INVASIVE ANNUAL SPECIES INCREASE WITH FIRE FREQUENCY IN THE NORTHERN GREAT BASIN

By

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A THESIS

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Wildfire, although a natural part of the Great Basin's sagebrush-steppe ecology, is poised to occur at more frequent intervals due to the combined influence of rampant annual grass invasion and increasingly long dry seasons. Deviations from the historic fire return interval of 25-75 years to a mere 3-5-year cycle disrupt the establishment of later-seral species, such as the keystone shrub, sagebrush (*Artemesia tridentata).* More frequent fire can also alter the structure of plant communities by favoring early colonizing annual grass and forbs. As fire frequency increases, the resilience of native species is diminished, and the site becomes more vulnerable to vegetation compositional conversions. The conversion of mixed sagebrush and perennial grass-dominated sites to monocultures of invasive annual species jeopardizes human and wildlife needs on the landscape. To better understand the effects of increased fire frequency on annual species invasion, I surveyed vegetation cover in sites with variable burn history at the North Great Basin Experimental Range in July of 2022. The relative abundance of plant functional groups, as well as two critical invasive annual species, cheatgrass (*Bromus tectorum*) and desert alyssum (*Alyssum desertorum)*, were recorded in plots burned in 5, 10, and 20 year intervals since 2002. The relationship between forb cover and fire frequency was the only statistically significant difference identified (p=0.02). General trends in the data supported the hypotheses that the mean percent cover of *Bromus tectorum* and *Alyssum desertorum* would be higher in sites burned more frequently. These preliminary findings indicate the relationship between fire frequency and invasive annual species warrants greater attention with future larger-scale vegetation surveys. A better understanding of fire frequency effects on vegetation conversion may help restoration practitioners effectively prioritize areas for post-fire restoration to limit loss of native species.

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KEY TERMS

Forb: herbaceous flowering plant other than grass

Perennial/Annual: Perennial plants regrow every spring, while annual plant individuals live for only one growing season.

Dominant/Subdominant: A dominant species is a species in an ecological community that has the highest abundance or highest biomass. A subdominant species has considerable importance in a community but less influence than the dominant species.

Seral stage: the various vegetation communities that occupy disturbed sites and make up an ecological community formed in succession. Seral-stage communities consist of vegetation types that are adapted to the site's particular set of physical and biotic conditions.

Burn edge: border region between areas burned and unburned.

Seed rain: the outcome of seed dispersal; the arrival of seeds into an area due to active dispersal by other species or via passive dispersal through gravity or wind.

Allelopathic: the chemical inhibition of one plant (or other organism) by another, due to the release into the environment of substances acting as germination or growth inhibitors.

INTRODUCTION

Overview:

Fire is a driving force of plant community structure in sagebrush-steppe of the Northern Great Basin. Wildfire is poised to occur more frequently in Basin and the competitive advantage of invasive annual grasses is likely to change as a result. This thesis reviews the scale of concern for native plant communities in the Basin as fire frequency increases and explores the influence of fire frequency as a regulator of plant community structure. I conclude with a discussion of trends observed in vegetation cover in plots of variable burn histories from field surveys I conducted at the North Great Basin Experimental Range in July of 2022.

A concerning trend: Sagebrush-steppe in decline:

The shrubland biome is a semi-arid ecosystem co-dominated by perennial grasses, forbs, and shrubs spanning thirteen states that makes up the largest terrestrial biome in the lower 48 (Natural Resources Conservation Service, 2021). Included within the shrubland biome is the sagebrush-steppe, an ecosystem in which the dominant shrubs are Dwarf sagebrush (*Artemisia arbuscula*) and Big sagebrush *(A. tridentata ssp. wyomingensis*). Though the sagebrush-steppe ecosystem is expansive, it is vulnerable to large-scale, biome-level threats such as annual grass invasion, conifer expansion, changing climate patterns, human land use changes, and altered wildfire regimes (USFWS, 2010; Davies et al., 2011).

Since the arrival of European settlers in the mid-1800s, the spatial extent of sagebrush-steppe has been reduced to half of its historic range. The loss is ongoing as an estimated 1.3

million acres continue to be converted to development or annual grass-dominated sites each year (Doherty et al., 2022).

Figure 1: Delineation of the floristic Great Basin ecoregion, adapted from Grayson, 2011

Intact sagebrush-steppe, much of which lies in the Great Basin (delineated above), retains some natural resistance to invasive species invasion if disturbance regimes are infrequent. However, as fire frequency increases and human land use intensifies, the natural resistance of native perennial bunchgrasses and sagebrush is diminished. Sagebrush habitats at lower elevations have particularly diminished resistance to invasion as they often have slightly warmer climates that foster more frequent fire and more substantial invasive growth (Chambers et al., 2014). As sagebrush-steppe sites are exposed to increasingly frequent disturbance, the structure of the plant community often transitions from shrub and perennial grass codominance to annual invasive species dominance (Mack et al., 1981; Brooks & Esque, 2002; Bradley & Mustard, 2005).

The conversion of sagebrush-steppe to monocultures of annual invasive species threatens native ecologies, and thus impacts plant and wildlife conservation as well as human lifestyles, values, and interests in the landscape. The loss of the keystone shrub *Artemisia sp.* is of particular concern as it supports approximately 350 other plant and animal species (Natural Resources Conservation Service, 2021). Amongst the dependent species is the greater sage-grouse (*Centrocercus urophasianus*), a species of focus for many conservation initiatives (Aldridge et al., 2007). Other sagebrush-reliant animals include the black-tailed jackrabbit (*Lepus californicus*) and the Paiute ground squirrel (*Spermophilus mollis*), which are significant sources of prey for golden eagles (*Aquila chrysaetos*) and prairie falcons (*Falco mexicanus*) (Knick et al., 2003). The stable root structure of the sagebrush also enables the establishment of many native grasses that are a preferred food source for both wildlife and cattle (Barga & Leger, 2018). When native species are lost, ranching and rangeland agriculture are threatened and the economic stability of rural communities is made vulnerable (Doherty et al., 2022).

The loss of *Artemisia sp.* to fire is particularly concerning as it is an extremely slow growing genus that does not resprout after burning. The non-sprouting phenological trait signifies a slow recovery; it can take 60 to 300 years of ecological succession for a sagebrush community to recover to its pre-burn state depending on the dominant sagebrush species (Britton

& Ralphs, 1979; Bunting et al., 1987). As the likelihood of large wildfires in the sagebrush biome increases due to annual grass invasion and longer dry seasons, it is critical to utilize a robust understanding of the influence of fire on plant community assembly in order to preserve and restore biodiversity.

