod et al. 2017).

Wildfires regimes are changing globally due to human activities including increases in the size and frequency of fires in arid ecosystems due to invasion by exotic annual grasses (Bradley

et al. 2018; D'Antonio and Vitousek 1992; St. Clair and Bishop 2019). Fire reduces biotic resistance of the native plant community by removing the native vegetation and decreasing competition for plant resources (Levine et al. 2004; St. Clair et al. 2016; Steers and Allen 2012). Differences in life-history traits between exotic annual plants and native desert plants have been associated with invasion success after disturbance. High nitrogen acquisition and nitrogen use efficiency by exotic plants has been linked to invasion success compared to natives particularly when soil resources increase (Funk and Vitousek 2007) such as in post-fire environments. But how disturbance modifies nutrient acquisition and competition between native and exotic vegetation has not been extensively tested (Perkins and Hatfield 2014; Schantz et al. 2015; Vila and Weiner 2004; Wainwright et al. 2012).

The Great Basin Desert of North America is an ideal study system for investigating the effects of changing precipitation patterns and fire on competitive interactions between exotic annual and native plants. The exotic annual grass *Bromus tectorum* L. (cheatgrass) and exotic annual forbs like *Sisymbrium altissimum* (tall tumblemustard) are spreading across the Great Basin thereby altering competitive interaction and changing fire regimes (Germino et al. 2016b). This desert is in jeopardy of losing native plants such as *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush)*,* that provide habitat for many key desert plant and animal species, due to exotic plant invasions and wildfire (Chambers et al. 2014a). Previous studies show that specific native species are sometimes successful in competing with or resisting exotic plant invasion (Blank 2010; Booth et al. 2003a; Callaway and Aschehoug 2000; St. Clair et al. 2016), and others), however, dominance of exotic annual species indicates potential superior competitive abilities (Allen and Meyer 2014; Dickson et al. 2012; Perkins and Hatfield 2014; Schantz et al. 2015).

The objective of this study was to determine how fall precipitation timing, fire, and competition between native and exotic plants influence plant community assembly and invasion in the Great Basin Desert. We hypothesize that: 1) faster germination and growth, and greater nitrogen acquisition and higher C:N ratios (nitrogen use efficiency) of exotic annual plants compared to native species will result in greater competitive exclusion of native plants than exotic plants when grown together; 2) exotics will respond more favorably than natives to resources made available by fire and earlier fall precipitation, which will increase their competitive advantage against natives.

METHODS

Experimental Design

Cores were planted and randomly assigned treatments in 4 replicated blocks in a full-factorial design: Burned- early precipitation, burned- late precipitation, unburned- early precipitation, and unburned- late precipitation. Burn treatments were imposed by placing seedless and sterilized *B. tectorum* straw collected from Rush Valley on the cores receiving the burn treatment. We placed 526 g m^{-2} of cheatgrass straw contained in an aluminum cylinder on top of 24 randomly selected cores and ignited it with a lighter. This amount of straw is similar to average fuel loads of 462 ± 20 g m^{-2} of cheatgrass biomass in Rush Valley (St. Clair 2016). The ash from the fully combusted straw was left on top of the soil surface resulting in an estimated 9.9 g m^{-2} of N input (St. Clair et al. 2016).

Experimental System

Soil cores were extracted from intershrub spaces at Rush Valley in Tooele County, Utah, USA (40°05'26.17" N 112°18'18.01" W) a latitudinally central location of sagebrush steppe

ecosystem of the Great Basin Desert ecoregion. The mid-low elevation (1650 m) area has classified soils as a silty, mixed mesic Haplic Natrargid Taylors Flat Loam (Soil Survey Staff 2015). There had been no recent fires and/or grazing activity evidenced by well-developed biological soil crusts, no evidence of *Bromus tectorum* invasion, and the native plants were mature shrubs and perennial grasses, primarily Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*) and squirreltail (*Elymus elymoides*). We extracted 48 soil cores in PVC cylinders from intershrub spaces that were 15 cm in diameter and 40 cm deep. To keep soils intact but still allow for water flow and root penetration, mesh screen was attached to the bottom of each core. We wetted the area of core extraction to reduce cracking and breakage of the biological soil crust. Biological soil crusts remained intact and the cores were void of any vegetation. The cores were transplanted and buried in the soil, with the top one cm above ground, outdoors in a common garden at Brigham Young University Life Sciences in Provo, Utah, USA (40.2518° N, 111.6493° W, elevation 1450 m), 48 km east of Rush Valley. A 2 m welded-wire fence was installed around the garden with 30cm below ground to deter any herbivores from entering. Cores were subject to natural weather conditions from early September 2016 until mid-June 2017, the study duration. Provo's mean annual temperature is 12.3 °C with a July mean of 24.2 °C and January mean of -1.1 °C and mean annual precipitation of 411 mm/year. Cores were watered to carefully collect germinated seed bank though very few seedlings emerged.

Timing was the main difference between the two precipitation treatments. All cores were subject to natural whether conditions from the beginning of the study period. The early precipitation treatment occurred September 6-19, 2016 and the later precipitation treatment occurred October 12-25, 2016. Precipitation treatments consisted of watering each core with 1.5

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mm of water once every morning and afternoon totaling 3 mm of water per day (Figure 1). There were two natural rain events on September 14, and October 24-25 in which we did not water on those days. There was one other natural rain event on September 23-24. These natural events led to an 18 mm increase in total cumulative water for the early precipitation treatment after taking into account not watering on natural rain event days (Figure 1). The total cumulative amount of water the cores received was 431 mm from September 6 until plant collection in mid-June and late August.

Seeding to create the plant community combinations included a mixture of invasive and native species harvested in Rush Valley or received by the Great Basin Research Center, Utah Division of Wildlife Resources. Twenty seeds of each species were divided into five seed mixes: 1) Exotic community of four exotic annual species: [*Bromus tectorum* L. (cheatgrass), *Sisymbrium altissimum* L. (tall tumblemustard), *Alyssum alyssoides* L. (pale madwort), and *Ceratocephala testiculata* (Crantz) Roth (curveseed butterwort)]; 2) Native community of five native species [*Elymus elymoides (Raf.) Swezey* (squirreltail), *Poa secunda* J. Presl (Sandberg bluegrass), *Achillea millefolium* L. car. *occidentalis* (western yarrow), *Linum lewisii* Pursh (Lewis flax), *Atriplex canescens* (four-wing saltbush), and *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush; hereafter *Artemisia tridentata*)]; 3) The combination of the exotic and native community grown together; 4) *Bromus tectorum* grown alone and 5) *Artemisia tridentata* grown individually. All exotic annuals (St. Clair et al. 2016; Young et al. 1972) and native species are found across the Great Basin (Chambers et al. 2016; Miller et al. 2013). The native species were chosen through prevalence in the experimental system and use in reseeding efforts post-disturbance (Miller et al. 2013; St. Clair et al. 2016). The ecological importance of *B. tectorum* and its close association with wildfire and *A.*

tridentata, a keystone native perennial shrub species, were selected to be grown individually in cores without competitive interactions. *Bromus tectorum* is widely known as an exotic annual grass that can fill intershrub spaces and that increases the size and frequency of fires in sagebrush shrublands (Germino et al. 2016b). *Artemisia tridentata* has been slow to recover in post-fire environments especially in the presence of *B. tectorum*. Sagebrush and cheatgrass were grown singly and in combination with the other species to experimentally test the competitive effects for those two dominant species. Seeds were sown on the top of each core with very little disturbance or any attempt to bury the seeds.

