Fire and Rodent Consumer Effects on Plant Community Assembly and Invasion in North American Deserts

Rebekah L. Stanton

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Fire and Rodent Consumer Effects on Plant Community Assembly and Invasion in North American Deserts

Rebekah L. Stanton

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

Samuel B. St. Clair, Chair
Phil S. Allen
Loreen Allphin
Richard A. Gill
Matthew D. Madsen

Department of Plant and Wildlife Sciences
Brigham Young University

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This dissertation explores the differential effects of fires and rodent communities on native and invasive desert plant communities. Chapter one examines the impacts of fire and repeat fires on fuel loads in two different Utah desert sites, one in the cool Great Basin Desert and one in the hyper-arid Mojave Desert, over the course of four years. We found that both desert sites responded with varying intensities to a single burn, but the effects of a reburn was not as pronounced. We also found that our Great Basin Desert site had a stronger response to fire than our Mojave Desert site, producing a higher plant fuel loads that could potentially exacerbate the changing fire regimes. These data can be used to help map the effects that climate change may have on fuel loads and the fire potential of these deserts. Chapter two uses a full factorial experimental design to compare the effects of rodent herbivory and fire on native versus invasive seedlings at our Mojave Desert field site. We found that rodent herbivory has a more negative impact on the survival of native seedlings than invasive seedlings. This could be because the invasives are grasses that tend to tolerate herbivory better than the native shrubs and forbs. Chapter three again uses a full factorial experimental design to assess the impacts of rodents and fire on the fate of native and invasive seeds at our field site in the Mojave Desert. We found that rodents removed seeds, and they did show preferences for some species of seed over others, but these preferences were not different between native and invasive seeds or seed mass. We propose that the preferences may be influenced by other seed traits such as water content, handling time or physical and chemical defenses. As with the seedlings in chapter two, fire did not have any impact on rodent seed preferences. These data highlight the importance of considering rodent effects on seeds used in restoration efforts following wildfires.

Keywords: plant invasion, rodents, fire, repeat fires, native plants, fuel load, seeds, seedlings
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CHAPTER 1

A comparison of the effects of fire frequency on fuel loads in two different deserts of North America

Rebekah L. Stanton, Samuel B. St. Clair, Baylie C. Nusink, Kristina L. Cass, Tara B.B. Bishop, Brianna Woodbury and David Armond
Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT
Doctor of Philosophy

ABSTRACT

Wildfire regimes are changing drastically across North American deserts with the spread of invasive grasses. These aggressive invaders thrive in disturbed areas and produce fuel loads that perpetuate invasive grass fire cycles, resulting in more frequent and larger fires. This study compares how fire and repeat fire influence fine fuel loads, consisting of native and invasive grasses and forbs, in two different desert types: a cold semi-arid desert (the Great Basin Desert) and a warmer, hyper-arid desert (the Mojave Desert). Our field sites consisted of full-factorial block design, replicated five times. Towards the end of summer 2011, we experimentally burned half of each block (a 30 m x 30 m plot). Half of these burned plots (30 m x 15 m subplot) were then reburned in the fall of 2016 to mimic the aforementioned increase in fire frequency. The remaining half (30 m x 30 m plot) stayed unburned and acted as an experimental control.

We conducted annual vegetation surveys every spring at each of our sites from 2017-2020. Each year we estimated average aboveground plant biomass in g m$^{-2}$, average plant percent cover and average plant density in individuals m$^{-2}$ in the treatment plots. Biomass did not vary between sites, but there was more plant cover and a lower density of plants in the Mojave and less plant cover and a higher plant density in the Great Basin. Fire did not significantly increase plant biomass or plant cover but did increase plant density across both desert study sites. All
three measurements varied from year to year, with greater annual fluctuations in the Great Basin. The initial fire (2011) increased plant biomass and density by around 1000 plants per m$^2$, but there was no significant effect of the repeat fire (2016). There was a fire by site interaction effect on plant density, indicating that the effect of fire on plant density was greater in the Great Basin than it was in the Mojave. There was also a fire by year interaction on plant cover, indicating that the effect of fire on plant cover varied between years. Overall, fuel loads vary between deserts, as do the effects of fire.

INTRODUCTION

Plant invasions are increasingly becoming more problematic on a global scale (Callaway and Ridenour 2004; Enders et al. 2019; Levine et al. 2004; Rejmánek and Richardson 1996). Human activity exacerbates plant invasions by creating areas of disturbance and dispersing the seeds of invaders to places that would otherwise be unreachable through natural dispersal (Bishop 2018; Seabloom et al. 2006; Vitousek et al. 1997). Often, plant invaders have traits, such as rapid and variable germination timing, and exhibit high phenotypic plasticity, which allows them to compete against native plants for light and soil resources (Knapp 1996). Plant invaders also often have a high fecundity (Leffler et al. 2011), so they can increase their establishment success and spread, particularly in disturbed environments (St.Clair et al. 2016).

North American desert ecosystems have historically been relatively resistant to wildfires, but plant invasions significantly alter these fire regimes (Brooks et al. 2004). As invasive grasses fill intershrub spaces, they provide the fine fuel necessary to carry fire from shrub to shrub resulting in larger and more frequent fires (St. Clair and Bishop 2019). Following a wildfire, the resulting reduction in plant cover significantly reduces biotic resistance from herbivores and native plants to exotic plant establishment (Levine et al. 2004; Levine et al. 2003; Pyke 1986;
St. Clair et al. 2016). In the absence of competition from native plants invasive grasses proliferate, providing more fine fuels for future fires (St. Clair and Bishop 2019; Whisenant 1989). These increases in invasive annual grasses have shortened the fire return interval from over a century to shorter than a decade in some places (Balch et al. 2013; Bukowski and Baker 2013; D'Antonio and Vitousek 1992). This cycle of fire and invasive grass production ultimately pushes a diverse native plant community over a tipping point which results in an invasive grass monoculture (Brown and Heske 1990; St. Clair et al. 2016) that can promote subsequent fires (St. Clair and Bishop 2019).

Repeated fires can be catastrophic as they prevent native restoration and affect soil nutrient contents in an already nutrient depauperate environment. Fundamentally, repeat fires are different to the initial fires, largely because of the fuel that perpetuates them. Woody native shrubs and other plants tend to burn hotter than invasive grasses (Fuentes-Ramirez et al. 2016), so an initial fire has the potential to do more damage to the soil, drastically reducing soil organic matter (Allen et al. 2011). Since fires result in higher numbers of invasive annuals and a significant loss of native diversity (Keeley and Brennan 2012), repeat fires tend to burn faster and at lower temperatures, so they do not do as much immediate damage to the soil (Fuentes-Ramirez et al. 2016; Jones et al. 2015). Despite these lower temperature burns, repeat fires still have a large impact on the available nutrients in a system as they reduce the carbon and nitrogen stored in the plant tissue to ash, which can then be lost as wind and water erode the top layers of the now exposed soil (Jones et al. 2015; Ojima et al. 1994). While there may be an initial pulse of nitrogen following a fire (Esque et al. 2010), over time, with as few as two burns, systems show decreases in soil organic nitrogen, microbial biomass and nitrogen availability, and increases in the C:N ratios of soil organic matter (Ojima et al. 1994). This kind of system
continues to favor invasive grasses over native communities, further perpetuating the invasive grass fire cycle (Bradley et al. 2017; Horn et al. 2012; Salo 2004; Whisenant 1989) and potentially leading to further desertification.

Ecosystems show varying degrees of susceptibility to invasions, and the influences of fire (Balch et al. 2013), but few studies have compared the impact of wildfire on fuel load production in different desert types. Different ecosystem characteristics among deserts could theoretically react differently to changing frequency. The Great Basin and Mojave deserts which are adjacent to each other provide an opportunity to compare invasion and fine fuel responses to fire frequency in an arid and semi-arid desert. The Great Basin Desert is a semi-arid, cold desert in the Intermountain West. The Mojave Desert is a hyper-arid desert in the southwestern US. The vegetation of both deserts is dominated by native perennial woody shrubs, interspersed with forbs and grasses. The Great Basin is mostly sagebrush steppe, whereas the Mojave is home to a diverse shrub community made up of iconic plant species such as Joshua trees (Yucca brevifolia Engelm.) and creosote bushes (Larrea tridentata (DC.) Coville). Cheatgrass (Bromus tectorum L.) is an aggressive plant invader of the Great Basin and the closely related red brome (Bromus rubens L.) dominate in the Mojave Desert (Mack 1981; Salo 2005). Both actively compete with native plant communities for the limiting resources of soil moisture and nitrogen (Young et al. 1972). These two Bromus species can significantly increase fire frequency and extent in both the Mojave and Great Basin Deserts (Bishop et al. 2020a; St. Clair and Bishop 2019).

Researchers have conducted studies that focus on the effects of fire on fine fuel load production (Bradley et al. 2017; Salo 2004), but less is known about the impacts of reburns, a phenomenon that is becoming more and more common (Bishop et al. 2020a). There is also less known about how the effect of fire on fine fuel loads differs between different desert types and
how these responses change over time (Horn and St.Clair 2017). The purpose of this study is to experimentally assess how fire and repeat fires influence the production of a fine fuel load, consisting of grass and forb plant species, in both the Great Basin and Mojave Deserts. We explore the following questions: 1) Does fire and repeat fire differentially affect the production of fine fuel loads? and 2) How do the effects of fire vary between years in different desert types? We hypothesize that the effects of a repeat fire would amplify the effects of a single fire on fuel loads as more native cover is lost.

MATERIALS AND METHODS

Study sites

Our Great Basin field site was just east of Vernon, Utah (40°05'26.17" N 112°18'18.01" W, elevation: 1650 m) in the sagebrush-steppe ecosystem of western North America. The average temperature of the area is 8.6°C, with the average January temperature being -3.2°C and average July temperatures being 22.3°C (Vernon GHCN:COOP, Utah Climate Center). Precipitation falls as both rain and snow at a rate of approximately 257 mm per year spread relatively evenly across all seasons. Soils have been classified as silty, mixed mesic Haplic Natrargid, Taylors Flat Loam. Native plants that are common to the area include Wyoming big sagebrush (Artemesia tridentata Nuttall) and bottlebrush squirreltail (Elymus elymoides (Raf.) Swezey). Several invasive plants common to the area include cheatgrass (Bromus tectorum) and bur buttercup (Ceratocephala testiculata Crantz. Bess.). There is no evidence of recent grazing or fire at the field site since the native shrub community is mature and the soil crusts are well developed. Wire fences surround the whole site to prevent any recent cattle grazing.
Our Mojave field site was near Lytle Ranch Preserve in the Beaver Dam Wash region of the Mojave Desert, approximately 25 miles West of St George, Utah (37°8'53.46" N, 114°0'49.59" W, elevation 915 m). The average temperature is 17.3°C, with the average January temperature being 7.2°C and the average July temperature being 29.4°C (Lytle Ranch GHCN:COOP, Utah Climate Center). An average of 206 mm of precipitation falls per year with a large portion of that falling in the winter months between October and April. The soil has been classified as young alluvium with a gravelly, sandy-loam texture. Common native plants in the area include Joshua trees (*Yucca brevifolia* Engelm.), white bursage (*Ambrosia dumosa* (A. Gray) Payne) and creosote bush (*Larrea tridentata* (DC.) Coville). Several invasive plants are common at the study site: cheatgrass (*Bromus tectorum*), red brome (*Bromus rubens*) and Arabian schismus (*Schismus arabicus* Nees). Wire fences surrounding the study site have prevented grazing from cattle for at least the last 30 years, and there is no evidence of recent fire.