Invasive species in the Great Basin

Disturbances in the sagebrush-steppe, such as frequent wildfire, provide opportunities for invasive species to establish quickly in degraded environments (Pastick et al., 2021). Invasive species are typically phenologically equipped to grow and reproduce quickly. An early colonizing advantage enables invasives to quickly become dominant before native species can establish. Once an invasive species is sufficiently dominant, it can remain the dominant species even after the source of disturbance is removed (such as future fire suppression) (Doherty et al., 2022). Ecosystem transformations can reduce wildlife habitat and livestock forage and alter fire regimes beyond the range of variation to which native species are adapted (D’Antonio et al., 1999).

Before invasion by annual grasses, intact sagebrush-steppe habitat can be characterized as a mix of perennial shrubs, perennial bunchgrasses, perennial forbes, and annual forbes (Young & Evans, 1975). Particularly widespread non-native species in the Great Basin include cheatgrass (*Bromus tectorum*), medusahead (*Taeniatherum caput-medusae*), desert alyssum (*Alyssum desertorum*), and pinyon-juniper woodlands. According to abundance in the study site selected for vegetation cover analysis, cheatgrass and desert alyssum are the focal species of this study.

Bromus tectorum

Cheatgrass, also known as downy brome or *Bromus tectorum,* is the most prevalent invasive annual grass in the Great Basin (Knapp, 1996) as its unique phenological traits make it highly competitive with native perennial bunchgrasses (Pellant, 1990). Cheatgrass invasion is a particular concern for ranchers as the species is not a reliable source of forage for cattle (Roberts et al., 1991). Already, approximately 20% of the sagebrush-steppe vegetation zone is dominated by cheatgrass to the extent that the establishment of native perennial species is made nearly impossible (Knapp, 1996).

Cheatgrass's phenological traits of early emergence, production of a high volume of above ground biomass, and heavy investment into the seedbank, make it a particularly effective competitor with native species (USDA, Fire Effects Information System). Cheatgrass emerges in the late winter, earlier than most native species, and is already an established seedling by the time native species begin to germinate in the spring. This early phenology enables the cheatgrass seedlings to be more resilient to fluctuations in temperature and precipitation in fickle spring weather (USDA, Fire Effects Information System). Once established, cheatgrass grows tall producing a high volume of above ground biomass that eventually forms a thatch of material on the soil surface. Due to the arid nature of the Great Basin, the thatch decomposes slowly, blocking light and water from reaching seeds beneath and inhibiting the establishment of native species (Welty, 2018). The final competitive advantage of cheatgrass lies in its ability to form persistent seed banks with seeds that can remain dormant in the soil for multiple years until conditions are favorable for germination (Hassan & West, 1986). When the cheatgrass seeds eventually emerge, the ecosystem is likely to become increasingly converted towards a monoculture of cheatgrass (Humphrey & Schupp, 2001).

The cheatgrass invasion of the Great Basin has not gone unchallenged. Manual removal, herbicide application, and reseeding of native species are the primary methods used to combat its spread. Unfortunately, these techniques can cost upwards of $350 per acre (Venhuizen), require repeat treatments, and restoration success rates are estimated at less than 30% (Pilliod et al., 2017).

Alyssum desertorum

Desert alyssum (*Alyssum desertorum*) is an invasive annual forb that also thrives in disturbed sites and brings with it unique environmental and economic burdens. While it does not demonstrate the same landscape altering abilities of cheatgrass, desert alyssum can displace native forb species through competition, though it only grows densely following disturbance. The spread of desert alyssum is also associated with increased soil erosion due to its shallow root systems (Meyer & Morey, 2021), decreased soil fertility, and a less-diverse surrounding soil microbial community (Hamilton & Hellquist, 2012). Desert alyssum also absorbs surface moisture inhibiting the establishment of native species (Meyer & Morey, 2021).

The removal of alyssum is challenging and costly. A project geared towards its removal in Yellowstone National Park estimated over $20,000 in expenses per acre for removal efforts (Renkin et al., 2014). The spread of desert alyssum, and the corresponding scale of restoration work required to combat it, is amplified by increased fire frequency (Evangelista et al., 2011).

Fire as a driver of non-native species invasion in the Great Basin

History of disturbance in the Great Basin

The invasion of non-native species in the Great Basin, in a painful parallel, aligns with the timeline of European colonization of the region. When Europeans settled in the Great Basin in the mid-1800's, they brought with them the seeds of highly competitive species combined with their straw seed mixes (cheatgrass and medusahead were among the stowaways) (Knapp et al., 1996). In addition to introducing new species to the ecosystem, European settlers began landscape-scale processes of disturbance in the shrubland biome via fire suppression and unregulated overgrazing practices (McAdoo et. al, 2013).

Settlers rotated their cattle across the landscape less frequently than previous mid-trophic herbivores ranged, such as the constant movement of bison, resulting in more concentrated consumption of vegetation and greater damage to soil structure and root communities of native species (Morris & Rowe, 2014). Unregulated grazing practices, coupled with a rapid increase in livestock stocking - up from 3 million cows in the Basin in 1870 to 23 million by 1975 - resulted in swift and significant native vegetation loss (West, 1983). Additionally, the removal of above ground vegetation through the process of herbivory and soil degradation further invited the establishment of early colonizing invasive species (Young & Sparks, 2002).

European settlers also disrupted the stability of plant communities in the Great Basin by criminalizing the historic fire regimes carefully maintained by indigenous communities since time immemorial. By interrupting the systematic burning techniques practiced by the Paiute people (McAdoo et. al, 2013), settlers in the Great Basin region enabled the encroachment of conifer woodlands historically kept at bay with regular burning and impeded the regular disturbance regime needed to maintain the diverse habitat niches that preserve biodiversity (Gruell, 1985).

Irregular and infrequent burning creates a mosaic of landscapes at different successional stages of burn response in the sagebrush-steppe. Over evolutionary time, fire regimes can partially determine the coevolution of plants and the species that depend on them at different stages of post-fire succession (Cowling, 1987). The resulting variety of post-fire successional stages (ranging from grass-dominant to shrub-dominant) provide a diversity of habitats for wildlife with preferences for particular plant functional group compositions (McAdoo et al., 2013). Cultural burning practices that maintain this "fire mosaic" are in keeping with the *Intermediate Disturbance Hypothesis* (Moi et al., 2020) in which moderate and semi-frequent disturbance support higher species diversity in an ecosystem. The species now considered native to the Great Basin evolved in relation to fire, consistently ignited via lightning or human ignition. Therefore, it can be reasonably assumed that fire regimes must remain within historical ranges to preserve native vegetation and high biodiversity.