Plant Measurements

All plants were destructively harvested beginning in early June 2017 by removing all above ground biomass and stored in separate paper bags. Harvested plants were dried at room temperature for six months. For *B. tectorum* and *S. altissimum*, a random subsample was used to count seeds for individuals and an allometric equation was derived based on the number of seeds per unit mass of the seed head ($R^2 = 0.88$) or silique ($R^2 = 0.97$) to calculate the total seed per core. All other seed was counted individually. Other plant measurements included average height, density, and biomass of above ground plant tissues.

Plant Tissue N and C Analysis

A homogenized plant tissue sample from each core (minus seed) was clipped from dry biomass that had already been measured for biomass. Subsamples were taken from each block, precipitation treatment, and seed mix however fire replicates were combined because of the lack of significant burn effect on plant growth. Plant tissue was homogenized and analyzed for % N and C:N ratios using the combustion method (TruSpec CN Determinator, LECO Instruments, St. Joseph, Mich., USA) at the Brigham Young University Environmental Analytical Laboratory.

Statistical Analysis

Linear mixed-effects analysis of variance models were used to test the main and interactive effects of fire, precipitation timing, and seed mix with experimental block as the random effect for the effect of competition on establishment, growth, and reproductive response of all planted species and community mixes using the 'nlme' package in Program R (Pinheiro et al. 2017). Linear mixed-effects analysis of variance models were used to test the main and interactive effects of precipitation timing, seed mix, and plant community (exotic, native) on N content and C:N ratios in plant biomass. Homogeneity of variance was achieved by using a varIdent covariance structure for precipitation or seed mix where needed.

RESULTS

Competitive Effects

Overall the native plant community and *Artemisia tridentata* exhibited greater sensitivity to competition than exotic plant community and *Bromus tectorum*. Exotics reduced the height (2-fold), density (2.3-fold), biomass (11-fold), seed production (200-fold), and C:N (1.3-fold) of native plants ($P<0.05$) but no effect on % N of native plant tissues ($P>0.05$) (Figure 4-2, Table 4-1). Competition negatively impacted *A. tridentata* where height, density, and biomass decreased 2.7-, 2.2-, and 95-fold when mixed with natives ($P<0.05$) and 24-, 23-, and 11,000-fold when mixed with exotics and natives together ($P<0.05$) compared to *A. tridentata* grown independently (Figure 4-3). In contrast, the exotic plant community response to competition with native plants only decreased exotic density 1.2-fold ($P<0.05$) with no effect on height, biomass, seed production, % N or C:N ratios ($P>0.1$) (Figure 4-2, Tables 4-1 and 4-2). Competition with exotics decreased *B. tectorum* height (1.2-fold), density (1.8-fold), biomass (1.6-fold), and seed production (2-fold) in comparison to being grown alone ($P<0.05$) (Figure 4-4). Competition with

exotics and natives decreased *B. tectorum* height (1.2-fold; P=0.08), density (2.7-fold), biomass (2.8-fold), and seed production (2.6-fold) compared to *B. tectorum* grown independently (P<0.05) (Figure 4-4).

Plant Community Responses to Precipitation Timing and Its Impact on Competition

Both exotic and native plant communities had positive responses to earlier fall precipitation. Earlier precipitation increased the mean exotic plant community height 18 cm (2-fold), density 1168 individuals m^2 (1.6-fold), biomass 5392 gm^{-2} (11-fold), seed production 4,846,573 seeds m^2 (12-fold) and C:N ratios (3-fold) compared with the late precipitation treatment (P<0.05) (Figure 4-2). Early precipitation increased the mean native plant community height 6 cm (3-fold), density 414 individuals m^2 (1.5-fold), biomass 258 gm^{-2} (11-fold), seed production (excluding *A. tridentata*) 12256 seeds m^2 (16-fold), and C:N ratios (1.4-fold) in comparison with the late precipitation treatment (P<0.05) (Figure 4-2, Table 4-1). However, early precipitation decreased % N of plant tissue for both exotic and native communities regardless of competitive mix (P<0.01) (Table 4-1)

Competitive effect of the exotic plant community on the native plant community was intensified by early precipitation as indicated by the significant competition by early precipitation interaction terms for native plant community density, height, biomass, seed production, and C:N ratios but not % N. The positive effect of early precipitation on the native plant community density, height, biomass, seed production, and C:N ratios was decreased or became non-existent when in competition with the exotic plant community (P<0.05) (Figure 4-2). Early precipitation also magnified the competitive effects of the exotic and native plant communities on *A. tridentata* as indicated by the severe reductions in height and biomass in early precipitation cores compared to late precipitation (P<0.05) (Figure 4-3). Early precipitation

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moderately increased the competitive effects of other exotics and native plants decreasing *B. tectorum* density, biomass and seed production (Figure 4-4).

Plant Community Responses to Fire and Its Impact on Competition

The main effect of fire and its interaction terms with precipitation timing and competition did not significantly impact the establishment, growth, or seed production of exotic or native plant communities ($P<0.05$) (Figures 4-2 and 4-3). Fire decreased the competitive effects of the exotic plant community on the native plant community density as indicated by the 3-fold decrease of density in unburned compared to the 1.7-fold decrease in burned cores ($P=0.07$) (Figure 4-2). Fire amplified the competitive effects of the exotic and native communities on *A. tridentata* density but had no effect on height or biomass (Figure 4-3). Fire did not influence the competitive effects of the native plant community on the exotic community or *B. tectorum* (Figures 4-2 and 4-4).