**Experimental design**

An identical experimental design was set up at both the Great Basin and Mojave study sites to test the effects of fire frequency on fuel load production. Five replicate blocks were installed at both sites each consisting of two 30 m x 30 m plots. Each plot was randomly selected as either a burn plot or unburned control. In 2016, burned plots at both study sites were split in half, with one side being randomly selected to serve as a reburn treatment and the other remaining in the single burn condition so that unburned, single burned and twice burned plots could be compared (Fig. 1.1).

Burn treatments at the Great Basin site were conducted on 20<sup>th</sup> September 2011. Because the site was uninvaded prior to this experiment, there was insufficient fine fuel to carry fire between native shrubs across the plots. We therefore spread wheat straw (300 g m<sup>-2</sup>) between the
shrubs to facilitate the burn (Esque et al. 2010). Drip torches were used initiate the experimental burns. Nitrogen released into the system by burning straw was comparable to nitrogen released by burned cheatgrass (St. Clair and Bishop 2019). The burn treatment was classified as high severity as measured by more than 99% plant cover loss. The reburn treatment was conducted in the middle of October 2016. During the reburn treatment cheatgrass cover was sufficient to carry the fire without the addition of straw. Drip torches were used to facilitate the burn.

Initial burn treatments at the Mojave site were conducted on 18th June 2011, using a drip torch. Because invasive grasses had already started to invade the site prior to the experiment, fine fuels from red brome, growing at a rate of 1319 stems m^{-2} in the intershrub spaces, were sufficient to carry the fire treatment across the burn plots without the addition of wheat straw. The severity of the burn was high, resulting in a 90% reduction in plant cover (Sharp Bowman et al. 2017c). Reburn treatments at the Mojave site occurred on 6th October 2016. Because of low fine fuel loads at our Mojave study site in the fall of 2016, wheat straw (300 g m^{-2}) was used to carry flames from drip torches across the reburn area.

Vegetation surveys

We conducted vegetation surveys to assess the effects of our burn and reburn treatments on the fuel loads produced. The surveys took place annually from 2017-2020 in April and May in the Mojave and in June in the Great Basin, when most of the fine fuel biomass reached its peak but before seed drop. We randomly placed four parallel 30 m transects in each plot at least 2 m away from the edge of the plots to prevent biases due to edge effects. The direction of the transects (North to south or east to west) alternated annually. Along transect lines, vegetation biomass, vegetation cover and vegetation density were measured.
We measured vegetation biomass in 2017 by placing a 25 cm x 50 cm modified Daubenmire frame every 4 m, six times, along each transect. From 2018 to 2020, we placed four frames along each transect to reduce fieldwork time. We used scissors to collect all above-ground plant matter from grasses and forbs that were rooted within each frame and sorted it into bags labelled by species. The biomass samples were taken back to the lab, dried in a drying oven for at least 72 hours at approximately 40 °C and were then weighed using a balance (Denver Instrument, Bohemia, New York, USA).

Plant cover was measured using the line-point intercept method (Herrick et al. 2006). We dropped a vertical pin systematically every 0.5 m along each transect line. For each vertical pin drop, we recorded the canopy layer, or the topmost plant that intersected the pin (Helm and Mead 2004).

To measure the vegetation density, we again placed a 25 cm x 50 cm modified Daubenmire frame every 2 m along each transect line. In 2020, we placed frames every 6 m along each transect due to constraints because of the global COVID-19 pandemic. We identified and counted every grass and forb that was rooted within the frame to get an average count for each species per m². For cheatgrass and bur buttercup in the Great Basin, and red brome and Arabian schismus in the Mojave, we measured density within a 10 cm x 25 cm subframe of the larger Daubenmire frame.

Statistical analysis

We conducted data exploration as outlined by Zuur et al. (2010), to ensure that the data met the assumptions for normality and equal variances. We modeled plant biomass, cover, and density using mixed-effects models in the program JMP®. Site, year, and burn were assigned as
fixed effects with block as a random effect (JMP® Pro 1989-2021). Pairwise analysis was then conducted using the Tukey HSD test in the program R, using the package emmeans (Lenth 2021; R Core Team 2018).

RESULTS

Plant biomass responses

Plant biomass was consistent across the two study sites when averaged across years \((F_{1,71} = 0.01, p = 0.91)\) but varied dramatically between years \((F_{3,71} = 130, p < 0.0001)\). In the Great Basin, the highest biomass year was in 2019 (219 g m\(^{-2}\), SE = 17), which decreased by 97% the following year, 2020 (5.78 g m\(^{-2}\), SE = 2.39), which was also the lowest biomass year. In the Mojave, the lowest biomass year was 2018 (19 g m\(^{-2}\), SE = 2.04), which increased almost 10-fold for the highest biomass year the following year, 2019 (185 g m\(^{-2}\), SE = 18). Fluctuation in biomass across years was greater in the Great Basin than the Mojave as evidenced by a significant site by year interaction term \((F_{3,71} = 6.4, p = 0.0007)\). When averaged across sites and years fire increased plant biomass by 24% from 71 g m\(^{-2}\) (SE = 15) in the unburned plots to 88 g m\(^{-2}\) (SE = 15) in the burned plots \((p = 0.08)\), but there was no statistically significant difference between the biomass in the burned and the reburned plots \((p = 0.61; F_{2,71} = 2.41, p = 0.10)\). The fire by site interaction \((F_{2,71} = 2.19, p = 0.12)\), the fire by year \((F_{6,71} = 0.90, p = 0.50)\) and fire by year by site interaction terms \((F_{6,71} = 0.73, p = 0.63)\) were not statistically significant (Fig. 1.2; Table 1.1).

Plant cover responses

There was approximately 24% more plant cover in the in the Mojave (61%, SE = 1.96) than there was in the Great Basin (49%, SE = 4.35; \(F_{1,71} = 26, p < 0.0001\)) when averaged across
years. Plant cover also varied between years ($F_{3,71} = 42, p < 0.0001$). In the Great Basin, the highest cover year was in 2019 (70%, SE = 6.31), which decreased by 77% the following year, 2020 (16%, SE = 3.09), which was also the lowest cover year. In the Mojave, the lowest cover year was 2017 (47%, SE = 2.00), which increased by 74% for the highest cover year in 2019 (82%, SE = 2.12). Fluctuation in percentage cover across years was greater in the Great Basin than the Mojave as evidenced by a significant site by year interaction term ($F_{3,71} = 24, p < 0.0001$). The main effect of burn and reburn did not have an impact on plant cover when averaged across site and year ($F_{2,71} = 1.50, p = 0.23$). The fire by site interaction was not statistically significant ($F_{2,71} = 0.45, p = 0.64$), but there was a fire by year interaction ($F_{6,71} = 2.14, p = 0.06$) with the effects of fire being greatest in 2019. The fire by year by site interaction term was also not statistically significant ($F_{6,71} = 2.05, p = 0.07$; Fig. 1.2; Table 1.1).

Plant density responses

There was a larger density of plants at our Great Basin site (2500 individuals m$^{-2}$, SE = 361) than our Mojave site (1661 individuals m$^{-2}$, SE = 106) when averaged across years ($F_{1,71} = 20, p < 0.0001$). Plant density also varied between years and sites resulting in a year by site interaction ($F_{3,71} = 33, p < 0.0001$). In the Great Basin, the highest density year was in 2019 (4403 plants m$^{-2}$, SE = 615), which decreased by 85% the following year, 2020 (675 plants m$^{-2}$, SE = 181), which was also the lowest density year. In the Mojave, the lowest density year was 2017 (895 plants m$^{-2}$, SE = 107), which increased by 189% for the highest density year in 2019 (2590 plants m$^{-2}$, SE = 215). When averaged across years, the effects of the initial fire increased the density of plants by 84% ($p < 0.0001$), from an average of 1302 individuals per m$^{2}$ (SE = 145) in the unburned plots, to 2393 individuals m$^{-2}$ (SE = 303) in the burned plots. However, there was no sizable difference between the density of plant individuals in the burned and the reburned
plots ($p = 0.82; F_{2,71} = 18.05, p < 0.0001$), but there was a fire by site interaction, indicating that the fire effect on plant density was stronger in the Great Basin than it was in the Mojave ($F_{2,71} = 6.90, p = 0.002$). There was not a significant fire by year ($F_{6,71} = 1.03, p = 0.42$), or fire by year by site interaction term ($F_{6,71} = 0.74, p = 0.62$; Fig. 1.2; Table 1.1).

**DISCUSSION**

*General summary of support for hypotheses*

Fire frequency, site, and year all had varying degrees of impact on plant biomass, cover, and density. We originally hypothesized that fire would increase fine fuel loads and fire potential. While the initial fire did increase plant biomass and density particularly in the Great Basin Desert the repeat fire had no amplifying effect on fine fuels.

*Effects of fire and repeat fire*

Repeat fires have different qualities to initial burns. Our data show that reburn did not have any effect on plant biomass, cover or density, especially when compared to the effects of the initial burn. The initial fire potentially removes a lot of shrub cover, leaving open space for invasions. The second fire happened too soon after the first fire for a productive native shrub community to regrow (Keeley and Brennan 2012) and so would burn only the invasion meaning the fire would burn cooler and not have such a destructive impact on the local plant community. Despite this lack of destruction, with every burn, nutrients are lost from the system as nutrients stored in plant material are reduced to ash and eroded away by wind and water (Jones et al. 2015; Ojima et al. 1994). The fact that there is no difference between the effects of one fire and the effects of two fires on fuel loads is likely because the system is losing the nutrients that could potentially produce more fine fuels, not providing a better environment for more growth. Based
on this, if this study was extended to include more repeated burns over a longer period of time, we would predict that fuel load production would actually decrease as the number of fires increased (Ojima et al. 1994).

Our data show that fire had a greater effect on the plant density in the Great Basin than on the plant density in the Mojave (Fig. 1.2). While the severity of the fires at both sites were similar, meaning that both sites experienced a significant loss of vegetation, the intensity, or the heat produced by the fire, likely would have varied. Fuentes-Ramirez et al. (2016) found that native plants burn slower and at much higher temperatures than invasive grasses. Shrub density surveys from our study sites have identified that in unburned areas, there is a 72% increase in native shrub cover from 0.57 shrubs per m² in the Mojave to 0.98 shrubs per m² in the Great Basin ($F_{1,19} = 19.32, p = 0.0004$; unpublished data). There was also a lot more of an invasion at the Mojave site than at the Great Basin site prior to the initial experimental burn. Although we did not measure the temperature of the burn, what we do know about the conditions can lead us to conclude that the experimental fires at our Mojave site were quicker, and of a lower intensity than the fires at our Great Basin site, which would have burned slower but with higher intensity. These findings would be in line with work by Brooks (2002) and Korfmacher et al. (2003), who both identified that the peak temperatures of fires at ground level are approximately 150-180°C in the Mojave and 253-337°C in the Utah Great Basin. Slow, high temperature desert fires do significantly more damage to soil crusts and disintegrate much more soil organic matter than quicker, low temperature fires (Allen et al. 2011), which may be why the effects of fire on density were larger in the Great Basin than in the Mojave.