Fire regimes

Ecosystems are balanced by disturbance regimes measured by frequency, intensity, severity, extent, type, and seasonality (White & Pickett, 1985). In the Great Basin, fire is a defining source of disturbance. **Fire frequency** measures the fire return interval, also known as fire recurrence interval or fire cycle, a metric capturing the average time before fire reburns a given area. **Fire intensity** describes the amount of heat released per unit of time. Intensity relates to **fire severity**, which is the effect of the heat release on biotic and abiotic ecosystem properties. **Fire extent** refers to the size and spatial homogeneity of the burn area. **Fire type** describes the type of fuel burned such as a ground fire, surface fire, and crown fire. Finally, **fire seasonality** captures the annual timeframe during which fire activity occurs (Brooks, 2004).

The historic fire regime in the Great Basin varies temporally and spatially; though in general, large wildfires appear historically infrequent (25 - 75 year fire return interval) in the desert shrublands and grasslands because of insufficient fuel to carry significant surface fire (Whisenant, 1990; Humphrey, 1974).

Shifting fire patterns

Euro-American fire suppression, a changing climate, and increased spread of flammable invasive species are increasing fuel loading on the landscape and extending the potential burn season. As a result, historic fire regimes in the Great Basin may shift towards larger acreage burns occurring at a higher frequency and higher intensity reaching more extreme maximum temperatures on the soil surface. If a new fire regime produces vast areas in homogeneous post-fire seral stages and couples with the localized loss of native species, local extinction events are likely to occur. To understand the mechanisms driving the fire regime changes, it is important to further explore the effects of fire suppression, changing climate patterns, and invasive grass characteristics.

Fire suppression

When Western fire suppression interrupted the historic “fire mosaic”, the natural fuel breaks provided by burn scars (regions previously burned) were removed and a continuous fuel bed was created. Continuous fuel loads make the shrub-steppe more vulnerable to high-acreage, high-intensity burns (McAdoo et al., 2013). Larger acreage burns have proportionally larger regions away from the burn edge, limiting opportunities for natural dispersal and the recovery of native species (Mueggler, 1956).

Climate change

Our changing climate compounds the increased risk of high-intensity fires resulting from fire suppression. Models produced by Abatzoglou & Kolden (2011) suggest warming will be amplified during the summer across the Great Basin, particularly in models that predict a reduction in summer precipitation. Abatzoglou & Kolden's models also predict a greater fraction of annual precipitation will fall between November and March across the Great Basin. Winter annuals germinate early and will be able to absorb a greater proportion of available moisture with this temporal shift in precipitation, a change likely to favor early emergent species such as cheatgrass. Furthermore, an earlier end to cool-season precipitation could promote a 1–4-week advancement in the median onset of fire season across the Basin (Abatzoglou & Kolden, 2011). In addition to concerning modeling predictions, sites in the Great Basin are already observing changes in precipitation patterns. At the North Great Basin Experimental Range, less than 75% of the 80-year precipitation average fell in 2012, 2013, and 2018 (Bates & Davies, 2022). These observations have significant implications for fire activity as longer and hotter seasons can "preheat" vegetation by removing moisture from fuel making it more vulnerable to ignition (Goodwin et al., 2021).

Invasive grasses

Fire regimes are also influenced by the invasion of highly flammable invasive grasses like cheatgrass (Whisenant, 1990). The invasion of cheatgrass poses a particular fire risk due to: 1.) fine leaves with a high ratio surface area, 2.) an earlier life cycle than native grasses that results in dry leaves earlier in the summer which extends the potential fire season, 3.) a tendency to grow densely and continuously, and 4.) phenological traits that favor above-ground biomass production via tall tufts that create a greater volume of fuel (Knapp, 1996; Pellant, 1990). The arid nature of the Great Basin reduces the rate of decomposition of plant material that enables the buildup of fuel over multiple growth seasons (Knapp et al., 1996).

Increases in the density of cheatgrass have been shown to lead to significant increases in fire frequency. For example, in the cheatgrass-invaded Snake River Plain of Southern Idaho, fires frequently burn at intervals of less than five years apart as compared to historic frequencies estimated at 60-year intervals (Whisenant, 1990). In the same region, over 50% of the fires that occurred between 1981 and 1987 were in previously burned, cheatgrass-dominated areas (Pellant et al., 1990). Hull et al. estimate cheatgrass rangeland is 10-500 times more likely to burn than native bunchgrasses, and that the presence of cheatgrass extends the fire season by one to three months (Hull et al., 1965).

Cheatgrass invasion has been observed to change to fire frequency to an interval at which native shrub–steppe species cannot recover between burns (e.g., D'Antonio & Vitousek, 1992; Mack & D'Antonio, 1998; D'Antonio et al., 2000; Whisenant, 1990). When fires are less than five years apart, cheatgrass quickly establishes dominance and can exclude the establishment of *Artemisia sp*. (Holmgren, 1956; Price & Brotherson, 1984).

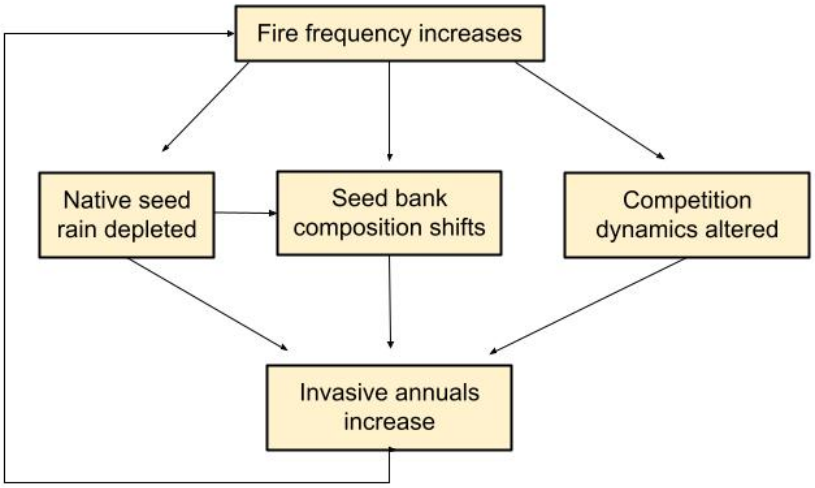

Figure 2: Positive feedback loop between fire frequency and invasive annual species dominance

Fire regimes shape plant communities

Fire regimes can drive the invasion of non-native species by influencing three critical plant community assembly forces: seed rain, seed banks, and inter-species competition dynamics. Fire does so by limiting natural seed dispersal, influencing germination from the seed bank, and shifting available light, water, and nutrient levels. Increases in fire frequency compound the impacts of an isolated burn and disproportionately favor species better equipped to take early advantage of available resources (Humphrey, 2001). If fire frequency increases, the relative competitive strength of early colonizers is also increased as the landscape is conducive to their establishment more frequently.