DISCUSSION

Competitive traits of exotic plants have a large influence in determining whether they become invasive or not (Levine et al. 2004; Mack et al. 2000). As outlined in our first hypothesis, native plant growth was greatly reduced when grown in competition with exotic species (Figure 4-2). And the effect of natives on exotics was minimal indicating that exotic plants were superior competitors to native species (Vila and Weiner 2004). Rapid germination, growth, nitrogen acquisition, and nitrogen use efficiency, as measured by C:N ratios, of exotic species likely increased their competitive ability against native species (Besaw et al. 2011; Davis et al. 2000; Ehrenfeld 2003; Perkins and Hatfield 2014; Wolkovich and Cleland 2011). Precipitation timing as opposed to total annual precipitation, is increasingly recognized as a critical driver of native plant establishment, and invasibility of ecosystems (Horn et al. 2017;

Pilliod et al. 2017; Prevéy and Seastedt 2014). In support of our second hypothesis early precipitation timing intensified the competitive effects of exotic plant species on the native plant communities likely due to increased N acquisition and nitrogen use efficiency (Table 4-1, Figure 4-2). However, our results did not show that fire had a major role in modifying competitive interactions between native and exotic plant species (Figures 4-2 and 4-3). While fire can provide resource pulses that can benefit plant growth (Allen et al. 2011; Bowman et al. 2011; D'Antonio and Vitousek 1992) some studies show that seed bank, pre-fire plant communities, and differences in fire severity may lead to more variable invasion outcomes (Schantz et al. 2015; Urza et al. 2017) .

Competitive Effects Between Exotic and Native Species and Communities

Certain native plant species, in our study particularly *Elymus elymoides* and *Poa secunda,* have been shown to compete with exotic species like *Bromus tectorum* (Booth et al. 2003a; Chambers et al. 2007; Uselman et al. 2015) but we found very little evidence of the native plant community having competitive effects on the exotic plant community (Figure 4-2). In contrast, exotic plant species have often been shown to competitively exclude native plants (Brooks 2000; Goodale and Wilsey 2018; Vila and Weiner 2004). Successful plant invaders often possess traits that facilitate rapid acquisition of soil resources (Brooks 2000; DeFalco et al. 2007; Goodale and Wilsey 2018; Melgoza et al. 1990; Prevéy and Seastedt 2014) that fuel rapid growth rate, resource use efficiency, and increase their competitive ability (Catford et al. 2012; Goldberg 1990; Shea and Chesson 2002; Vila and Weiner 2004). Higher C:N ratios in the exotic community and decrease of C:N of the native community in response to competition would indicate that higher resource use efficiency is a possible mechanism explaining stronger competitive abilities of exotic plant species (Table 4-1). Thomsen (2006) showed that the exotic

perennial grass *Holcus lanatus* had higher root:shoot ratio, relative growth rate, and greater competitive effects on neighboring plants than other native plant species in California perennial grasslands. Though, these effects and responses were variable across other species (Thomsen et al. 2006a). While early seral species (*Elymus elymoides*) seemed to fair best against the exotic annual species, slower establishment and growth of native plants generally make it difficult to compete with exotics (Figure 4-2, Table 4-2) (Adler et al. 2009; Chesson 2000). Native plant communities have shown varying degrees of robustness at resisting exotic plant invasions (Humphrey and Schupp 2004; Vaughn and Young 2015; Young et al. 2015) and biotic resistance is typically highest in intact, mature native plant communities that have not experienced recent disturbance (Chambers et al. 2017; St. Clair et al. 2016). Therefore, long term biotic resistance is unlikely to be maintained in the presence of increased disturbance in where native seedling are competing against exotic seedlings (Chambers et al. 2014b; Germino et al. 2016b; St. Clair and Bishop 2019).

Competition decreased *Artemisia tridentata* growth so severely that in some cases complete exclusion of *A. tridentata* occurred (Figure 4-3). *Artemisia tridentata* has shown to have mixed success at post-fire recovery even with active seeding (Chambers et al. 2014b; Davies 2011; Miller et al. 2013) and can vary widely based on environmental conditions (DiCristina and Germino 2006; Schlaepfer et al. 2014). Our results indicate that interspecific competition, regardless of fire or precipitation timing, is a major limiting factor in *A. tridentata* growth (DiCristina and Germino 2006; Schlaepfer et al. 2014) and sources therein). When certain native plant species establish first post-fire, such as *Elymus elymoides, A. tridentata* recruitment can be enhanced, but those effects are largely non-existent in the presence of exotic annuals (Germino et al. 2016b; Miller et al. 2013). The rapid vertical growth of exotics (Figures 4-2 and 4-3) in our

study also suggest that in addition to below-ground competition, above-ground competition for light availability may be a factor. Exposure to light is necessary to break *A. tridentata* seed dormancy and the faster growth of both the other natives and the exotics may limit its germination and recruitment (Meyer 1994; Schlaepfer et al. 2014).

Bromus tectorum exhibited some sensitivity to competition but overall experienced only limited reductions in establishment and growth when grown in competition with exotic and native plant communities (Figures 4-2 and 4-4). *Bromus tectorum* is an aggressive plant invader capable of inhabiting a wide variety of habitats and has successfully spread across large expanses of deserts in western North America (Bishop et al. 2019; Germino et al. 2016b). *Bromus tectorum* can germinate early in the fall, tolerate cold winter conditions, acquire N and water quickly, and has faster growth rates compared to the native plant species in our study (Germino et al. 2016b). *Bromus tectorum* is a prolific seed producer (Figure 4-4) which is a principal mechanism by which *B. tectorum* establishes and spreads in new environments (Allen and Meyer 2014; Schantz et al. 2015; St. Clair and Bishop 2019; Thomsen et al. 2006b) even though it may be sensitive to competitive interactions with native perennial grasses (Booth et al. 2003a; Germino et al. 2016b).

Effects of Precipitation on Native and Exotic Plant Communities and Competitive Interactions

Native and exotic plants benefitted from earlier precipitation timing (Figure 4-2). Water limitation is often seen as the first environmental filter constraining plant establishment in arid systems (Miller et al. 2006; Noy-Meir 1979; Wainwright et al. 2012). Predicted changes in the timing of the precipitation in the Great Basin for wetter winter and fall periods are likely to benefit plants established during those time periods (Abatzoglou and Kolden 2011; Pilliod et al. 2017; Prevéy and Seastedt 2015). Earlier precipitation can release water limitation for seedling

emergence and extend the growing period into more favorable fall temperatures for increased emergence and establishment (Bates et al. 2006; Slate et al. 2018; Ulrich and Perkins 2014). Longer favorable growing periods created by earlier fall precipitation can also affect nitrogen fixation rates and increase plant available nitrogen in the soil (Belnap 2002; Bishop et al. *in review*).