Water, nitrogen, and phosphorus are limiting factors in the desert, which will result in a point whereby the amount of vegetation in an area reaches a limit and can grow no further
(Brown et al. 1979; DeLucia et al. 1989). Since the base level of invasive grasses, a large component of the plant community, was higher in the Mojave prior to the beginning of this experiment, it could have been closer to that limit, so a disturbance in the form of fire would not encourage much further growth, resulting in a smaller fire effect. Invasive grass levels in the Great Basin were low compared to the Mojave prior to beginning this experiment, so the competitive release from a fire disturbance would be more significant, allowing for a more drastic fire effect. The soil crust is also much more developed at our Great Basin site than at our Mojave site. Fires also burn hotter in the Great Basin (Korfmacher et al. 2003), causing more damage to the soil crust (Ojima et al. 1994), potentially having a more drastic effect on the Great Basin soil physiology than the Mojave, again resulting in a more substantial release from biotic resistance (Ponzetti et al. 2007) and a greater effect of fire on the subsequent fuel load. These thoughts are supported by our data that show there is not much difference between the plant density in burn vs reburn treatments, even in the Great Basin where the effects of fire are significant (Fig. 1.2).

Interactions of fire and year

Climates in the Great Basin and the Mojave Deserts fluctuate from year to year, with periods of drought followed by relatively wet periods (Hereford et al. 2006; Soulard 2012). Our data show a significant fire by year interaction for plant cover, indicating that the intensity of the fire effect also varies from year to year. This variation is primarily seen in the Great Basin data, with the strongest fire effect taking place in 2019 (Fig. 1.2). This result also correlates with 2018-2019 being Utah's tenth wettest water year in recorded history (since 1875) at the time (NOAA 2021). Kerns and Day (2017) identified that the growth of invasive grasses is strongly regulated by the timing of fires and the climate around the time of the burn. They showed that
low precipitation following a burn results in low levels of invasive grasses, but a fall fire would generally burn with greater severity, which provides better conditions for a larger post-fire invasion (Kerns and Day 2017). Since water is a limited resource in the desert, desert annuals exhibit a much stronger response to larger amounts of precipitation than their counterparts in wetter climates, growing quickly and in abundance when precipitation levels are high (Salguero-Gomez et al. 2012). This increase in growth in high precipitation years may increase the plant cover in plots where they are present, i.e., the burn and reburn plots, thus accentuating the fire effect.

Just as the weather fluctuates from year to year, so do rodent populations (Sharp Bowman et al. 2017a). Since rodents can provide strong biotic resistance against plant invasions (Allington et al. 2013; St.Clair et al. 2016) and have strong top-down effects on plant community establishment following a wildfire (Brown and Heske 1990), a year where their population is low could potentially provide predation release from rodents that would increase plant establishment and growth.

*Contrast in the responses of the two desert systems*

Climate varies between the two sites, and studies have shown that invasive grass growth changes with changing climate (Bishop et al. 2020b; Horn and St.Clair 2017). Our data show that both plant cover and density significantly varied between the two sites; Plant cover was greater in the Mojave than in the Great Basin, but the plant density was larger in the Great Basin than in the Mojave. The plant biomass was about the same in both deserts, so productivity was about the same. The Mojave Desert is a hyper-arid system with most precipitation falling in the cooler months between October and April, but it also experiences unpredictable monsoonal rain events in the summer (Hereford et al. 2006; Wells 1979). The Great Basin Desert is at a much higher
elevation than the Mojave (Hunter 1991) and is characterized by extremely cold, wet winters and extremely hot, dry summers (Soulard 2012). The majority of precipitation in the Great Basin falls as snow in the winter (Soulard 2012). Invasive *Bromus* species form a large part of the plant community in these two deserts. The traits and genetics of these species are different and are suited to the desert climate where they grow. Young red brome plants cannot withstand the extreme oscillations in temperature that occur in the Great Basin but can thrive in the less variable climate of the Mojave (Bykova and Sage 2012). It could be that the Great Basin climate favors high numbers of small plants because plants are more opportunistic because of these oscillating temperatures, but Mojave plants are more likely to invest in less opportunistic larger plants because of the more stable climate.

As an essential part of desert ecosystems, cryptobiotic soil crusts provide robust biotic resistance to plant invasion. There is a significant negative correlation between many lichens and mosses that make up a healthy soil crust and *Bromus* cover (Belnap et al. 2006). Cattle grazing is another thing that can drastically alter the structure of soil crusts. Any disturbance that damages soil crusts results in reduced nitrogenase activity and opens up space for an invasion to occur (Belnap 2002; Knapp 1996). Our site in the Great Basin has a much more well-developed soil crust and was subject to much less grazing than our Mojave site before treatment implementation. It could be that the soil crust in the Great Basin prevents larger plants from establishing, but cracks provide an ideal microclimate for many smaller vascular plants to grow (Rahmonov et al. 2006).

Herbivores, such as rodents, can suppress plant invaders and exert top-down control over plant community establishment following a fire (Allington et al. 2013; Brown and Heske 1990; St.Clair et al. 2016). The rodent communities at the two sites vary drastically. It is possible that
differences in plant cover and density between sites is due to the varying food preferences of the different rodent communities at each site.

Conclusions and implications

Overall, our data have shown that the effects of fire on fine fuel load production are not the same at our contrasting field sites. Fire has a greater effect on fine fuel load production in the Great Basin Desert than in the Mojave Desert. Fire also had a greater effect on fine fuel load production some years than others. While our results may be interesting, they may not be representative of the whole desert that they are a part of. The Mojave and the Great Basin Deserts both span multiple US states and experience variability in topography, climate, and biological composition. But while we may have lost extrapolation potential by having a spatially smaller study, we may have gained in terms of temporal data by having a study that spans four years. Throughout the four years of this study, we have experienced variabilities in precipitation and temperature, going from an extremely wet year in 2019, to an extreme drought in 2020. Not only is it good to consider that the fuel loads of different deserts respond differently to fire when implementing management strategies for land restoration, but it also good to identify that fuel loads change with climate. This kind of information can be extremely valuable when assessing the potential impacts that climate change can have on fire regimes.
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**Figure 1.1:** A pictorial representation of a single block in our experimental design, containing an unburned (white) plot, a plot that was burned (light grey) in 2011 and a plot that was reburned, or burned twice (dark grey), once in 2011 and again in 2016. Treatments, including the direction (N-S or E-W) of the reburn, were randomly assigned to each plot and blocks were replicated five times at each of our two desert sites, one in the Mojave and one in the Great Basin.
Figure 1.2: Time series showing how the main and interactive effects of fire (unburned, burned, reburned), field site (Great Basin or Mojave) and year (2017-2019) influence fuel load production in the form of total plant biomass, cover, and density. Light grey points represent our control areas that were left unburned, dark grey represent plots that were burned once in 2011 and black points represent plots that have been reburned, or burned twice, in 2011 and again in 2016. Error bars are ±S.E. For significance values see table 1.1.
**Table 1.1:** The main and interactive effects of the change in year (2017-2019), site (Mojave or Great Basin) and fire (unburned, burned, reburned) on total plant biomass, cover and density. For a graphical representation of these results, see figure 1.2.

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CHAPTER 2

Rodent folivory preference for native seedlings increases invasion potential in the Mojave Desert

Rebekah L. Stanton, Carrie Evans Saunders, Tara B.B. Bishop and Samuel B. St. Clair
Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT
Doctor of Philosophy

ABSTRACT

Rodents can confer strong biotic resistance to the establishment of weak and aggressive plant invaders. Rodent herbivory preferences for native or invasive seedlings have the potential to affect the direction of plant community re-establishment in post-fire environments when invasion potential is high. This study's objective was to examine the effects of rodent herbivory and wildfire on the survival of native and invasive plants at the seedling stage of development. Our field site was composed of a full factorial design, replicated five times to test the individual and interactive effects of past fire and rodent exclusion on seedling survival. We used fencing to create rodent exclusion plots. In 2011, one rodent exclusion and one access plot in each block were experimentally burned. We grew several plant species, five native and four invasive (Table 2), in pots to the seedling stage and placed one pot of each species in each of our treatment plots. Seedling fate was assessed over one week. Rodent exclusion increased seedling survival across species by 15%. Seedling survival was nearly twice as high for invasive seedlings (85%) than native seedlings (47%). Rodent exclusion increased the survival of native seedlings from 36% to 59% but did not significantly impact the survival of invasive seedlings. Fire did not significantly impact the survival of the seedling community. When comparing across functional groups, the
survival of shrubs was increased from 31% to 58% in rodent exclusion plots compared to rodent access plots and forb seedling survival was increased from 57% in the rodent access plots to 76% in exclusion plots, with no differences for grasses. When considering individual species, *Yucca brevifolia* seedling survival was 47% in unburned plots with no seedling survival in burned plots. Fire did not have a significant impact on any other species. *Larrea tridentata* and *Erodium circutarium* showed the greatest sensitivity to rodent herbivory with much smaller effects on the other species. These results suggest that rodents may be contributing to the establishment of plant invaders at the seedling stage by showing preferences for native plants over invasive.

**INTRODUCTION**

Plant invasion outcomes are influenced by both the environmental characteristics of the invaded ecosystem (Enders et al. 2019; Levine et al. 2004) and traits of the plant invaders (Callaway and Ridenour 2004; Rejmánek and Richardson 1996). Reductions in the establishment success of exotic plants can occur through mechanisms of competition and herbivory. This biotic resistance is conferred upon invasive plants by native plant and rodent communities (Levine et al. 2004; St. Clair and Bishop 2019). Invasive grasses are growing prolifically in the North American deserts due to traits that allow them to overcome key environmental constraints to their establishment, particularly in post-fire conditions. Traits such as rapid and variable germination timing and phenotypic plasticity allow invasive grasses to strongly compete for light and soil resources with native seedlings (Knapp 1996). They also produce large numbers of seeds (Leffler et al. 2011), increasing their establishment success and spread in post-fire environments (St.Clair et al. 2016).

Rodents influence plant community assembly through seed dispersal and herbivory (Brown and Heske 1990; Clements and Harmon 2017; St.Clair et al. 2016; Vander Wall 1994)
and can create biotic resistance to plant invasion through granivory and folivory (Parker et al. 2006; Pearson et al. 2012; St.Clair et al. 2016). They also show strong species preferences based on seed and seedling characteristics, driving shifts in plant community composition (Connolly et al. 2014). Several studies have shown that rodents can reduce the establishment success of weak plant invaders (Allington et al. 2013; Pearson et al. 2012; St.Clair et al. 2016), and there is emerging evidence that they can also suppress aggressive invaders (Pyke 1986; St.Clair et al. 2016). A large amount of research in this area has focused on understanding the top-down control of rodents on plant community assembly based on seed preference (Connolly et al. 2014; Lucero and Callaway 2018; Maron et al. 2012; Price 1983). Recent studies have shown that rodents can also influence patterns of plant community composition due to variability in seedling herbivory preference based on seedling traits (Sharp Bowman et al. 2017a; Sharp Bowman et al. 2017c).