EXPERIMENTAL STUDY

Research Question: How does variable fire frequency influence the structure of the plant community and the spread of invasive species at the North Great Basin Experimental Range?

HYPOTHESES:

1.) As the interval between burns decreases, the mean percent cover of annual grasses and forbs will increase while the mean percent cover of perennial bunchgrasses will decrease.
2.) As the interval between burns decreases, the mean percent cover of the invasives *Alyssum desertorum* and *Bromus tectorum* will increase.

METHODS

A. Study Site:

Sampling took place in the North Great Basin Experimental Range, approximately 56 km west of Burns, Oregon (known from here out as NGBER) at N 43.490142, E -119.712763. NGBER is an agricultural and plant sciences research station jointly managed by Oregon State Extension and the USDA. The site was chosen for the extremely unique opportunity to sample before and after a scheduled burn in the shrub-steppe ecosystem in areas with known variability in burn history.

The NGBER falls within the High Desert Ecoregion (Anderson et al., 1998) and experiences a semi-arid climate with a 90-year average of 280 mm of precipitation falling mostly between October and May (Bates & Davies, 2022). The soil is predominantly characterized as Ninemile (cobbly loam) and Carryback soil (silty clay loam) (Lentz & Simonson, 1986).

NGBER vegetation reflects the typical vegetation of the sagebrush-steppe and includes a mix of shrubs, perennial bunchgrasses, annual grasses and annual forbs. The dominant shrub is *Artemisia sp*., and *phlox sp.* is a subdominant shrub. The dominant perennial bunchgrasses are Idaho fescue (*Festuca idahoensis*), Sandberg's bluegrass *(Poa secunda*), bluebunch wheatgrass (*Pseudoroegneria spicata*), prairie Junegrass (*Koeleria macrantha*), and Thurber's needlegrass (*Achnatherum thurberianum*).

Vegetation sampling occurred in late July 2022 and late October 2022. Paired study sites (burn, control) were established at elevations of 1430–1560 m on a west-facing aspect with slopes between 0-5% grade. Burned sampling sites were quarter-acre units burned every 5 years, 10 years, and 20 years located in the NGBER range 9, plot 16. Control sample sites were quarter acre units in range 8, plot 13 and are estimated to have last burned at least 50 years ago.

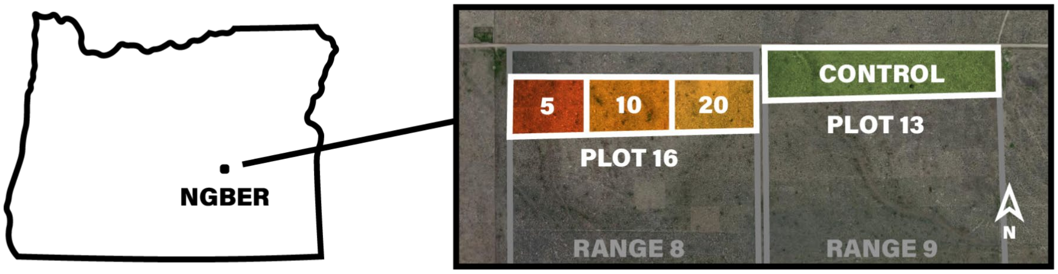

Figure 3: NGBER study site orientation. Background image source: Google Earth

Image 1: Perennial bunchgrasses visible in this east-ward perspective from within the 20 year burn interval site in Plot 16 at the NGBER.

B. Vegetation data collection

A transect method was utilized to assess vegetation cover. A 50-meter transect tape was laid out in each subplot (5 year, 10 year, 20 year, and three times in the unburned control) every 10 meters along the east/west border of the site. Four 1 square meter quadrat sampling frames were placed along the transect at 10 meter intervals in each subplot (3 burned subplots, 3 unburned subplots = 6 subplots x 1 transect x 4 quadrats each = a total of 24 quadrat sites).

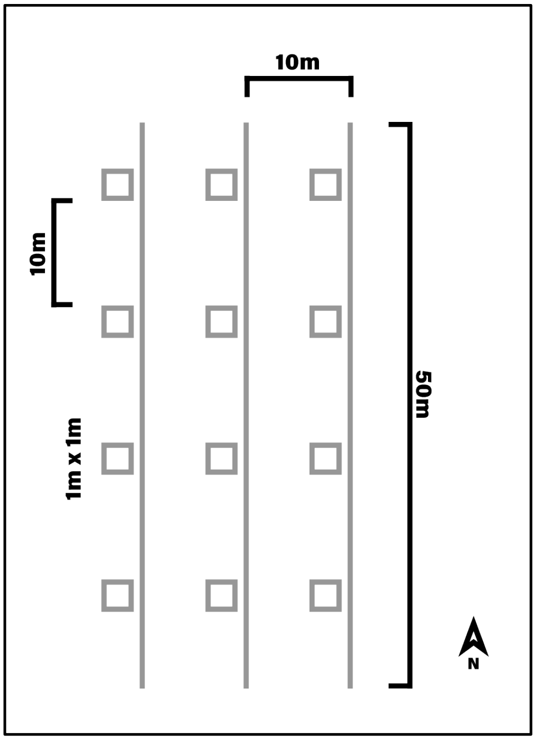

Figure 4: Vegetation sampling scheme

Image 2: Identifying *Achnatherum thurberianum*

Sample quadrats were placed at least 50 centimeters from a shrub or ant hill. If a shrub was present, the sample quadrat shifted west until an area appropriately clear of shrubs and without evidence of ants was found. These steps were taken so that the top 10 centimeters of soil could be collected from each corner of the quadrat for seed bank analysis (not included in this thesis). The species of each plant captured in the quadrat was identified and recorded by cover class. Unidentifiable species were photographed with a sample collected for future identification. Percent cover was recorded to the nearest 1% between [0-10] and recorded in intervals of 5% between [10, 100]. A GPS coordinate was collected at each sampling site with a Trimble GPS unit for spatial representation of the data.

C. Statistical analyses

Rstudio, JMP, and Excel were used to produce figures and statistically evaluate the data. A mixed-effect linear model and post-hoc Tukey tests were used to compare significance in the percent cover of species across transects. Significance was determined with an alpha of 0.05. A linear mixed-effects model fit by REML (REstricted Maximum Likelihood) was performed to analyze the effect of burn interval on the percent cover of *B. tectorum, A. desertorum*, and the functional groups of perennial grasses, annual grasses, and forbs with quadrat replication nested within transect as a random effect.