Competitive reduction of natives by exotic plants was intensified by early precipitation timing (Figures 4-2 and 4-3). The priority effects hypothesis posits that early season establishment by exotics, as in our study (Germino et al. 2016b; Meyer et al. 1997) provides a competitive advantage (Goodale and Wilsey 2018; Thomson et al. 2017; Ulrich and Perkins 2014). Exotic species decreased the positive effect of early precipitation for native species, while natives had little effect on exotics (Figure 4-2). This suggests that priority effects may be a mechanism driving competitive outcomes in our study system (Figure 4-2) (Dickson et al. 2012; Perkins and Hatfield 2014; Wainwright et al. 2012). However, with greater resource availability competition typically decreases (Davies et al. 2007; Davis et al. 2000), therefore more available water in favorable temperature conditions during the fall period may cause a shift towards nutrient limitation as being a driver of plant community assembly (Allen et al. 2011; Miller et al. 2006; Slate et al. 2018).

Though the native plants had higher nitrogen acquisition (Table 4-1) the exotic plant species were most nitrogen use efficient with earlier fall precipitation (Table 4-1). The higher C:N ratios but low nitrogen concentrations of the exotic community with earlier precipitation provides supporting evidence that exotic plant species are effective in rapidly acquiring soil nutrients, particularly nitrogen, and more resource use efficient than native plants in this study (Table 4-1) (Booth et al. 2003a; DeFalco et al. 2007; Huxman et al. 2008). Higher nitrogen nitrogen use

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efficiency can lead to increased relative growth rate and biomass accumulation and, in our study appear to provide a competitive advantage (Table 4-1 and Figure 4-2). Native desert annual plants commonly exhibit low relative growth rate and maintain high leaf nitrogen concentrations to increase stress tolerance and water use efficiency in response to soil resource limitation (Funk 2013; Huxman et al. 2008) Native plant adaptation for low-resource environments opens a temporal niche for invasion and resource pre-emption in early fall when temperatures are warmer and historically precipitation has been less consistent (Funk 2013).Therefore, early season exotic forbs and grasses have an opportunity particularly with increased early season precipitation due to climate change, to acquire nitrogen and grow quickly and establish thereby competitively excluding native plants (Berry et al. 2014; Prevéy and Seastedt 2014; Vila and Weiner 2004).

Effects of Fire on the Plant Community and Competitive Interactions

   The fire treatment did not strongly impact the establishment and growth of cheatgrass (Figure 4-4) or the exotic and native plant communities (Figure 4-2) but did increase the density and biomass of *Artemisia tridentata* (Figure 4-3). The effect of fire on *A. tridentata* was mainly seen when grown alone which is possibly due to the enhanced microsite conditions and darker soils, which can increase favorable growing conditions (Blank et al. 1996; Boyd et al. 2017; Schlaepfer et al. 2014)

   Fire did not enhance the competitive ability of the exotic plant community (Figures 4-2 and 4-4). Increases in plant growth in post-fire conditions, particularly exotic annuals, has commonly been reported (Besaw et al. 2011; Condon et al. 2011; Germino et al. 2016a) and others) and largely attributed to soil resource-pulses (Allen et al. 2011; Booth et al. 2003b; Davis et al. 2000) and reductions in biotic resistance of the native community (plants, consumers, biological soil crusts) (Levine et al. 2003; St. Clair et al. 2016). Our data suggests that successful plant

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invasions in post-fire conditions are more likely indirect effects of fire by reducing established native perennials that can resist invasion than nutrient pulses alone (Booth et al. 2003a; Callaway and Aschehoug 2000; Catford et al. 2012; Kraft et al. 2015; St. Clair et al. 2016). Biological soil crusts have varying effects on plant species growth, inhibiting both exotic and native plant species (Germino et al. 2018; Reisner et al. 2013; Slate et al. 2018) but also in some cases, providing more hospitable microsites for seedling emergence and growth (Boyd and Obradovich 2014; Deines et al. 2007; Ferrenberg et al. 2017; Germino et al. 2018; Zhang et al. 2016). Our experimental fires more likely mimicked a secondary fire where fine fuels from exotic grasses are the dominant fuel type rather than woody native shrubs. Fires that remove native woody shrubs typically create resource islands wherein shrub sub-canopies also have less developed soil crusts (Davies et al. 2009). Post-fire spatial heterogeneity can lead to differences in soil temperatures and recovering plant communities where native perennial bunchgrasses were favored in burned sub-canopies compared to burned interspaces (Boyd and Davies 2010; Davies et al. 2009). As our soil was removed from interspaces and our biomass fuel may not have increased temperatures into the soil layers as rooted plants would, it may not have mimicked wildfires adequately to result in damaging biological soil crusts severely enough to benefit seedling emergence and establishment. But the experimental fires may have provided a small pulse of nutrients affecting the growth responses for some species (Tables 4-1, 4-2, and 4-3) although the suggested nutrient pulse did not strongly alter plant community growth or strongly affect competitive interactions (Figure 4-2).

Conclusion

Biological invasions are restructuring native plant communities across the Earth's ecosystems including the Great Basin Desert (Chambers and Wisdom 2009). Responsiveness of

plant communities to changes in precipitation timing and disturbance regimes and how they modify plant-plant interactions will be a strong determinant of system vulnerability to vegetation state changes (Chambers et al. 2014b). Early precipitation timing positively affected exotic and native plant species (Figures 4-1 and 4-2, Table 4-1). The competitive advantage of exotic vegetation over native vegetation demonstrated in this study is consistent with shifts in vegetation observed in the Great Basin Desert in recent decades (Chambers et al. 2014b; Prevéy and Seastedt 2014; Prevéy and Seastedt 2015). Furthermore, the responsiveness of exotic annual plants to increases in fall precipitation not only increase their competitive advantage but also may reduce the potential benefits of early fall moisture to the native plant community (Figure 4-2) (Knapp et al. 2002; Schantz et al. 2015; van Kleunen et al. 2010). The reduction of growth of *B. tectorum* in the presence of competition of both exotics and natives (Figure 4-3) may offer limited opportunities to mitigate its success that has contributed to the spread of invasive grass fire cycles in the Great Basin Desert (Bradley et al. 2009; St. Clair and Bishop 2019). Conservation of established native plant communities by reducing disturbance may increase resistance to invasion and resilience in post-disturbance environments by reducing opportunities for priority advantaged exotic annual species that will be most benefitted by climate change and early fall precipitation (Booth et al. 2003a; James et al. 2012; Madsen et al. 2016).