Life-history strategies and functional traits of plants strongly influence their sensitivity to rodent herbivory and establishment success. In post-fire environments, the emergence of seedlings in low-density plant communities can increase their vulnerability to herbivory (Sharp Bowman et al. 2017a). Rodents have strong preferences for vegetation with higher tissue N and moisture content, both limiting factors in deserts (Paul et al. 2012; Pérez-Harguindeguy et al. 2003; Sharp Bowman et al. 2017a). Seedlings with a high moisture content are important water sources for desert rodents (Bailey 1923; Borruel et al. 1998). Young seedlings also sometimes lack the physical and chemical defenses found in adult plants, making them even more susceptible to rodent herbivory (Elger et al. 2009; Fenner 1987). Invasive and native plants often exhibit differences in leaf functional traits, such as lignin content and specific leaf area, and defense strategies, both physical and chemical, that are likely to affect their sensitivity to rodent
herbivory (Poorter et al. 2004). The role that rodent herbivory plays in the establishment success of invasive species has not been adequately explored in the context of changing disturbance regimes, particularly fire that is linked to invasion success.

Wildfires are increasing in size and frequency in desert ecosystems due to plant invasions which can have legacy effects on post-fire plant community assembly (St. Clair and Bishop 2019). Wildfire can reduce biotic resistance to invasion by removing competition from the native plant community and altering the rodent communities in ways that could differentially impact the post-fire establishment success of native and invasive seedlings (Levine et al. 2004). Above ground-dwelling rodents, such as *Neotoma*, are particularly susceptible to fire as their homes are flammable, and they are notoriously reluctant to leave when threatened by fire (Simons 1991). Subterranean species of rodents, while less susceptible to the direct effects of fire, often experience a reduction in community abundance and diversity in post-fire environments (Horn et al. 2012) due to emigration or increased predation rates related to losses in native shrub cover (Leahy et al. 2016; Simons 1991). Quadrupedal rodents prefer areas rich in cover and vegetative diversity, while bipedal rodents, such as *Dipodomys* species, have a much higher affinity for open spaces (Simons 1991; Vamstad and Rotenberry 2010), which can result in dramatic shifts in rodent community structure in post-fire environments (Sharp Bowman et al. 2017a). Since rodents can have strong top-down effects on plant community regeneration and invasion (St.Clair et al. 2016), shifts in rodent communities in response to post-fire conditions are likely to have substantial impacts on post-fire plant community composition and succession. Variation in functional traits of seeds and seedlings will also likely impact herbivory preferences by rodents in post-fire environments.
The Mojave Desert provides a good location for studying the impacts and preferences of a diverse community of rodent herbivores on native and invasive seedling in response to changing fire regimes. The Mojave Desert rodents are abundant and diverse and show evidence of conferring biotic resistance to plant invasions (Bishop et al. 2020a; Hafner 1977; Sharp Bowman et al. 2017b). Red brome (*Bromus rubens* L.) and Arabian schismus (*Schismus arabicus* Nees), common invaders of the Mojave Desert, compete directly with a diverse native plant community (Brooks 2000; DeFalco et al. 2003), which allows us to test how variation in functional traits among these two groups influences their vulnerability to rodent herbivory. Fine plant fuels of invasive grasses have established novel fire regimes in the Mojave Desert, whereby fires have become larger and more frequent over time (Brooks et al. 2004; Horn and St.Clair 2017). This cycle is likely to have indirect effects on plant community assembly and invasion by altering patterns of rodent herbivory (Sharp Bowman et al. 2017b; Simons 1991).

The objectives of this study were to assess how current rodent seedling preferences differ in areas that have experienced past fires compared to areas that have not, and to identify how some of a seedling’s traits, which differ between native and invasive seedlings, influence their susceptibility to rodent herbivory. We hypothesized that rodents would consume native seedlings more than invasive seedlings because of variations in functional traits, such as growth form, between native and invasive species. We also hypothesized that the survival of some seedling species would be reduced in previously burned areas because of the reduced food sources available and the potential that fire has to alter the rodent community, and therefore, their preferences.
MATERIALS AND METHODS

Study site

Our field site was located near Lytle Ranch Preserve in the Beaver Dam Wash region of the Mojave Desert, approximately 25 miles West of St George, Utah (37°8'53.46" N, 114°0'49.59" W, elevation 915 m). The average temperature is 17.3°C, with the average January temperature being 7.2°C and the average July temperature being 29.4°C (Lytle Ranch GHCN:COOP, Utah Climate Center). An average of 206 mm of precipitation falls per year with a large portion of that falling in the winter months between October and April. The soil has been classified as young alluvium with a gravelly, sandy-loam texture. The most common native shrubs in the area include Joshua trees (Yucca brevifolia Engelm.), white bursage (Ambrosia dumosa (A. Gray) Payne) and creosote bush (Larrea tridentata (DC.) Coville). Several invasive plants are common at the study site: cheatgrass (Bromus tectorum), red brome (Bromus rubens) and Arabian schismus (Schismus arabicus Nees). Rodent trapping at the site identified Merriam's kangaroo rat (Dipodomys merriami Mearns), long-tailed pocket mouse (Chaetodipus formosus Merriam) and the desert woodrat (Neotoma lepida Thomas) as the most common rodent species. In this part of the Mojave, fire regimes are changing because of increases in invasive grasses. With fire return intervals becoming shorter (Brooks and Matchett 2006). Wire fences surrounding the study site have prevented grazing from cattle for at least the last 30 years, and there was no evidence of recent fire.

Experimental design

To assess the influence of fire and rodent exclusion on the survivability of native and invasive seedlings, we used a full factorial block design, replicated five times. 60 m x 60 m
blocks were quartered into four adjacent 30 m x 30 m quadrants. Fences surrounding the plots were constructed from 1 cm welded wire fencing and reached a height of 65 cm aboveground and extended 35 cm belowground. Within each block, one of four treatment combinations was randomly assigned to each plot: burned exclusion (preventing rodent access), burned rodent access, unburned exclusion, and unburned rodent access (Fig. 2.1).

The fences surrounding the rodent exclusion plots were fitted with 20 cm metal flashing along the top of the outward-facing side to prevent rodents from climbing over into the plots (Brown and Munger 1985; Curtin et al. 2000). The rodent access plots had 10 cm x 12 cm holes cut in the fencing at ground level every 4 m to allow the free movement of rodents into and out of the plots. Visible rodent trails through these holes indicate that they were utilized.

The burn treatments took place on 18th June 2011. Drip torches were used to initiate the burns. Due to the area already being invaded, fine fuels from red brome, which were growing at a rate of approximately 1319 stems m\(^{-2}\) in the intershrub space, were sufficient to carry the fire treatment across the burn plots without the addition of extra fuel. The burn reduced the shrub cover from 21% to 2.1% (90% reduction in shrub cover), which is typical of high severity burns in the Mojave Desert (Horn et al. 2015; Sharp Bowman et al. 2017c).

**Species selection**

This study aimed to assess the impacts of rodents and past fire on the vegetation found in the Mojave Desert. Because of this goal, we took a visual inventory of the most common species at our field site and selected nine of the most common plant species in the Mojave Desert for this experiment. Five of these common species were natives, and the remaining four common species were classified as invasive. Descriptions of the species used can be found in table 2.1. Seeds for
invasive plants were collected by hand from the Mojave Desert, close to our field site. Native seeds were commercially available and obtained from Granite Seed and Erosion Control (Lehi, Utah, USA).

_Greenhouse trials and seedling propagation_

In the beginning of 2017, a preliminary trial of twenty seeds of each species were planted in a 70% compost and 30% sand mix in plastic pots that were 10 cm in diameter and 2.5 cm high. Seedlings were grown in a climate-controlled greenhouse at 30°C daytime temperature and watered daily to saturation. Germination and height of seedlings were recorded daily, which made it possible to determine the germination rate and timing and average growth rates.

Using this germination data, we determined the average number of seeds needed to grow approximately ten seedlings of each species per pot. We grew these seedlings in the same greenhouse conditions as with our trials, but used our growth rate data to stagger the planting of each species so that when the time came to place them in our experimental plots, they were all approximately the same height of 2.5 cm.

_Data collection_

In the spring of 2017, we placed one pot of seedlings for each species in a randomized order along a transect in each of the twenty experimental plots (four treatment plots replicated five times). Each pot along a transect was placed approximately 2 m apart. All pots were more than 2m away from the plot boundary to avoid edge effects (Fig. 2.2). Pots were anchored in place using a metal clip.

The pots were watered daily to saturation throughout the experimental period to prevent seedling death via desiccation. Seven days after the initial placement of the seedlings in the field,
we recorded the number of seedlings left living in each pot. Seedlings were counted as dead if no leaves remained and there was no evidence of resprouting, according to methods described by Sharp Bowman et al. (2017c).

*Rodent trapping*

We surveyed the rodent population by live trapping within each plot during the new moon following the seedling experiment, April 27-29, 2017. Traps were set just before sunset at 8 pm and emptied just after sunrise between 6:30-8 am for each consecutive day in the 3-day trapping period for a total of approximately 36 trapping hours. Eight Sherman live traps were placed in each experimental plot and baited with commercially available birdseed. Captured rodents were given an individually numbered ear tag and marked by shaving a small patch of fur to identify them as recaptures following subsequent trapping nights. After marking, the rodents were released at the point of capture unless they were caught within an exclusion plot. In such cases, the rodent was released at the nearest point outside of the plots. Abundance was measured as the number of live rodents captured in each plot.

*Statistical analysis*

Data exploration was conducted based on the methods described by Zuur et al. (2010), creating box plots and conducting tests for normality and equal variances to ensure that all model assumptions for analysis were met. We used analysis of variance (ANOVA) to assess how rodent exclusion and fire influenced the survival of the seedlings in the program, R (R Core Team 2018). We fit three separate models, all of which included rodent exclusion, burn treatment, as fixed effects, block as a random effect, with seedling survival as a response variable. In the second model, invasion status (invasive or native) was included as a fixed effect and growth
form (grasses, forbs, shrubs) was included as a fixed effect in the third model. Pairwise comparisons were then made for each treatment combination using the Tukey function in R. The rodent data were analyzed using Wilcoxon signed-rank tests to assess how abundances varied between the exclusion and burn treatments.

RESULTS

Seedling survival across species

The historical fire treatment had no significant impact on seedling survival when averaged across species ($F_{1,189} = 0.37, p = 0.69$; Table 2). Rodent access lowered overall seedling survival across species by 21% from a proportion survival of 0.73 (SE = 0.03) to 0.58 (SE = 0.04; $F_{1,189} = 7.74, p = 0.006$), while the fire by rodent interaction term was not significant ($F_{1,189} = 0.11, p = 0.89$; Fig. 2.3; Table 2.2).

Native vs invasive species responses

Seedling survival was nearly twice as high for invasive seedlings (0.85, SE = 0.02) compared to native seedlings (0.47, SE = 0.04; $F_{1,185} = 67.6, p < 0.001$). Fire did not have a significant impact on the survival of native ($p = 0.80$) or invasive ($p = 0.49$) seedlings. Rodents decreased the survival of native seedlings by 39%, from a proportion survival of 0.59 (SE = 0.05) in exclusion plots to 0.36 (SE = 0.06; $F_{1,99} = 10, p = 0.002$), while rodents had no effect on invasive seedling survival ($F_{1,99} = 0.79, p = 0.38$), resulting in a significant rodent x invasion status interaction ($F_{1,185} = 4.5, p = 0.04$; Fig. 4). There were no significant three-way interactions of fire, rodent exclusion, and native vs. invasives ($F_{1,185} = 0.028, p = 0.87$; Fig. 2.4; Table 2.3).
**Growth Form comparison**

Shrubs had a lower survival rate (0.44, SE = 0.05) than forb (0.67, SE = 0.05) and grass (0.86, SE = 0.02) seedlings as indicated by the substantial main effect of growth form \(F_{2,181} = 28.0, p < 0.001\). The effect of fire on seedling survival did not vary between growth forms as indicted by a non-significant fire by growth form interaction term \(F_{2,181} = 0.881, p = 0.35\).