RESULTS

Effects of burn interval on functional group relative abundance

Table 1:

Table 1 provides the average percent cover of functional groups per burn interval

Burn interval (years)	n	% Annual Grass	% Forbs	% Perennial Grass
5	4	10.5 ± 5.11	27.5 ± 2.25	17.0 ± 1.96
10	4	8.75 ± 3.47	20.5 ± 3.28	19.8 ± 1.89
20	4	3.75 ± 3.75	18.3 ± 2.36	29.0 ± 6.20
Control	12	3.08 ± 1.61	12.3 ± 2.27	19.3 ± 1.18

Values are presented as mean ± standard error

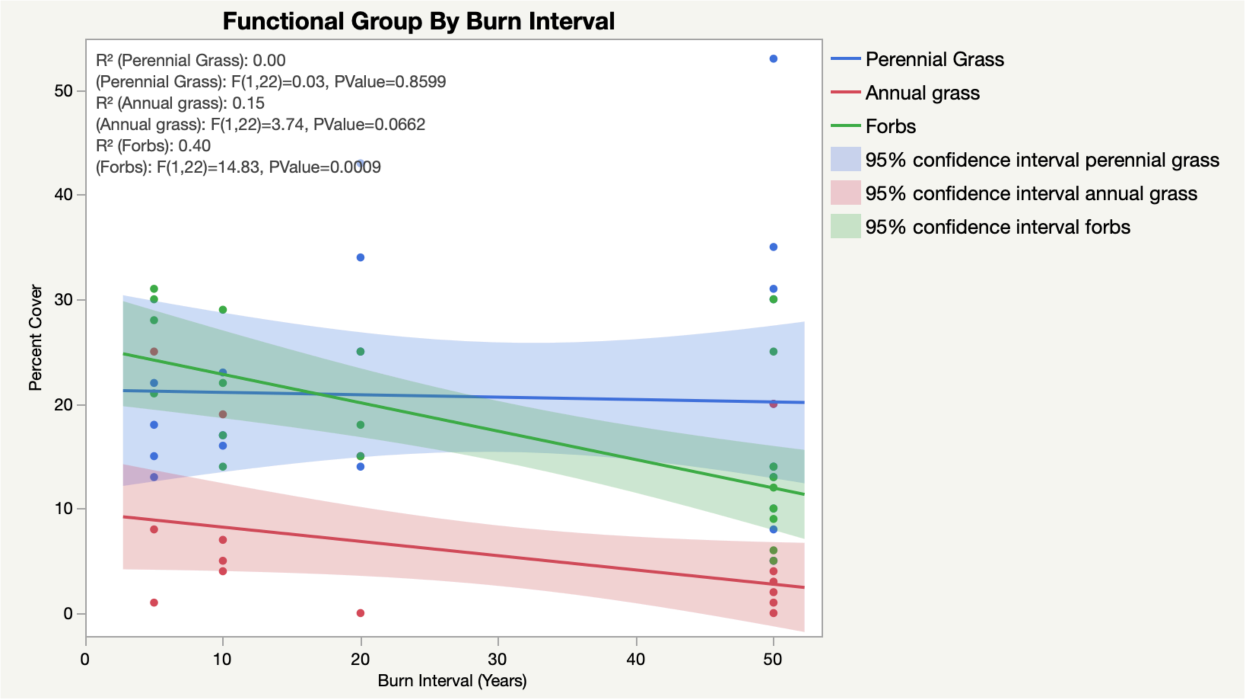

Figure 5:

Forbs and annual grass decrease as fire return interval increases. Perennial grasses remain consistent. Lines represent smoother lines of fit (Method: Spline, Lambda: 0.05). Shaded regions represent 95% confidence intervals around the fit line. Points represent percent cover of functional groups in each sampling quadrat.

Perennial grass cover weakly increased with longer burn interval ($F_{3,9} = 1.92$, $p = 0.197$). Annual grass cover did not statistically change with burn interval ($F_{3,9} = 1.55$, $p = 0.269$). Forb cover significantly decreased with longer burn interval ($F_{3,9} = 5.45$, $p = 0.0206$). Simple main effect analysis showed that random effects of quadrat replication did not statistically significantly affect the percent cover of any functional group.

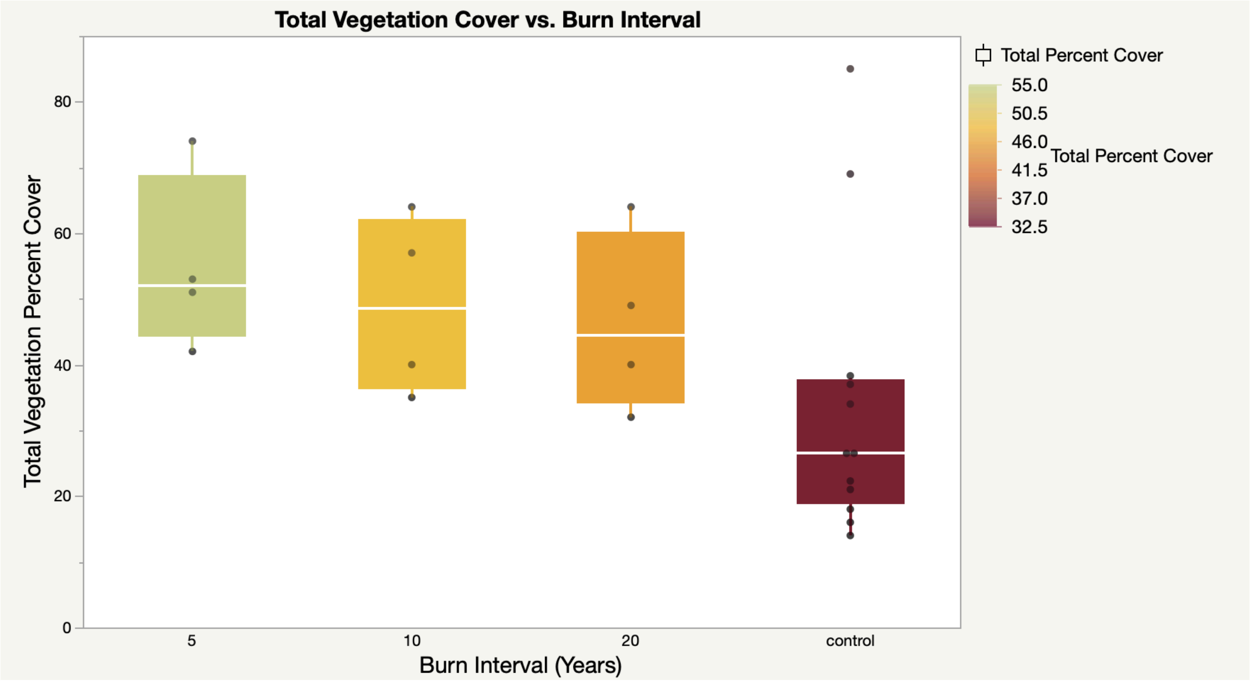

Figure 6:

Total vegetation cover decreases with time between burns. Box plots show five number summaries of total percent cover grouped by burn interval (5, 10, 20, control). Points represent individual cover data collected once per sampling quadrat. The 5-year interval has a median of 52% with a lower quartile of 44% and an upper quartile of 69%. The 10-year interval has a median of 49% with a lower quartile of 36% and an upper quartile of 62%. The 20-year interval has a median of 45% with a lower quartile of 34% and an upper quartile of 60%. The control group has a median of 27% with a lower quartile of 19% and an upper quartile of 38%.