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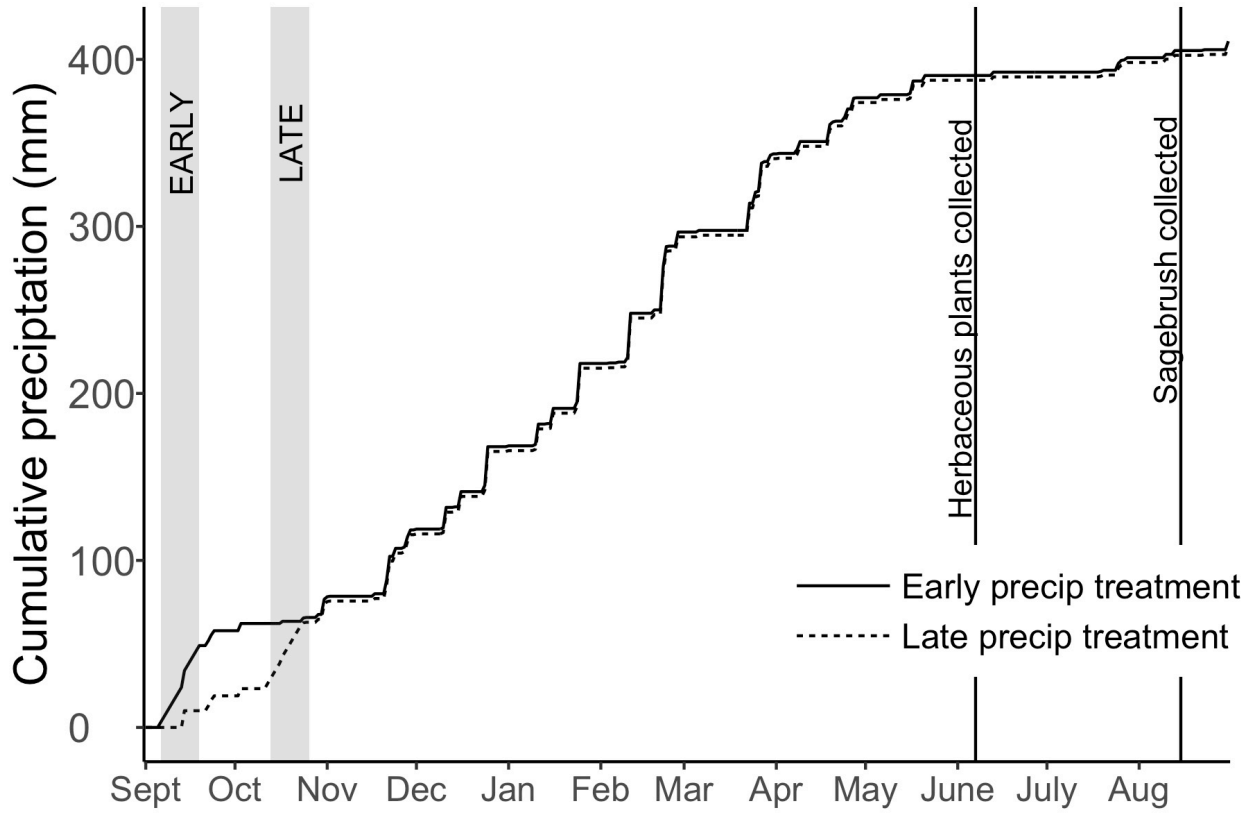
Figure 4-1 Cumulative precipitation between the two precipitation treatments. The timing of the precipitation treatments (early and late) is denoted by the two vertical grey bars. Time of plant harvest is denoted by the two vertical black lines.
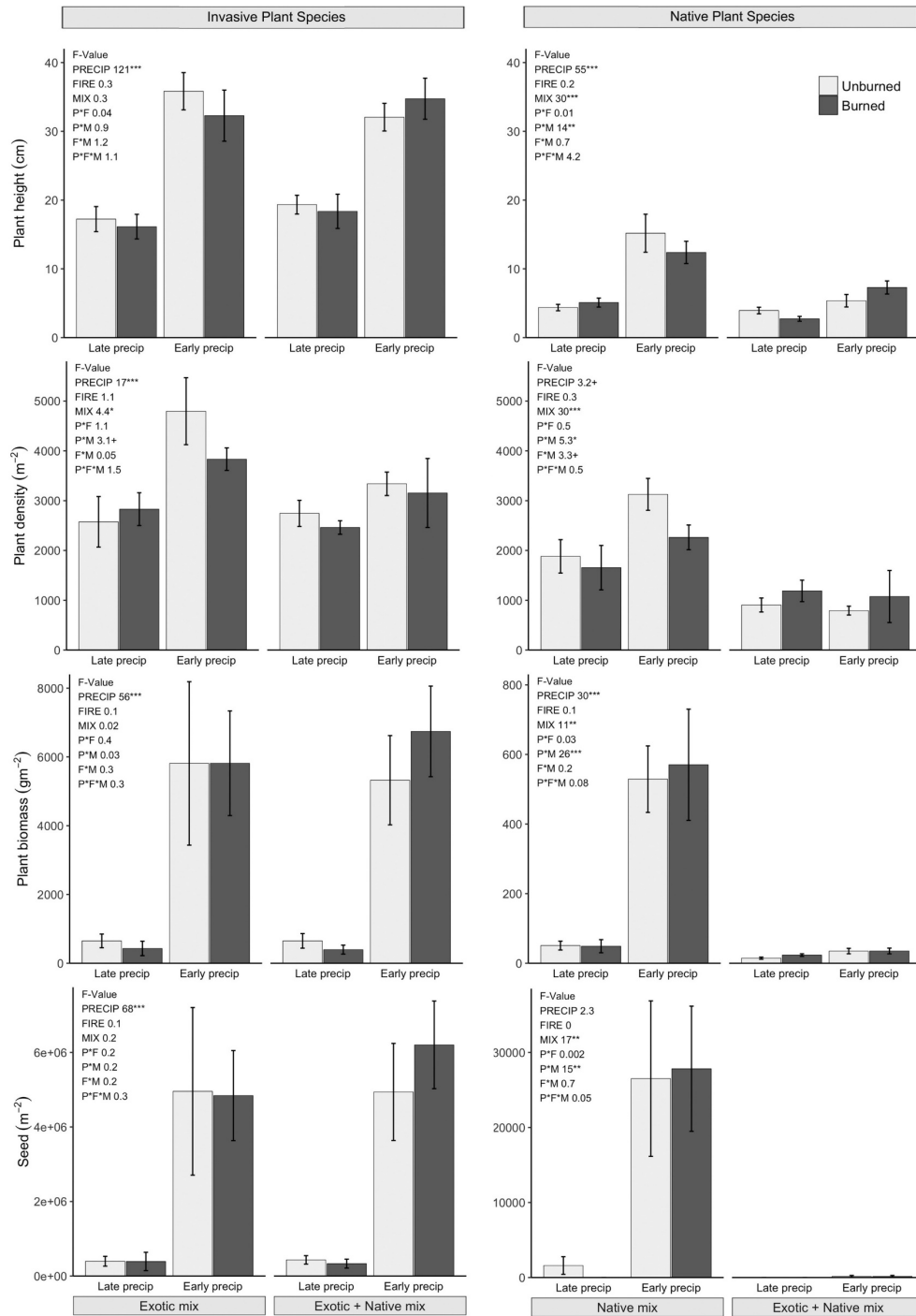
Figure 4-2 Plant growth, establishment, and seed production response of the exotic plant community and herbaceous native community grown in competition mixes modified by precipitation and fire treatment combinations. Native shrubs were removed. Means presented ± SE. F-statistic presented with P-value significance (*). P<0.05 (*), P<0.001 (**), P<0.0001 (***).