Rodents had no significant impact on the survival of grass seedlings \(p = 0.67\) but decreased forb seedling survival \(p = 0.04\) from a proportion survival of 0.76 (SE = 0.06) in the exclusion plot to 0.57 (SE = 0.07) in the allowed plots, and shrub seedling survival \(p = 0.006\) from a proportion survival of 0.58 (SE = 0.06) in the exclusion plot to 0.31 (SE = 0.07) in the allowed plots. These effects resulted in a rodent by growth form interaction \(F_{1,181} = 3.69, p = 0.03\;\text{Table 2.4}\). The three-way interaction of fire by rodent exclusion by growth form was not statistically significant \(F_{2,181} = 0.18, p = 0.84\;\text{Fig. 2.5}\).

**Individual species responses**

Fire reduced the survival of Joshua tree (Yucca brevifolia Engelm.) seedlings, with the proportion survival being 0.47 (SE = 0.18) in unburned plots and no seedling survival in burned plots \(F_{1,14} = 13.5, p = 0.003\), but did not have a significant impact on any other seedling species (Fig. 2.6; Table 2.2). The presence of rodents reduced the survival of creosote (Larrea tridentata (DC.) Coville), desert globemallow (Sphaeralcea ambigua A. Gray) and red stem stork’s bill (Erodium circutarium L.) seedlings by approximately 55% \(F_{1,25} = 10.7, p = 0.003\), 52% \(F_{1,24} = 4.69, p = 0.05\) and 22% \(F_{1,24} = 3.15, p = 0.09\) respectively, but did not have a significant impact on any other species (Table 2.2; Fig. 2.6). The rodent by fire interaction was not significant for any seedling species (Fig. 2.6; Table 2.2).
Rodent abundance

In the spring of 2017, we captured a total of 70 individual rodents and five species of rodent in our experimental plots during the 36-hour sampling period. 77% of the rodents captured were Merriam’s kangaroo rat. The difference in average rodent abundance in the burned vs the unburned plots was not significant ($W = 519.5, P = 0.29$), but rodent abundance was reduced in exclosure plots by approximately 62%, from an average of 1.70 (SE = 0.18) individuals per plot in control plots to 0.63 (SE = 0.13) in exclusion plots ($W = 178, p < 0.0001$).

DISCUSSION

Rodents had significant effects on seedling survival, particularly for native plants, while fire had much less impact. Our first hypothesis that rodents would consume native seedlings more than invasive seedlings because of variations in functional traits such as growth form was confirmed as our data suggest that rodents did prefer native seedlings more than invasive seedlings and there was evidence that traits associated with different growth form affected sensitivity to herbivory, with rodent showing a greater preference for shrubs than forbs and grass. Concerning our second hypothesis that the survival of some seedling species would be reduced in previously burned areas because of the potential that fire has to alter the rodent community, and therefore, their preferences, there was no evidence that fire directly or indirectly affected seedling survival via means of rodent herbivory.

Rodent herbivory

Studies show that rodents can suppress plant invaders (Allington et al. 2013; Pearson et al. 2012; Pyke 1986; St.Clair et al. 2016) but our data focus more on the mechanisms underlying consumer control of invasive species. Our results demonstrate that rodent seedling herbivory has
a strong suppressive effect on native seedling survival but little effect on invasive species in our study system (Fig. 2.3). Three of the four problematic invasive species in our study system are grasses, which likely make them less appealing to rodent herbivores due to lower palatability and higher C:N ratios compared to forb and shrub seedlings (Pirhofer-Walzl et al. 2011). Grasses typically have a higher silica content, in the form of phytoliths, that have the potential to act as a defense against herbivory (Strömberg et al. 2016), and higher C:N ratios, another key trait that lowers herbivory (Massey and Hartley 2009; Thomas and Asakawa 1993; Vargas et al. 2006). Seedling morphology that differs between grasses, forbs and shrub seedlings can also create visual cues that affect herbivory preference, in a similar way to how animals recognize yellow and black as dangerous colors (Pérez-Harguindeguy et al. 2003).

*Fire*

It is well documented that fire can alter the composition and abundance of rodent communities (Horn et al. 2012; Zwolak et al. 2010) which could in turn affect herbivory pressure on emerging seedlings in post-fire environments. Our results showed no effect of fire on rodent community abundance, which is consistent with other studies that show losses in the diversity, but not abundance of rodents in post-fire environments (Horn et al. 2012). These changes in diversity can have top-down implications on the local plant community, depending on the food preferences of the different rodent species (Horn et al. 2012; Simons 1991). Our data suggest that there is not a difference in herbivory preferences of rodent communities in burned and unburned rodent communities since the burn treatment did not significantly influence seedling survival. This result may be partially influenced by the dominance of Merriam’s kangaroo rat in our study system, which is less sensitive to post-fire burn conditions (Horn et al. 2012; Simons 1991; Vamstad and Rotenberry 2010). It is also important to note the size of our experimental plots.
Each burned plot is 900 m², but the range of Merriam’s kangaroo rat has been recorded as up to 5200 m² (Behrends et al. 1986), meaning that there is potentially significant overlap between burn and unburn rodent communities. This overlap would result in a blurry boundary between the burned and unburned parts of our study, causing little differentiation between communities. More studies with larger burn treatments would be required to get an accurate idea of the impact that fire has on rodent diversity and herbivory preferences.

**Growth form differences**

Rodents' food preferences can have top-down effects on the survival and ultimate establishment of plant communities (St.Clair et al. 2016). While it is understood that rodents actively consume vegetative plant tissues, it is less understood how these top-down effects regulate seedlings and ultimate plant community establishment. Our data suggest that rodents show a general preference for forbs and shrubs over grasses (Fig. 2.5; Fig 2.7). This result is in line with work in the Great Basin Desert by Sharp Bowman et al. (2017c), who also shows that grass and forb seedlings exhibit greater survivability than shrub seedlings. This phenomenon could be because of the nutritional content of shrubs and forbs compared to grasses. Shrubs and forbs have a more significant amount of crude protein and phosphorous and greater digestibility than grasses (Holechek 1984) that greatly influence the food preferences of herbivores (Pérez-Harguindeguy et al. 2003). Carmona et al. (2011) suggest that plants' chemical composition is less of a deterrent to herbivores than morphological features. Looking at the morphology of grasses, forbs, and shrubs, they are relatively different, even at the seedling stage. Grass seedlings are composed of a single thin leaf that grows quickly upward. Most shrub seedlings were slower to grow and had two cotyledons. They were more robust and had a bit more of a substantial, "woody" feel. Forbs also have a significantly higher moisture content than grasses
(Sharif and West 1968), while the moisture content of shrubs may be lower than grasses at maturity (Sharif and West 1968), which can drive preferences due to water limitation in deserts.

**Conclusions and implications**

This experiment within our study system has shown that rodents do have some influence on which plants can establish, not just following a disturbance, but at any time. Knutson et al. (2014) suggest that native seeding failure is primarily due to weather, but our data show that there is a significant reduction in certain native seedlings’ survival in the presence of rodents, both in and out of small fire disturbed areas, up to 55% for some species. While weather may be influential in native plant recruitment failure, rodents are also a significant driver of recruitment failure for some native species.

Considering rodent herbivory while developing management strategies for land restoration following wildfires can better predict post-fire plant community establishment. It is relatively easy to assess local rodent communities by conducting short-term trapping surveys and thus predict the impact that rodents may have on seeding efforts. It would be wise to reserve seeding efforts for times when rodent activity is low to minimize the adverse effects of herbivory on seedling establishment and augment the seed of native species that are more sensitive to rodent herbivory to compensate for recruitment failure.

Bailey V (1923) Sources of water supply for desert animals. The Scientific Monthly 17:66-86


Leffler AJ, Monaco TA, James JJ (2011) Morphological and physiological traits account for similar nitrate uptake by crested wheatgrass and cheatgrass. Natural Resources and Environmental Issues 17:10


Sharp Bowman TR, McMillan BR, St Clair SB (2017a) Rodent herbivory and fire differentially affect plant species recruitment based on variability in life history traits. Ecosphere 8


**FIGURES**

**Figure 2.1:** A pictorial representation of our full factorial experimental design, replicated five times. A random two out of four plots in each block were left unburned plots (light grey) and the remaining two plots were experimentally burned (dark grey) in June 2011. A random unburned and burned plot in each block were assigned to be rodent exclusion plots, which are represented by the no rodent symbol.

**Figure 2.2:** A pictorial representation the placement of the seedlings in one of the blocks. The burned plots are dark grey, and the unburned plots are light grey. Rodent exclusion plots are identified with the rodent exclusion symbol. Transects that our seedlings were placed along were randomly placed and are represented in this figure as dotted lines. One pot of each species was placed in a random order along each transect and were at least 2 m away from each other and the edge of the plot.
Figure 2.3: A graph showing how the main and interactive effects of rodents and a historical burn influence proportion seedling survival (after seven days) of all the seedlings used in this experiment (four invasive plant species and five native plant species). Cross hatched bars represent rodent exclusion plots, grey bars represent plots that were burned in June 2011 and white bars represent unburned plots. Mean values are presented with error bars as ±1SE. For significance values see table 2.2.

Figure 2.4: A graph showing how the main and interactive effects of rodents and a historical burn influence proportion seedling survival (after seven days) of five native species and four invasive species in the spring of 2017. Cross hatched bars represent rodent exclusion plots while open bars represent rodent access plots. Grey bars represent plots that were burned in June 2011 and white bars represent unburned plots. Mean values are presented with error bars as ±1SE. For significance values see table 2.3.
Figure 2.5: The main and interactive effects of a historical burn and rodent exclusion on the proportion survival (after seven days) of three shrub, three forb, and three grass seedling species in the spring of 2017. Cross hatched bars represent rodent exclusion plots, grey bars represent plots that were burned in June 2011 and white bars represent unburned plots. Mean values are presented with error bars as ±1SE. For significance values see table 2.4.

Figure 2.6: The main and interactive effects of a historical burn and rodent exclusion on the proportion survival (after seven days) of nine different seedling species in the spring of 2017. Cross hatched bars represent rodent exclusion plots, grey bars represent plots that were burned in June 2011 and white bars represent unburned plots. Mean values are presented with error bars as ±1SE. For significance values see table 2.2.
Figure 2.7: A representation of the effects of rodents on three grass, three forb, and three shrub seedling species from the Mojave Desert during our experiment in the spring of 2017. The thickness of the arrow correlates with the strength of the effect; the effect of rodents was greatest on shrub seedlings and least on grass seedlings. For the significance values representing these relationships, see table 3.
### Table 2.1: Descriptions of all the plant species used in this study looking at the effects of rodents and fire on seedling survival in the Mojave Desert.