Effects of burn interval on invasive annual dominance

Table 2:

Table 2 provides average percent cover of *B. tectorum*, *A. desertorum*, and total vegetation per burn interval.

Burn Interval (Years)	n	% Cover *B.tectorum*	% Cover *A.desertorum*	Total % Vegetation Cover
5	4	10.5 ± 5.11	18.75 ± 4.27	55.0 ± 6.77
10	4	4.25 ± 1.79	16.25 ± 2.39	49.0 ± 6.87
20	4	3.75 ± 3.75	16.25 ± 3.15	46.25 ± 6.86
50+	12	3.0 ± 1.6	8.75 ± 2.10	33.92 ± 6.31

Values are presented as mean ± standard error

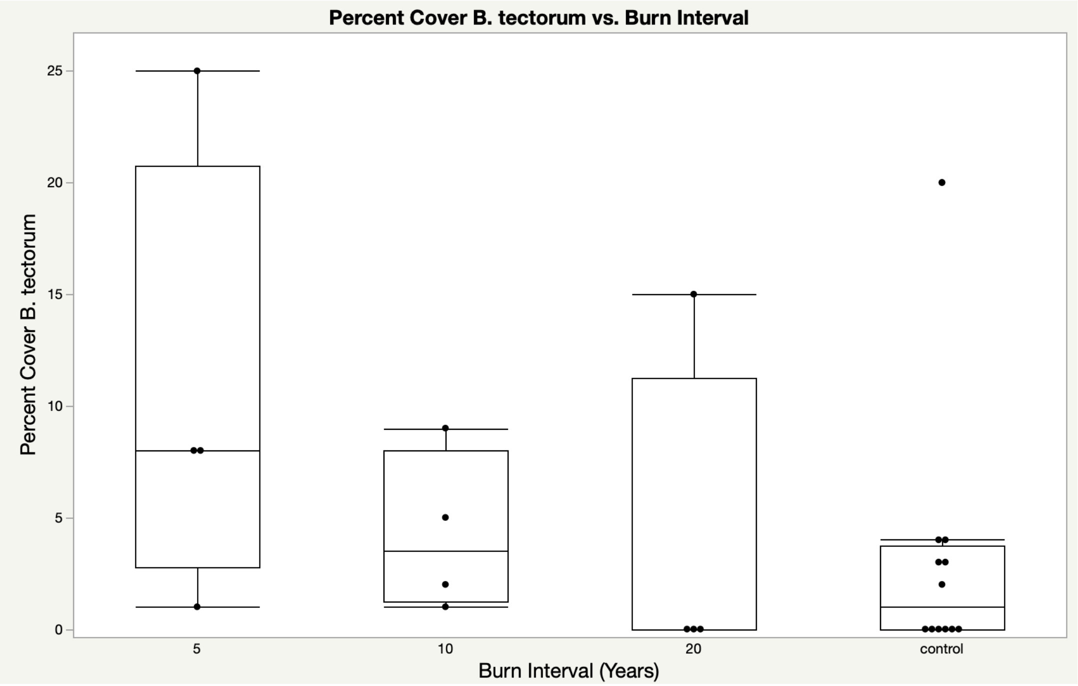

Figure 7:

Highest median percent cover *B. tectorum* observed in the 5 year burn interval. Box plots show five number summaries of percent cover *B. tectorum* grouped by burn interval (5, 10, 20, control). Points represent individual data collected once per sampling quadrat. The 5-year interval has a median of 8% with a lower quartile of 2.75% and an upper quartile of 20.75%. The 10-year interval has a median of 3.5% with a lower quartile of 1.25% and an upper quartile of 8%. The 20-year interval has a median of 0% with a lower quartile of 0% and an upper quartile of 11.25%. The control group has a median of 1% with a lower quartile of 0% and an upper quartile of 3.75%. No significant differences were found between the mean values in each burn interval.

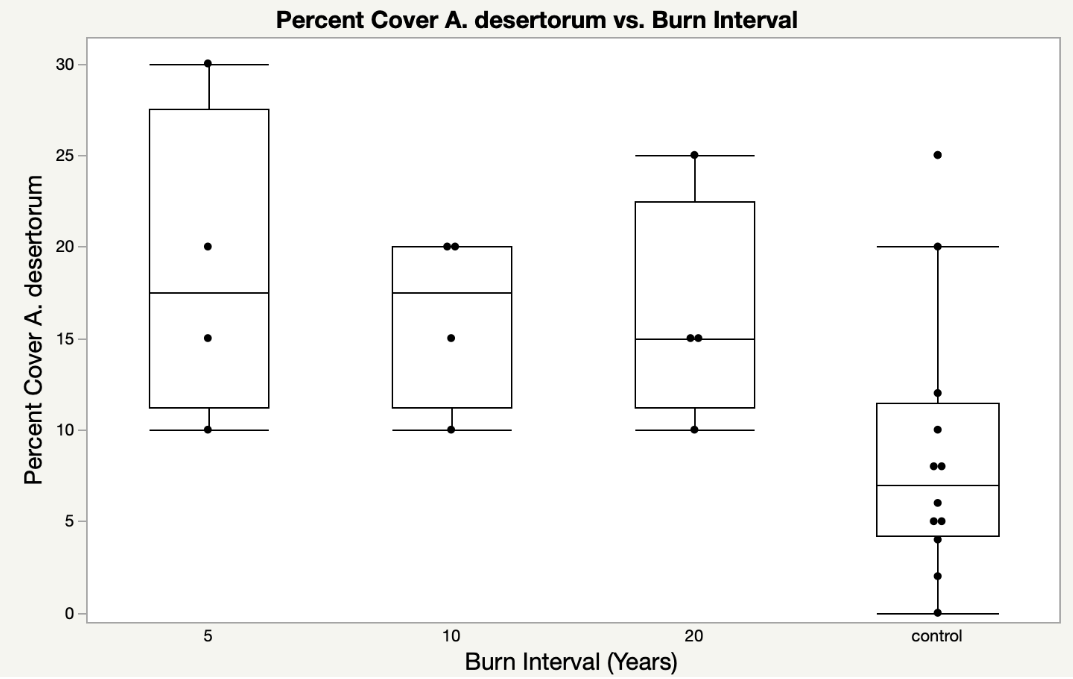

Figure 8:

Median cover *A. desertorum* higher in sites that received burn treatment than in the control. Box plots show five number summaries of percent cover *Alyssum desertorum* grouped by burn interval (5, 10, 20, control). Points represent individual data collected once per sampling quadrat. The 5-year interval has a median of 18% with a lower quartile of 11% and an upper quartile of 28%. The 10-year interval has a median of 18% with a lower quartile of 11% and an upper quartile of 20%. The 20-year interval has a median of 15% with a lower quartile of 11% and an upper quartile of 23%. The control group has a median of 7% with a lower quartile of 4% and an upper quartile of 12%. No significant differences were found between the mean values in each burn interval.

Simple main effects of linear mixed effects model analysis showed that burn interval did not have a statistically significant effect on percent cover *B. tectorum* ($F_{3,9} = 1.33$, $p = 0.323$). Burn interval also did not have a statistically significant effect on percent cover *A. desertorum* *(*$F_{3,9} = 2.92$, $p = 0.093$).

DISCUSSION

Results summary

The initial hypothesis (1) that the mean percent cover of annual grasses and forbs would increase while the mean percent cover of perennial bunchgrasses would decrease as the interval between burns decreased was supported by general trends but the only statistically significant difference between groups was observed in the forbs.

The initial hypothesis (2) that the mean percent cover of the invasives *A. desertorum* and *B. tectorum* would increase as the interval between burns decreased was supported by general trends in the data but differences between burn groups were not statistically significant.

Burn interval and functional group relative abundance

Although we failed to reject the null hypothesis that burn interval does not affect the mean percent cover of plant functional groups, a few interesting trends emerged that could be explored further in a more extensive study.

As exemplified by the trends observed in the abundance of the annual grass *B. tectorum*, the relative abundance of annual grasses increased from the control, 5, 10, and 20 year subplots respectively (Table 1). Also mirroring the observed pattern in the forb *A. desertorum*, the percent cover of forbs increased with every incremental increase in burn frequency. The increase in the percent cover of forbs and annual grasses may be explained by the functional groups' role as early-seral species in the Great Basin plant successional gradient (Tueller & Platou, 1991). After a major disturbance, forbs and annual grasses are often the first to return. Forbs and annual grasses produce a high volume of seeds and can rely on this heavy investment into the seed bank for post-fire germination and early colonization of a disturbed site (Allen et al., 2008).

Perennial grass abundance remained relatively consistent across the burn treatments. The consistency of their abundance across burn interval groups was a surprising finding compared to my assumption that perennial grasses would be more vulnerable in high fire-return intervals. Rather than jumping to the conclusion that native perennials are more resilient to frequent fire than previously understood, the characteristics of the specific species observed must first be considered. The consistency of perennial abundance may partially be explained by variation among the specific species of perennial grasses found in the burn interval groups that varied in relative size. In the unburned plots, the non-native, non-bunching perennial crested wheatgrass (*Agropyron cristatum*) was observed. Non-bunching grasses take up relatively less ground cover per individual due to their non-bunched stem structure. This phenological difference limits the efficiency of percent cover as a measure of abundance and likely contributed to the surprising finding of less perennial grass cover in the control plot than in the 20 year plot (Table 1). The greater abundance of perennials in the 20 year plot than in the control plot may also be due to the presence of sagebrush at more advanced stages of establishment in the control sites. Sagebrush can limit establishment of adjacent plant individuals via allelopathic interactions (Preston et al., 2002) and the tendency to absorb a significant portion of available water (Welch, 2005). Later seral-stages of the sagebrush-steppe have a greater proportion of overall bare ground as a result of the water uptake of established sagebrush (Williams et al., 2022). The trends in observed total vegetation cover are in keeping with this pattern with the lowest overall vegetation cover observed in the control plot, the only plot with intact sagebrush individuals (Figure 6, Table 2).

Given these variables, it is not possible to draw strong conclusions about the resilience of native perennial grasses to increased fire frequency from these data.

Why did functional group levels shift?

The shifts in relative cover of different functional groups may also have been influenced by indirect effects of fire such as the water repellency of the soil and available nutrient levels (Tilman, 1984).

Water repellency effects

Changes to available moisture content in the soil as the result of fire-induced hydrophobic soil properties may favor the establishment of particular functional groups with different water needs. Fire increases the hydrophobic layer of topsoil that repels water droplets, thereby inducing a temporary water repellency effect that decreases the moisture content in the soil (Madsen et al., 2012). The depth and duration of the water repellent zone is proportional to the maximum temperature of the fire, duration at temperature peaks, and the interval between burns; therefore, as fire intensity and frequency increases, soil water content can be reduced more significantly (DeBano & Krammes, 1966; Hubbert, 2006; Granged et al., 2011) (though some studies suggest the effects are reverse if soil reaches above 240 degrees Celsius (Zavala et al. 2010)). Plant functional groups less resilient to moisture variability, such as shrubs, could be disproportionately adversely affected (Wilson et al., 2018).

Cheatgrass has been shown to thrive in soil with less water content and out-compete native species in water restricted conditions (Johnston & Garbowski, 2020). The disruption of water percolation in the soil caused by the hydrophobic upper layer can also disrupt soil nutrient cycling (Austin et al., 2004).

Shifting nutrient availability

Changes to available nitrogen in the soil post-fire may favor the establishment of particular functional groups (Davis & Pelsor, 2001). Nitrogen is a particularly influential nutrient on plant community structure and is a principle limiting factor for plant growth in sagebrush steppe during times of moisture availability (Krueger-Mangold et al., 2004). Available inorganic nitrogen (NH4 and NO3 that are accessible for plants), increases in the soil after a wildfire due to the release via the combustion of vegetation, the influx of nitrogen-rich ash, and increased microbial processes associated with ammonification (Christensen, 1973). The nitrogen pulse in the soil following a fire can last from weeks upwards of three years (Kavanagh et al. 2007) and the extent of the nitrogen pulse is proportional to the intensity of the fire (Stephan, 2007). Sudden high nitrogen availability supports fast growing species which can more effectively utilize the nutrient and can increase annual dominance (Vinton & Burke, 1995). However, the specific relationship between nitrogen availability in soil and invasive species success is still unclear (Yoder & Caldwell, 2002).