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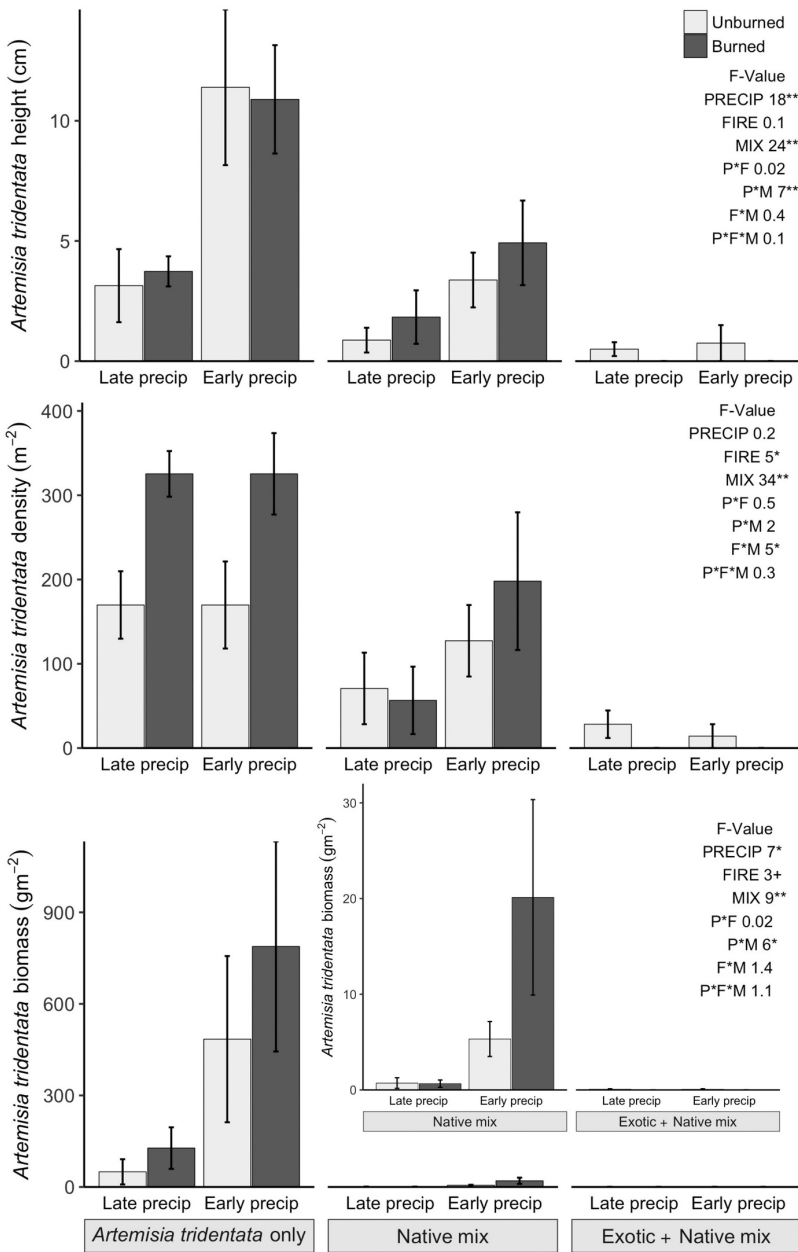
Figure 4-3 Plant growth and establishment of *Artemisia tridentata* grown alone and in competition mixes modified by precipitation and fire treatment combinations. Means presented ± SE. F-statistic presented with P-value significance (*). P<0.05 (*), P<0.001 (**), P<0.0001 (***). Note: biomass figure (bottom) has inset of *A. tridentata* growth in competition mixes due to the large magnitude difference of growth response to competition.

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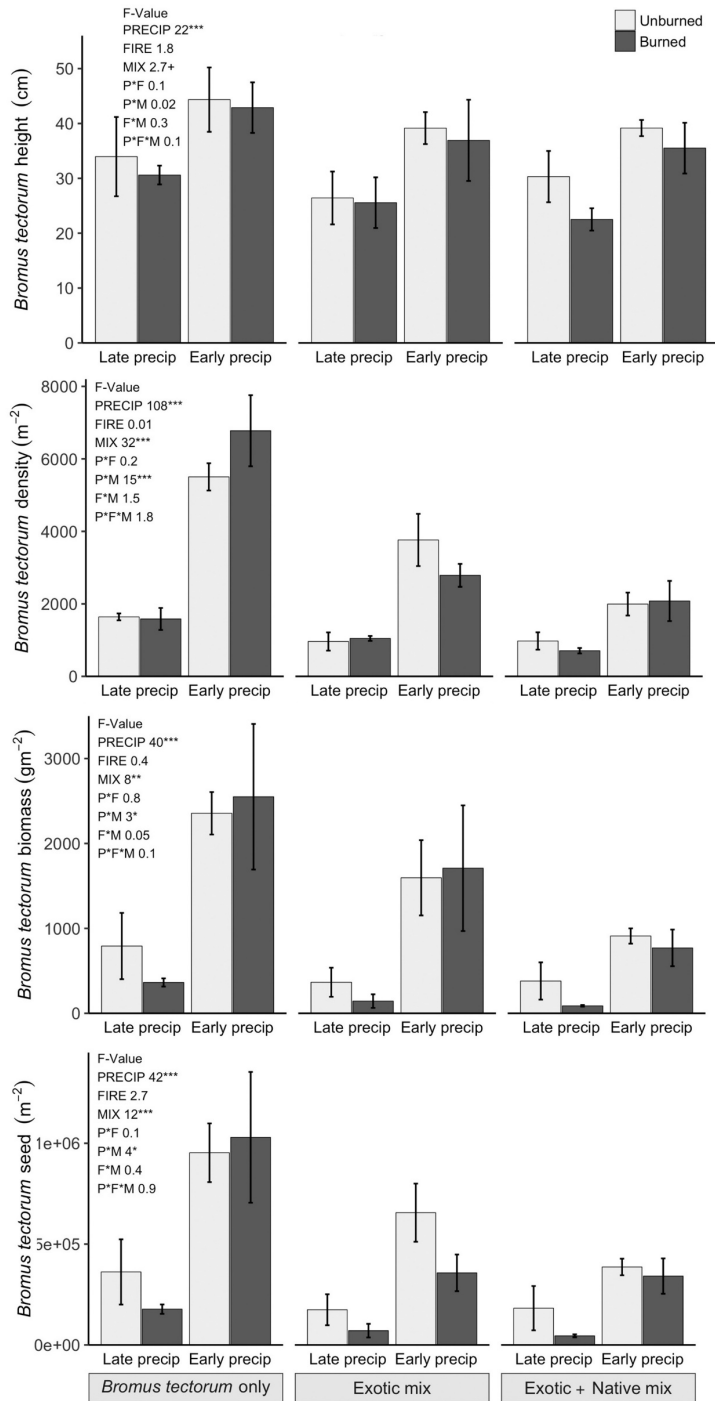
Figure 4-4 Plant growth, establishment, and seed production of *Bromus tectorum* grown alone and in competition mixes modified by precipitation and fire treatment combinations. Means presented ± SE. F-statistic presented with P-value significance (*). P<0.05 (*), P<0.001 (**), P<0.0001 (***). P<0.05 (*), P<0.001 (**), P<0.0001 (***).