<table>
<thead>
<tr>
<th>Species</th>
<th>Code</th>
<th>Common name</th>
<th>Status</th>
<th>Growth form</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bromus rubens L.</td>
<td>BRRU</td>
<td>Red brome</td>
<td>Invasive</td>
<td>Grass</td>
</tr>
<tr>
<td>Bromus tectorum L.</td>
<td>BRTE</td>
<td>Cheatgrass</td>
<td>Invasive</td>
<td>Grass</td>
</tr>
<tr>
<td>Erodium circuitarium L.</td>
<td>ERCI</td>
<td>Redstem stork's bill</td>
<td>Invasive</td>
<td>Forb</td>
</tr>
<tr>
<td>Schismus arabis Nees</td>
<td>SCAR</td>
<td>Arabian schismus</td>
<td>Invasive</td>
<td>Forb</td>
</tr>
<tr>
<td>Ambrosia dumosa (A. Gray) Payne</td>
<td>AMDU</td>
<td>White bursage</td>
<td>Native</td>
<td>Shrub</td>
</tr>
<tr>
<td>Baileya multiradiata Harv. &amp; A. Gray</td>
<td>BAMU</td>
<td>Desert marigold</td>
<td>Native</td>
<td>Forb</td>
</tr>
<tr>
<td>Larrea tridentata (DC.) Coville</td>
<td>LATR</td>
<td>Creosote</td>
<td>Native</td>
<td>Shrub</td>
</tr>
<tr>
<td>Sphaeralcea ambigua A. Gray</td>
<td>SPAM</td>
<td>Desert globemallow</td>
<td>Native</td>
<td>Forb</td>
</tr>
<tr>
<td>Yucca brevifolia Engelm.</td>
<td>YUBR</td>
<td>Joshua tree</td>
<td>Native</td>
<td>Shrub</td>
</tr>
</tbody>
</table>

### Table 2.2: The main and interactive effects of rodent exclusion and a historic burn on the proportion survival (after seven days) of the individual seedling species and all the species together that were used in our experiment during the spring of 2017.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>RODENTS</th>
<th>BURN</th>
<th>RODENTS x BURN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Status</td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>SHRUB</td>
<td>AMDU</td>
<td>2.99</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>LATR</td>
<td>11</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>YUBR</td>
<td>0.36</td>
<td>0.47</td>
</tr>
<tr>
<td>FORB</td>
<td>BAMU</td>
<td>0.34</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>ERCI</td>
<td>3.15</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>SPAM</td>
<td>4.69</td>
<td>0.05</td>
</tr>
<tr>
<td>GRASS</td>
<td>BRRU</td>
<td>0.42</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>BRTE</td>
<td>0.93</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>SCAR</td>
<td>0.41</td>
<td>0.53</td>
</tr>
<tr>
<td>All species</td>
<td></td>
<td>7.74</td>
<td>0.006</td>
</tr>
</tbody>
</table>
Table 2.3: The main and interactive effects of a historic burn and rodent exclusion on the proportion survival (after seven days) of the four invasive and five native seedling species used in our experiment during the spring of 2017.

<table>
<thead>
<tr>
<th>STATUS</th>
<th>RODENTS</th>
<th></th>
<th>BURN</th>
<th></th>
<th>RODENTS x BURN</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p</td>
<td>F</td>
<td>p</td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Invasive</td>
<td>0.79</td>
<td>0.38</td>
<td>0.73</td>
<td>0.49</td>
<td>0.09</td>
<td>0.92</td>
</tr>
<tr>
<td>Native</td>
<td>10</td>
<td>0.002</td>
<td>0.22</td>
<td>0.8</td>
<td>0.08</td>
<td>0.92</td>
</tr>
</tbody>
</table>

Table 2.4: The main and interactive effects of a historic burn and rodent exclusion on the proportion survival (after seven days) of the three shrub, three forb and three grass seedling species used in our experiment during the spring of 2017.

<table>
<thead>
<tr>
<th>GROWTH FORM</th>
<th>RODENTS</th>
<th></th>
<th>BURN</th>
<th></th>
<th>RODENTS x BURN</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p</td>
<td>F</td>
<td>p</td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Shrub</td>
<td>8.23</td>
<td>0.006</td>
<td>0.005</td>
<td>&gt; 0.99</td>
<td>0.03</td>
<td>0.96</td>
</tr>
<tr>
<td>Forb</td>
<td>4.63</td>
<td>0.04</td>
<td>1.74</td>
<td>0.19</td>
<td>0.54</td>
<td>0.58</td>
</tr>
<tr>
<td>Grass</td>
<td>0.18</td>
<td>0.67</td>
<td>0.48</td>
<td>0.62</td>
<td>0.22</td>
<td>0.81</td>
</tr>
</tbody>
</table>
CHAPTER 3

The effects of fire and rodent exclusion on the seed fate of native and invasive plant species in the Mojave Desert

Rebekah L. Stanton, Samuel B. St. Clair, Kristina L. Cass, Baylie C. Nusink, Eliza Burdett and Rachel Watts
Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT
Doctor of Philosophy

ABSTRACT

Plant invaders are becoming increasingly problematic globally due to altered disturbance regimes driven by human activity. Rodents are active seed predators that can create strong biotic resistance against the establishment of plant invaders. The objective of this study was to assess the impacts of rodent granivory and fire on the fate of key native species and problematic invaders in desert ecosystems. Using rodent fencing and experimental burns in a factorial design, we examined the influence of rodents and fire on seed fate of seven native and three invasive species in the Mojave Desert. We placed seeds in dishes in each of the experimental treatment plots in a randomized order. When averaged across all species, rodent exclusion reduced seed removal from 80% (SE = 1.33) in the exclusion plots to 33% (SE = 1.60) in rodent allowed plots.

Rodents had an effect on all individual species used in this experiment ($p < 0.1$), most significantly on blackbrush (*Coleogyne ramosissima* Torr.) and Joshua tree (*Yucca brevifolia* Engelm.) seeds, leaving an average of less than 1% of seeds for both species. Rodents did not differentially favor native or invasive seeds. There was not a significant correlation between seed mass and the preferences of rodents, indicating that factors other than seed size are influential in determining which seeds the rodents choose. Fire did not have a strong or consistent effect on
seed removal by rodents ($p > 0.01$), likely because they did not influence the abundance of rodents in the plots ($W = 56, P = 0.70$). Management initiatives could use our data to know how to best compensate for seeds lost to rodent herbivory. Future studies should examine what seed traits drive rodent seed preferences.

INTRODUCTION

The life history traits of plant invaders (Callaway and Ridenour 2004; Rejmánek and Richardson 1996) and the characteristics of the invaded ecosystem (Enders et al. 2019; Levine et al. 2004) influence plant invasion outcomes. Exotic annual grasses native to Eurasia, particularly in the genus *Bromus*, have spread broadly across the North American continent and have been particularly problematic in desert ecosystems (Knapp 1996). These annual grasses are strong competitors for soil resources, leading to rapid growth and prolific seed production, along with long-distance dispersal mechanisms that drive their expansion (Knapp 1996; Leffler et al. 2011; St.Clair et al. 2016). Biotic resistance by native organisms can reduce invasion success. Native plant communities and established cryptobiotic soil crusts actively compete with invasive plants for space and resources and can successfully hinder their establishment (Belnap et al. 2006; Knapp 1996). In addition, native herbivore communities can reduce exotic seedling establishment through seed predation and herbivory (Allington et al. 2013; St.Clair et al. 2016).

There have been several hypotheses posited to explain the success of invasive species. The enemy release hypothesis is just one hypotheses that outlines a mechanisms by which exotic species can perform better in their introduced range (Callaway and Ridenour 2004; Keane and Crawley 2002). The enemy release hypothesis suggests that an invasive plant has no natural enemies in a new system, allowing them to grow unencumbered by predation (Keane and Crawley 2002). Some cases have shown that generalist herbivores are less active at preventing
the establishment of invasive plant species than native plant species, which would support this hypothesis (Adams et al. 2009; Lucero et al. 2019; Vila et al. 2005). This hypothesis highlights how a lack of shared co-evolutionary history with a new system could give invasive plants a competitive edge over their native counterparts.

Rodents can influence plant community assembly and provide biotic resistance against invasion through seedling herbivory and seed predation (Connolly et al. 2014; Parker et al. 2006; Pearson et al. 2012; St.Clair et al. 2016). Rodents have been shown to suppress the establishment success of invasive annual grasses in North American deserts (Pyke 1986; St.Clair et al. 2016). Seeds have the highest caloric value of any plant material and are targeted by rodents as a preferred food source (Golley 1961; Reichman 1975; Simberloff and Dayan 1991). The size of a seed often determines their caloric content and can be a factor in influencing rodent seed preferences and ultimate plant establishment (Chen and Valone 2017; Davidson et al. 1984; Willson 1971). While studies have shown that some rodents prefer larger and more energy-dense seeds over smaller seeds (Chen and Valone 2017; Maron et al. 2012; Soholt 1973), nutrient and water content and chemical and physical defenses can also influence rodent seed preferences (Blate et al. 1998; Frank 1988; Soriano et al. 2015). In addition, seed coat characteristics and their influence on handling time can also determine which seeds are chosen for consumption (Taraborelli et al. 2003; Willson and Harmeson 1973). While there has been significant research into what influences rodent seed preferences (Blate et al. 1998; Frank 1988; Murray and Dickman 1994), there is limited research on how rodent seed preferences vary between native and invasive seed species.

The emergence of invasive grass fire cycles increases fire and plant invasions in desert ecosystems (D'Antonio and Vitousek 1992). Fire can alter the composition and activity of rodent
communities changing their top-down effects on plant community assembly (Levine et al. 2004). *Neotoma* species that dwell above ground have flammable homes that are particularly susceptible to wildfire's direct effects (Simons 1991). On the other hand, subterranean rodent species are less vulnerable to the direct impacts of wildfire but may still be reduced in post-fire environments because of emigration and increased predation due to the loss of vegetation cover (Leahy et al. 2016; Simons 1991). Rodent species demonstrate different sensitivities to post-fire environments; quadrupedal mice species tend to have a higher affinity for unburned plant communities with plenty of cover (Sharp Bowman et al. 2017a), whereas bipedal rat species are far more likely to be found in open spaces, like those created following a fire (Simons 1991; Vamstad and Rotenberry 2010). Together, all of these factors can result in dramatic changes in post-fire rodent community structure, and ultimately the top-down effects on plant community regeneration and invasion outcomes (Sharp Bowman et al. 2017b; St.Clair et al. 2016).

The Mojave Desert is an ideal location for studying the influences of a diverse rodent community on native and invasive seeds' fate in response to wildfire. Rodent communities in the Mojave are abundant and diverse and target both native and invasive species (Bishop et al. 2020a; Sharp Bowman et al. 2017b). In addition, several annual invasive species, including red brome (*Bromus rubens* L.), Arabian schismus (*Schismus arabicus* Nees.), cheatgrass (*Bromus tectorum* L.), and red stem stork's bill (*Erodium cicutarium* L.), are common invasives in the Mojave Desert. They also directly compete with native plant species for water and soil resources (Brooks 2000; DeFalco et al. 2003), and have contributed to the invasive-grass fire cycles in Mojave Desert, making fires larger and more frequent over time (Brooks et al. 2004; Horn and St.Clair 2017). These changing fire regimes are known to affect the abundance and diversity of the rodent communities (Sharp Bowman et al. 2017b; Simons 1991), but less is known about
how shifts in rodent communities in response to fire, and rodent seed preferences may alter plant
community assembly and invasion outcomes.