The frequency of fire on the landscape can also impact how post-fire nitrogen pulsing impacts plant community structure. Long periods of fire exclusion can result in low levels of available inorganic nitrogen as microbes and plants hold it in organic form (Covington & Sackett, 1986). Post-fire nitrogen pulses can have particularly significant effects on community assembly in these fire-excluded areas (Tilman & Wedin, 1991). Frequent fires can change total soil nitrogen storage by altering the quantity and chemistry of plant inputs through changes in plant biomass and composition as well as the decomposition of soil organic matter (Pellegrini et al., 2020).

Burn interval and invasive annual dominance

Both *B. tectorum* and *A. desertorum* increased as the burn interval decreased though the changes were not statistically significant.

Why did B. tectorum cover increase?

B. tectorum may have been trending towards greater dominance in sites burned more frequently due to its non-obligate relationships with vesicular arbuscular mycorrhizae (Knapp, 1996), and its ability to form persistent seed banks with seeds entry dormancy for up to two growing seasons (Meyer et al. 2018).

Non-obligated VAM relations

In disturbed soil, *B. tectorum* has a competitive edge over native shrubs and perennial grasses in that it does not rely on relationships with vesicular arbuscular mycorrhizae (VAM). VAM are symbiotic fungi that extract carbon from the root of a plant, but in return facilitate nutrient and water absorption via the hyphal network (Crawley, 1986). Most grasses, including *B. tectorum*, are facultatively mycotrophic signifying that they only form fungal relationships when advantageous, while most shrubs, such as big sagebrush, are obligately mycotrophic and require the presence of fungal propagules (equivalent to fungal reproductive units) (Allen et al., 1990). Therefore, after a disturbance such as fire or grazing facilitates topsoil erosion and reduces or eliminates propagules of mycorrhizal fungi, the successional establishment of native species can be limited by available propagule density (Powell et al., 1980).

Seed Bank Investment

Additionally, *B. tectorum* is more equipped to re-establish after a fire than native shrub and bunchgrass species due to its ability to form persistent seed banks. After dispersal from established individuals, ungerminated seeds can accumulate and persist in the soil in a seed bank (Hopfensperger, 2007). This is a particularly important ability for plants in semi-arid environments, like the Great Basin, when variable water availability makes some seasons ill-suited for germination (Pérez-Noyola et al., 2005). Annual species, such as *B. tectorum*, produce more seeds than shrubs and perennial species as they need to reseed themselves every year. The greater volume of seed production corresponds to a greater density of seeds from annual species in the seed bank. After a fire, seed banks help preserve species that were made locally extinct above ground (Pekas & Schupp, 2013). Given that the seedbank is largely composed of annual species including *B. tectorum*, when seeds germinate out of the seed bank, the ecosystem is likely to become increasingly dominated by *B. tectorum*. Changes to the survivorship of above ground individuals after a fire influence which species can disperse seeds on the landscape. When seed rain patterns change, inputs to the seed bank change as well. This positive feedback loop can promote the eventual conversion of the site towards a monoculture of *B. tectorum* (Humphrey & Schupp, 2001).

Why did *A. desertorum* cover increase?

The increase in *A. desertorum* is likely due to its early phenology in disturbed sites. It is difficult to predict how the effects of microbial relationships or seed bank investment may have impacted *A. desertorum*'s spread as the literature is lacking on seed bank longevity and associated microbial communities.

Study limitations

While these trends are interesting to explore, the findings of this experimental study were significantly limited by my initial sampling design. The sample scheme was constructed to prioritize replication for a seed bank study exploring the effects of fire frequency on ungerminated seeds in the soil. Therefore, the sampling design was fundamentally oriented to ensure sufficient replication in soil collection rather than above ground cover. Vegetation cover data was collected alongside soil samples as a covariant to compare the correlation between above and below ground plant community composition. Challenges arose when attempting to meet the species-specific germination needs of the seeds in the collected soil. In order to complete the thesis within the allotted timeline, the intended greenhouse experiment was paused and vegetation cover data shifted to the focal point of study. A future *vegetation-specific* survey could utilize point-line-intercept methodology with at least 10, 50-meter transect replicates per burn unit for more efficient data collection with more robust results.

Additional limitations of this study include unknowns in the burn history of the study site, sampling late in the growing season, and minimal species-specific observations. The NGBER made for an advantageous study site because of the unique opportunity to sample in adjacent areas with different burn history. However, the burn intensity was not necessarily consistent between burns. The first burn on the landscape had greater fuel loading from the intact sagebrush plants. Therefore, subsequent fires without sagebrush occurred at an inherently lower intensity. Furthermore, the burn history before 2002 is poorly understood which makes it difficult to identify the number of years since fire occurred in the control sites.

Additionally, greater temporal variation in sampling with increased replication within each burn interval would provide more robust results. Given that sampling took place in late July, many annual forbs had already senesced and may therefore be underrepresented in the percent cover of their functional group. Sampling at various times in the growing season would ameliorate this issue.

Finally, the only species-specific effects explored were *B. tectorum* and *A. desertorum*. Future work could explore fire frequency effects on other invasive annual species such as medusahead (*Taeniatherum caput-medusae*) or on select native species. Fire frequency effects on overall species diversity would also warrant closer attention.

If the scope of the study could be scaled up to include other potentially significant variables influencing plant community composition, it would be worthwhile to investigate water repellency effects and analyze inorganic nitrogen levels in the soil.

Implications

As fire frequency continues to increase in the Great Basin, close attention ought to be paid to corresponding increases in invasive annual species. With a better understanding of fire frequency effects, restoration practitioners may anticipate trends in vegetation conversion to effectively prioritize areas for restoration to limit loss of native species.

The effects of fire frequency on invasive species spread must also be considered when applying prescribed burns to the landscape as a management tool. If burns are applied infrequently in the spring on healthy and intact shrub steppe ecosystems in cooler areas (often at slightly higher elevations), with established populations of native perennials, prescribed fire can be an effective tool to mitigate future wildfire intensity by preemptively removing fuel (Pellant, 1990) and creating natural fire breaks. Reducing the risk of high intensity fire is valuable as high intensity burns have been shown to correspond with a lower species richness of natives up to ten years after the fire (Barga & Leger, 2018). However, the results of this study indicate that prescribed fire should be applied with sufficiently long intervals between applications in a variety of locations to restore a mosaic of post-fire on the landscape. If prescribed fire is applied in intervals <10 years in the same location, the effects of increased frequency may exacerbate the spread of invasive annuals (Hassan & West, 1986). Understanding how to appropriately restore a fire mosaic in the Great Basin will be an essential proactive ecosystem management technique to alleviate factors driving biome-wide collapse in the sagebrush steppe.

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