TABLES

Table 4-1 %N and C:N ratios of homogenized plant tissue based on exotic and herbaceous native plant communities by seed mix and precipitation timing. Means presented with ±SE. Letters denote statistically different C:N ratios based on seed mix and precipitation timing. F-statistic presented with p-values denoted by asterisks; P=0.08[+], P<0.001 ***, P<0.0001 ****.

Seed Mix Precipitation treatment	df	Exotic spp % N	Native spp % N	Exotic spp C:N	Native spp C:N
Exotics only					
Early precipitation		0.34 ± 0.02 [a]		138 ± 10 [a]	
Late precipitation		0.63 ± 0.2 [ac]		84 ± 22 [b]	
Natives only					
Early precipitation			0.94 ± 0.2 [c]		51 ± 12 [c]
Late precipitation			1.51 ± 0.1 [d]		28 ± 2 [d]
Exotics + Natives					
Early precipitation		0.39 ± 0.1 [a]	1.31 ± 0.1 [de]	124 ± 18 [a]	33 ± 2 [d]
Late precipitation		0.52 ± 0.1 [ae]	1.45 ± 0.1 [d]	94 ± 20 [b]	29 ± 1 [d]
F-statistics for mixed-effects model					
Species by Mix	3,21	36 ****		27 ****	
Precip timing	1,21	12 ***		12 ***	
*SbM * P t*	3,21	1.6		2.7 [+]	
R^2_c		0.8		0.61	

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Table 4-2 Individual exotic plant species response to fire, precipitation timing, and competition. Means presented ± SE. F-statistic presented with P-value significance (*). P<0.05 (*), P<0.001 (**), P<0.0001 (***).

|		Sisymbrium altissimum				Alyssum alyssoides				Ceratocephala testiculata				Bromus tectorum			
Seed Mix		height (cm)	density (m^{-2})	biomass (gm^{-2})	seed (m^{-2})	height (cm)	density (m^{-2})	biomass (gm^{-2})	seed (m^{-2})	height (cm)	density (m^{-2})	biomass (gm^{-2})	seed (m^{-2})	height (cm)	density (m^{-2})	biomass (gm^{-2})	seed (m^{-2})
Treatment	df																
Exotic mix																	
Late-Unburned		29 ± 3	267 ± 48	222 ± 196	175361 ± 6899	10 ± 1	891 ± 180	63 ± 26	44989 ± 1816	3.3 ± 1	453 ± 179	15 ± 6	12124 ± 452	26 ± 5	962 ± 251	366 ± 171	174597 ± 7689
Late-Burned		22 ± 9	340 ± 122	217 ± 197	263056 ± 23985	12 ± 1	920 ± 220	70 ± 23	48017 ± 1528	1.4 ± 0.8	523 ± 323	10 ± 5	9507 ± 577	26 ± 5	1047 ± 67	144 ± 80	70973 ± 33798
Early-Unburned		56 ± 10	396 ± 165	4149 ± 221	4259250 ± 22249	16 ± 1	566 ± 95	66 ± 21	40122 ± 1312	2.4 ± 1	71 ± 42	0.8 ± 0.3	835 ± 63	39 ± 3	3763 ± 721	1596 ± 443	655917 ± 14418
Early-Burned		81 ± 8	552 ± 27	4076 ± 106	4212839 ± 93748	11 ± 1	467 ± 118	31 ± 17	21193 ± 2249	1.1 ± 0.7	28 ± 16	0.3 ± 0.2	424 ± 26	37 ± 7	2787 ± 316	1709 ± 730	357474 ± 90883
Exotics + Natives mix																	
Late-Unburned		28 ± 10	283 ± 106	174 ± 75	165667 ± 11748	12 ± 2	1146 ± 212	96 ± 28	68163 ± 1887	2.5 ± 1	340 ± 197	8 ± 6	7017 ± 475	30 ± 4	976 ± 239	380 ± 219	182388 ± 109797
Late-Burned		36 ± 7	340 ± 69	186 ± 102	210386 ± 11621	12 ± 1	1146 ± 93	122 ± 26	72039 ± 1322	3.7 ± 0.5	269 ± 42	6 ± 3	5602 ± 159	23 ± 2	707 ± 75	88 ± 10	45321 ± 7281
Early-Unburned		75 ± 8	608 ± 58	4355 ± 129	4514853 ± 12823	13 ± 1	722 ± 133	57 ± 18	37830 ± 1124	1.1 ± 1	14 ± 14	0.5 ± 0.5	297 ± 29	39 ± 1	1995 ± 316	910 ± 90	386639 ± 41210
Early-Burned		87 ± 8	538 ± 54	5929 ± 125	5832502 ± 11582	14 ± 0.5	481 ± 177	44 ± 20	29144 ± 1359	2.4 ± 1.4	57 ± 33	0.6 ± 0.4	707 ± 43	36 ± 5	2080 ± 524	770 ± 215	341475 ± 87614
Fire	1,21	0.09	0.7	0.3	0.3	0.7	0.5	0.06	0.3	0.05	0	0.4	0	1.8	0.01	0.4	2.7
Precipitation	1,21	98 ***	11 **	43 ***	44 ***	5 *	17 **	6 *	6 *	1.6	12 **	11 **	13 **	22 ***	108 ***	40 ***	42 ***
Mix	1,21	0.2	0.7	0.5	0.5	0.6	2	1.9	1.6	0.3	0.9	1	0.2	2.7 +	32 ***	8 **	12 ***
F x P	1,21	0.09	0.03	0.3	0.2	2.3	0.7	1.6	0.7	0.07	0	0.3	0.2	0.14	0.16	0.8	0.1
F x M	1,21	2.2	0.9	0.4	0.2	1.6	0.1	0.4	0.07	4 +	0.02	0.2	1	0.3	1.5	0.05	0.4
P x M	1,21	0.8	0.5	0.6	0.5	0	0.5	1.6	1	0.2	0.7	1	1	0.02	15 ***	3 *	4 *
F x P x M	1,21	0.02	0.7	0.4	0.3	6 *	0.06	0.004	0.05	0.04	0.3	0.09	0.002	0.1	1.8	0.1	0.9

Table 4-3 Individual native grass species response to fire, precipitation timing, and competition. Because many native grass individuals did not produce seed, not all individuals were able to be differentiated between the two native species but distinguishable from *B. tectorum.* We present all growth first, followed by any identifiable to species growth response. Means presented ± SE. F-statistic presented with P-value significance (*). P<0.05 (*), P<0.001 (**), P<0.0001 (***).