Previous studies have explored how fire and rodents influence native plant community
establishment, but the impact of rodent granivory on ecosystem invasibility in the context of fire
is less studied (Brown and Heske 1990; Clements and Harmon 2017). This study aims to assess
how fire and rodent granivory influence native and invasive seed species' fate in the Mojave
Desert. We hypothesized that rodent preference would be greater for native species than
invasives because of their shared co-evolutionary history would create greater familiarity and
adaptations for optimizing their use. We predicted that rodents would show preferences for
species that produce larger seeds. Finally, we hypothesized that burn treatments would indirectly
affect seed fate by altering the composition and abundance of the rodent community.

MATERIALS AND METHODS

Study system

Our study site is in the Beaver Dam Wash region of the Mojave Desert, near Lytle Ranch
Preserve, approximately 25 miles West of St George, Utah (37°8'53.46" N, 114°0'49.59" W,
elevation 915 m). The average temperature is 17.3°C, with the average January temperature
being 7.2°C and the average July temperature being 29.4°C (Lytle Ranch GHCN:COOP, Utah
Climate Center). An average of 206 mm of precipitation falls per year with a large portion of that
falling in the winter months between October and April. The soil has been classified as young
alluvium with a gravelly, sandy-loam texture. By rodent trapping in the area, we have
determined that the most common rodent species are Merriam's kangaroo rat (Dipodomys
merriami Mearns), long-tailed pocket mouse (Chaetodipus formosus Merriam) and the desert
woodrat (*Neotoma lepida* Thomas). The most common native plants in the area include Joshua trees (*Yucca brevifolia* Engelm.), white bursage (*Ambrosia dumosa* (A. Gray) Payne) and the creosote bush (*Larrea tridentata* (DC.) Coville). Common invasive plants include cheatgrass (*Bromus tectorum*), red brome (*Bromus rubens*), Arabian schismus (*Schismus arabicus* Nees) and redstem storksbill (*Erodium circutarium* L.). Wire fences surrounding the study site have prevented grazing from cattle for at least the last 30 years, and there is no evidence of recent fire.

**Experimental design**

We used a full factorial block design, replicated five times, to assess the influence of rodent exclusion and fire on seed fate. Each block consisted of four 30 m x 30 m plots which were each randomly assigned one of four treatment combinations: burned, rodent excluded, burned with rodent access, unburned, rodent excluded, and unburned with rodent access (Fig. 3.1).

We implemented the burn treatments on 18th June 2011. Drip torches were used to ignite the fires, and red brome, which had already invaded the system and was growing at a rate of 1319 stems m\(^{-2}\) (Bishop et al. 2020a), provided enough fine fuel in the intershrub spaces to carry the fire across the burn plots. Fire severity was high, with approximately 90% of the vegetation cover being removed due to these experimental burns (Sharp Bowman et al. 2017c).

We constructed fences made of 1 cm welded wire around each of the 20 treatment plots. Fencing extended 35 cm below the ground and 65 cm above the ground. Rodent access plots had 10 cm x 12 cm openings in the mesh fencing every 4 m at ground level to facilitate rodent entry. Exclusion plots had 20 cm metal flashing along the top of the outward facing side to prevent rodents from climbing in (Fig. 3.1).
Species selection

Because this study aims to assess the impacts of rodents and a historical burn on the dominant vegetation found in our study area, we selected ten plant species common in this area and across the Mojave Desert to use in this experiment (three common invasives in the area and seven common native species). Descriptions of each of the species used can be found in table 3.1. We collected invasive seeds for this experiment from the areas surrounding our field site in the Mojave Desert by hand. Mark Borchert at the USDA Forest Service provided Joshua tree seeds, which he collected by hand from approximately 6 km north northeast of Big Bear City, California. The remaining seeds were obtained from Granite Seed and Erosion Control (Lehi, Utah, USA), a company that specializes in native seed collections.

Rodent trapping

We surveyed the rodent population by live trapping within each plot during the new moon prior to the seed experiment, July 9-12, 2018. Traps were set just before sunset at 8:30 pm and emptied just after sunrise between 6-8 am for each consecutive day in the 3-day trapping period for a total of approximately 27 trapping hours. Eight Sherman live traps were placed in each experimental plot and baited with commercially available birdseed. Captured rodents were given an individually numbered ear tag and marked by shaving a small patch of fur to identify them as recaptures following subsequent trapping nights. After marking, the rodents were released at the point of capture unless they were caught within an exclusion plot. In such cases, the rodent was released at the nearest point outside of the plots. Abundance was measured as the number of live rodents captured in each plot.
Seed experiment

On June 5th, 2018, during the summer when most plants drop their seeds, we placed our seeds out in our Mojave study site. We placed groups of four 100 mm Petri dishes for each species in each of the experimental plots. The groups of four Petri dishes were placed along a transect in a randomized order, 2 m apart, and with the end dishes at least 2 m away from the plot boundary to avoid edge effects. Each dish contained one hundred of their respective seeds mixed with soil. Mixing the seeds with soil prevented loss from wind and ensured that the only seed predators assessed in this experiment were rodents, as rodents, unlike other seed predators, can seek out seeds via olfactory means (Vander Wall et al. 2003). We collected the soil from the side of Bull Valley Road, approximately 1 mile southwest of our field site. Since seed presence is minimal below a depth of 10 cm in the Mojave desert (Guo et al. 1998), we dug down at least 15 cm before collecting the soil to get past the current seed bank.

We collected one dish of each species from each plot one, three, seven and fourteen days after placement in the field and brought them back to the lab. We used a series of different sized sieves to separate most of the soil from the remaining seeds, then our own eyes to differentiate seeds from the rest of the soil. We then counted the separated seeds.

Seed mass

For each species, a random selection of 50 seeds was weighed using a balance (Denver Instrument, Bohemia, New York, USA). That mass was then divided by 50 to get an average mass per seed for each seed species.

Statistical analysis
Following Zuur et al. (2010), explored the data in R to check if the data met the model assumptions of normality and equal variances required for parametric analysis. Since the assumptions for equal variances could not be met, we used a non-parametric rank-based ANOVA model from the Rfit package in R (Kloke and McKean 2012; R Core Team 2018) to test how the proportion of seeds left in the dishes varied with the rodent and fire treatments and how the seeds left in the dishes varied with the number of days they were left out in the field. Unfortunately, since this type of analysis did not allow for mixed-effects, block could not be added to the model as a random effect. Since the effects of the number of days on the proportion of seeds remaining plateaued after 7 days, only the data from day 7 were used to analyze the effects of fire and rodents on individual seed species. The fire effect was not significant so, for figure 3 showing the comparative effects of rodents on the different species, we averaged the species comparisons across burned and unburned treatments. A Mann-Whitney U test was used to see if rodents differentially influenced native and invasive seed fate. We included the proportion of seeds remaining on day seven as the response variable and again averaged the comparison across burned and unburned treatments. We then used Pearson's correlation to test how the proportion of seeds remaining in the dishes varied with seed mass. A Mann-Whitney U test was again used to test the effects of fire and the exclusion fences on rodent abundance.

RESULTS

Rodents: native vs invasive and seed size

When averaged across species, the percentage of seeds remaining in rodent exclusion plots after seven days was 80% (SE = 1.33), and 33% (SE = 1.60) in rodent allowed plots ($F_{1,1167}$
= 796, \( p < 0.001 \)). The amount of time the seeds were left in the field reduced the percentage of seeds left remaining in the dishes \((F_{3,1167} = 98, p < 0.001)\). There was a significant rodent by time interaction in which the rodent effect increased over time \((F_{3,1167} = 35, p < 0.001; \text{Fig. 3.2})\).

The presence of rodents reduced the number of seeds left in the dishes of all ten species after seven days \((p < 0.05; \text{Table 3.3; Fig. 3.3})\). Blackbrush \((\text{Coleogyne ramosissima} \ \text{Torr.})\) and Joshua tree \((\text{Yucca brevifolia} \ \text{Engelm.})\) seeds were the most affected by the rodents, both having an average of less than 1% of their seed remaining in rodent allowed plots (Fig. 3.3). White bursage \((\text{Ambrosia dumosa} \ (\text{A. Gray}) \ \text{Payne})\) was least affected by the rodents, having approximately 62% \((\text{SE} = 8.41)\) of its seed remaining in the rodent allowed plots on day 7 (Fig. 3.3). These variances in preference were not however, due to the invasion status of the seed species as rodents had similar effects on the removal of native seeds \((27\% \text{ seeds remaining on day 7, SE} = 3.33)\) as they did on the removal of invasive seeds \((16\% \text{ seeds remaining on day 7, SE} = 4.52; W = 1969, p = 0.21; \text{Fig. 3.4})\). There was no significant correlation between the percentage of seeds left remaining and the average mass of the seed \((r^2 = 0.21, p = 0.19)\).

**Fire**

The main effect of fire legacy did not have a significant impact on seed fate when averaged across species \((F_{1,1167} = 0.97, p = 0.32; \text{Fig. 3.2})\). Both the fire by rodent interaction \((F_{1,1167} = 0.29, p = 0.59)\), the fire by time left in the field interaction \((F_{3,1167} = 0.93, p = 0.42)\) were and the fire by rodent by time in the field interaction were all insignificant \((F_{3,1167} = 0.45, p = 0.72; \text{Fig.3.2})\).
Fire legacy did not have a significant effect on the remaining seeds of any of the individual species studied \((p > 0.1; \text{Table 3.3})\) and there was no significant rodent by burn interaction on the remaining seeds of any species \((p > 0.1; \text{Table 3.3})\).

*Rodent abundance*

In the summer of 2018, we captured a total of 34 individual rodents and six species of rodent in our experimental plots during the 27-hour sampling period. 68% of the rodents captured were Merriam’s kangaroo rat. The difference in average rodent abundance in the burned vs the unburned plots was not significant \((W = 56, p = 0.70)\), but rodent abundance was reduced in exclusion plots by approximately 79%, from an average of 2.8 (SE = 0.48) individuals per plot in control plots to 0.60 (SE = 0.21) in exclusion plots \((W = 11, p = 0.003)\).

**DISCUSSION**

Rodents had a significant effect on the seed fate of all species used in this experiment, while fire had no impact (Fig. 3.2). Our first hypothesis predicted that rodent preference would be greater for native species than invasives, which was not validated by our data. Rodents did show varying preferences between seed species, but these preferences appear to unrelated to invasive status of a species (Fig. 3.4). We predicted that rodents would show preferences for species that produce larger seeds, which was not supported by the data. Our final hypothesis that burn treatments would indirectly affect seed fate by altering the composition and abundance of the rodent community was rejected as our burn treatments did not significantly alter the fate of any of the seed species used in this study (Fig. 3.2).
Rodent granivory: native vs invasive seeds

Rodents can suppress plant invaders (Allington et al. 2013; St.Clair et al. 2016), but we know less about the mechanisms that drive this consumer control of the plant community. Our data suggest that rodents impact seed fate but do not show differential preferences for native or invasive seed species (Fig. 3.4), which may indicate that their potential to suppress invasion that St.Clair et al. (2016) identified, may occur at the seedling stage. This result appears to be contrary to studies by Lucero and Callaway (2018) and Pearson et al. (2011), who both propose that generalist rodents avoid invasive seeds. It could be that the seed preferences of rodents vary across different locales. The aforementioned studies took place in cooler, northern territories (Idaho and Montana, respectively), whereas the Mojave system in this study is a hotter, hyper-arid desert system. Seeds are an essential source of energy and water (Brown et al. 1979), limiting factors in the hyper-arid Mojave desert. Rodents have been known to select certain seeds proportional to their availability so it may be that rodents are less selective in more resource limiting environments where seeds are less available (Ivan and Swihart 2000). It is also important to note that our study standardized the number of seeds by providing 100 of each species. Even though rodents may eat invasives at the same rate as other species, the number of invasive seeds produced during an invasion can saturate the consuming capacity of rodents (St. Clair and Bishop 2019).