Seed Mix		Native perennial grasses - total				*Elymus elymoides* - identifiable				*Poa secunda* - identifiable			
Treatment	df	height (cm)	density (m^{-2})	biomass (gm^{-2})	seed (m^{-2})	height (cm)	density (m^{-2})	biomass (gm^{-2})	seed (m^{-2})	height (cm)	density (m^{-2})	biomass (gm^{-2})	seed (m^{-2})
Native Mix													
Late- Unburned		4.8 ± 0.6	1273 ± 195	37 ± 12	1599 ± 118	9 ± 1	736 ± 69	32 ± 11	1245 ± 1245	4 ± 0.8	524 ± 159	4 ± 1	524 ± 159
Late- burned		4.6 ± 0.7	962 ± 321	14 ± 6	0	6 ± 2	396 ± 142	10 ± 4	0	6 ± 3	509 ± 308	4 ± 2	509 ± 308
Early- Unburned		13 ± 2.5	2122 ± 233	245 ± 38	26512 ± 1036	14 ± 3.2	1613 ± 274	232 ± 35	7158 ± 3588	24 ± 5	509 ± 61	14 ± 2	509 ± 61
Early- Burned		8.7 ± 1.7	1118 ± 314	111 ± 20	27828 ± 834	11 ± 0.6	707 ± 246	92 ± 20	1273 ± 738	15 ± 5	410 ± 156	18 ± 7	410 ± 156
Exotics + Natives Mix													
Late- Unburned		4.4 ± 0.5	623 ± 69	10 ± 1.5	0	7 ± 0.9	495 ± 42	8 ± 1	0	1 ± 1	42 ± 42	0.1 ± 0.01	42 ± 42
Late- burned		3.2 ± 0.5	552 ± 121	13 ± 2	0	7 ± 0.3	410 ± 81	10 ± 2	0	1 ± 1	85 ± 85	1 ± 1	85 ± 85
Early- Unburned		4.8 ± 0.5	623 ± 83	29 ± 8	141 ± 14	12 ± 1	538 ± 105	27 ± 8	0	0	0	0	0
Early- Burned		8 ± 1.7	382 ± 139	22 ± 10	141 ± 14	14 ± 2.6	297 ± 129	19 ± 9	0	7 ± 7	14 ± 14	0.4 ± 0.4	14 ± 14
Fire	1,21	0.3	6 *	1.7	0								
Precipitation	1,21	23 ***	1.7	15 ***	2.2								
Mix	1,21	8 **	26 ***	49 ***	17 ***								
F x P	1,21	0.03	1.8	1.9	0								
F x M	1,21	2.8	2.4	10 **	0								
P x M	1,21	3 +	3 +	33 ***	15 ***								
F x P x M	1,21	5 *	0.7	5 *	0.05								

Table 4-4 Individual native forb and shrub species response to fire, precipitation timing, and competition. Means presented ± SE. F-statistic presented with P-value significance (*). P<0.05 (*), P<0.001 (**), P<0.0001 (***). F-statistics for *A. tridentata* models specified in Figure 4-3.

Seed Mix		Native perennial forbs – total				*Achillea millefolium* var. *occidentalis* – identifiabl				*Linum lewisii* – identifiable				*Artemisia tridentata* ssp. *wyomingensi*		
		height	density	biomass	seed	height	density	biomass	seed	height	density	biomass	seed	height	density	biomass
Treatment	df	(cm)	(m^{-2})	(gm^{-2})	(m^{-2})	(cm)	(m^{-2})	(gm^{-2})	(m^{-3})	(cm)	(m^{-2})	(gm^{-2})	(m^{-2})	(cm)	(m^{-2})	(gm^{-2})
Native mix																
Late–Unburned		4 ± 1	608 ± 139	14 ± 4	0	3 ± 1	382 ± 145	11 ± 4	0	4 ± 1	226 ± 40	3 ± 1	0	1 ± 1	71 ± 42	1 ± 0.5
Late–Burned		6 ± 1	693 ± 88	35 ± 14	0	6 ± 1	167 ± 63	31 ± 13	0	5 ± 1	226 ± 77	4 ± 1	0	2 ± 1	57 ± 40	1 ± 0.4
Early–Unburned		19 ± 4	1004 ± 96	284 ± 57	14275 ± 579	19 ± 3	424 ± 75	219 ± 43	8998 ± 356	19 ± 4	580 ± 71	64 ± 22	4541 ± 246	3 ± 1	127 ± 85	5 ± 2
Early–Burned		18 ± 2	1146 ± 170	460 ± 141	22325 ± 805	19 ± 2	651 ± 164	405 ± 153	18307 ± 873	17 ± 2	495 ± 166	55 ± 20	3353 ± 115	5 ± 1	198 ± 81	20 ± 10
Exotics + Natives mix																
Late–Unburned		3 ± 1	283 ± 155	4 ± 1	0	4 ± 1	156 ± 58	3 ± 1	0	2 ± 1	127 ± 109	1 ± 1	0	1 ± 1	28 ± 16	0.1 ± 0.04
Late–Burned		2 ± 0.2	637 ± 109	11 ± 3	0	4 ± 0.5	637 ± 109	11 ± 3	0	0	0	0	0	0	0	0
Early–Unburned		6 ± 2	170 ± 61	6 ± 3	142 ± 142	4 ± 1	85 ± 37	1 ± 1	0	8 ± 5	85 ± 67	4 ± 3	127 ± 127	1 ± 1	14 ± 14	0.1 ± 0.1
Early–Burned		6 ± 2	693 ± 384	13 ± 5	0	8 ± 2	623 ± 399	12 ± 5	0	5 ± 3	71 ± 54	1 ± 1	0	0	0	0
Fire	1,21	0.01	3 +	5 *	0.9											
Precipitation	1,21	41 ***	8 *	0.6	1.1											
Mix	1,21	34 ***	11 **	25 ***	14 **											
F x P	1,21	0.04	0.2	0.05	0.9											
F x M	1,21	0.2	1.7	1.4	0.7											
P x M	1,21	17 ***	3 +	20 **	14 **											
F x P x M	1,21	0.9	0.05	1	0.7											