Rodent granivory: seed size

Studies have shown that seed consumers can be selective of particular species or seed types, thus controlling which plants can establish to maturity (Marone et al. 2008). Our data demonstrate that the rodent effect, while significant for each species, is greater for some species than for others, implying that rodents may also show preferences for some species over others.
We hypothesized that this variation in granivory preference would be due to seed size; however, our data do not support this, as the relationship between seed mass and granivory in our study was not significant. This result seems consistent with Blate et al. (1998) and Radtke (2011), who suggests that there may be more to seed preference than just size. We did not measure the water content of the seeds we used in this study, but Frank (1988) and Murray and Dickman (1994) suggest that water content is a greater indicator of granivore preference than the seed size particularly in arid environments. Water is very limiting in the hyper-arid Mojave Desert, and seeds have the potential to provide much-needed hydration to their consumers (Brown et al. 1979). Rodents of similar sizes will often prefer and forage for similarly sized seeds (Ivan and Swihart 2000). The rodent community in the Mojave Desert is diverse, which may be why preferences are shown for the many different sized seeds; different sized rodent species may prefer and utilize the different parts of a given resource.

Different species of seeds also have various physical and chemical defenses that may protect them from seed predation (Blate et al. 1998). For example, the least eaten seed in our study was *Ambrosia dumosa* (61% remaining in rodent allowed areas; Fig. 3.3). This seed is relatively average in size compared to the other seeds in the study but has obvious physical defenses that may make it a less desirable food source in the form of spikes. Blate et al. (1998) also identify that the physical defense provided by the hardness of a seed's coat may be a better indicator of granivore preference. In their system, nutrient rewards within harder seed coats were harder to access, therefore not predated upon as much. In a cafeteria study on seed preferences, Auger et al. (2016) compared rodent seed preferences of five common native species in the Mojave to the human palatability ranking of the same seed species, ultimately finding that the rankings were very similar. Seeds that ranked lower on the scale were reported to have a more
bitter taste, indicative of secondary chemical compounds that act as a defense against predation. This suggests that seed preferences may be driven by chemical defenses in the seed.

Fire

Fire can change rodent communities, which can potentially change the top-down impacts that rodents have on the establishment of a plant community (Horn et al. 2012; Zwolak et al. 2010). Our data, however, suggest that fire did not have a significant effect on the fate of any seed species used in this study. Summer 2018 rodent surveys in the plots confirm that the dominant rodent at this site is Merriam’s kangaroo rat, a bipedal kangaroo rat less sensitive to post-fire burn conditions (Horn et al. 2012; Simons 1991; Vamstad and Rotenberry 2010). A total of 34 individual rodents were caught throughout a 36-hour trapping session, 17 in burned plots and 17 in unburned plots. Of the rodents in the burned plots, 82% were Merriam’s kangaroo rat, but in the unburned plots only 53%, were Merriam’s kangaroo rat, with the other 47% being made up of quadrupedal long-tailed pocket mice and desert woodrats. These data correlate with other rodent studies in the area which show that fire lowers the rodent diversity but not the abundance and that rodent communities in burned areas consist of primarily bipedal species, such as kangaroo rats, which feel more at ease in larger, open spaces common in post-fire environments (Horn et al. 2012). Despite fire causing these differences in rodent community composition, our data indicate that seed preferences do not differ between these communities. This result may be caused by the size of our burn treatments. The typical range of a Merriam’s kangaroo rat can reach up to 5200 m² (Behrends et al. 1986), whereas our burned plots are only 900 m², meaning there could be too much overlap between rodent ranges to have really defined burned and unburned rodent communities. Although we have seen fire reduce rodent abundance and diversity in these plots in previous years (Sharp Bowman 2017a) To get a more reliable
estimation of the effects of fire on rodent community seed preferences, future researchers should undertake a larger scale study where burn treatments can encompass the whole range of the rodents in question.

Conclusions and implications

Overall, our study highlights the critical role that rodents play in plant community establishment. Rodents significantly reduced the number of seeds of all seeds within the study. Knutson et al. (2014) suggest that recruitment failure following seeding efforts is primarily due to the weather; however, our data indicate that rodents may be a large part of the cause. Rodents also prefer some seed species over others, which is essential to consider when developing and implementing management strategies for post-fire land restoration. Therefore, it may be best to consider local rodent activity when deciding when to seed an area and tailor the seed mixes used to better compensate for seeds lost to rodent granivory.

While our results are useful, they are not representative of the whole Mojave Desert. The Mojave Desert spans multiple US states and experiences variability in topography, climate, and biological composition. These variabilities will likely cause variances in rodent community composition and their potential food preferences. Future should get data to see how these granivory preferences vary across different parts of the Mojave Desert.

In this paper we discussed different factors that may be responsible for the rodent preferences of some seeds over others, things like water and nutritional content of seeds, as well as physical and chemical defenses that may be in place. Future studies would do well to assess these factors and the role they play in determining rodent food preferences to get a better overall understanding of the vulnerability of desert plant species in post fire environments.
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**FIGURES**

**Figure 3.1:** A pictorial representation of our full factorial experimental design, replicated five times. A random two out of four plots in each block were left unburned plots (light grey) and the remaining two plots were experimentally burned (dark grey) in June 2011. A random unburned and burned plot in each block were assigned to be rodent exclusion plots, which are represented by the no rodent symbol.

**Figure 3.2:** A time series showing how the main and interactive effects of fire and rodent exclusion on seed fate changed over a period of 14 days in the summer of 2018. Each point represents a selection of dishes of seeds that were taken out of our experimental plots on various days. The dark points represent dishes that we placed in plots that were burned in June 2011, and the open points represent dishes that we placed in unburned plots. Points paired with a solid line represent dishes that we placed in rodent exclusion plots whereas the points paired with dashed lines represent dishes that we placed in rodent access plots. Mean values are presented with error bars as ±1SE. For F statistics and significance values, see table 3.2.
Figure 3.3: A comparison of the seeds left remaining in rodent access plots after being left in the field seven days during our experiment in the Summer of 2018. Mean values are presented with error bars as ±1SE. We tested comparisons using pairwise Wilcoxon rank sum tests, with correction for multiple testing. Significant differences at the p < 0.05 level are denoted by different letters.
**Figure 3.4:** The main and interactive effects of rodent exclusion on the seed fate of native and invasive species after seven days in the field in the summer of 2018. Cross hatched bars represent rodent exclusion plots while open bars represent rodent access plots. Light grey bars represent data from native seeds and dark grey bars represent data from invasive seeds. Mean values are presented with error bars as ±1SE. We tested pairwise comparisons using pairwise Wilcoxon rank sum tests, with correction for multiple testing. Significant differences at the p < 0.05 level are denoted by different letters.
### Table 3.1: Descriptions of all the seed species used in this study looking at the effects of rodents and fire on seed fate in the Mojave Desert. For each species, the average seed mass was obtained by weighing a random 50 seeds of that species using a balance (Denver Instrument, Bohemia, New York, USA) and then dividing that mass by 50 to get an average mass per seed.

<table>
<thead>
<tr>
<th>Species</th>
<th>Code</th>
<th>Common name</th>
<th>Status</th>
<th>Average seed mass (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bromus rubens</em> L.</td>
<td>BRRU</td>
<td>Red brome</td>
<td>Invasive</td>
<td>1.80</td>
</tr>
<tr>
<td><em>Bromus tectorum</em> L.</td>
<td>BRTE</td>
<td>Cheatgrass</td>
<td>Invasive</td>
<td>3.24</td>
</tr>
<tr>
<td><em>Erodium circutarium</em> L.</td>
<td>ERCI</td>
<td>Redstem stork's bill</td>
<td>Invasive</td>
<td>1.75</td>
</tr>
<tr>
<td><em>Ambrosia dumosa</em> (A. Gray) Payne</td>
<td>AMDU</td>
<td>White bursage</td>
<td>Native</td>
<td>5.31</td>
</tr>
<tr>
<td><em>Baileya multiradiata</em> Harv. &amp; A. Gray ex A. Gray</td>
<td>BAMU</td>
<td>Desert marigold</td>
<td>Native</td>
<td>6.66</td>
</tr>
<tr>
<td><em>Coleogyne ramosissima</em> Torr.</td>
<td>CORA</td>
<td>Blackbrush</td>
<td>Native</td>
<td>17.0</td>
</tr>
<tr>
<td><em>Larrea tridentata</em> (DC.) Coville</td>
<td>LATR</td>
<td>Creosote</td>
<td>Native</td>
<td>5.38</td>
</tr>
<tr>
<td><em>Sphaeralcea ambigua</em> A. Gray</td>
<td>SPAM</td>
<td>Desert globemallow</td>
<td>Native</td>
<td>0.87</td>
</tr>
<tr>
<td><em>Krascheninnikovia lanata</em> (Pursh) A. Meeuse &amp; Smit</td>
<td>KRLA</td>
<td>Winterfat</td>
<td>Native</td>
<td>3.36</td>
</tr>
<tr>
<td><em>Yucca brevifolia</em> Engelm.</td>
<td>YUBR</td>
<td>Joshua tree</td>
<td>Native</td>
<td>78.6</td>
</tr>
</tbody>
</table>

### Table 3.2: The main and interactive effects of rodents, fire, and time in the field on the percentage of seeds left remaining in dishes during our seed fate experiment in the summer of 2018 averaged across all species used. For graphical representation of data see figure 3.2.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>df</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rodents</td>
<td>1, 1167</td>
<td>796</td>
<td>$&lt; 0.0001$</td>
</tr>
<tr>
<td>Fire</td>
<td>1, 1167</td>
<td>0.97</td>
<td>0.32</td>
</tr>
<tr>
<td>Time in</td>
<td>3, 1167</td>
<td>98</td>
<td>$&lt; 0.0001$</td>
</tr>
<tr>
<td>R x T</td>
<td>3, 1167</td>
<td>35</td>
<td>$&lt; 0.0001$</td>
</tr>
<tr>
<td>R x F</td>
<td>1, 1167</td>
<td>0.29</td>
<td>0.59</td>
</tr>
<tr>
<td>F x T</td>
<td>3, 1167</td>
<td>0.93</td>
<td>0.42</td>
</tr>
<tr>
<td>R x F x T</td>
<td>3, 1167</td>
<td>0.45</td>
<td>0.72</td>
</tr>
</tbody>
</table>
Table 3.3: The main and interactive effects of rodent exclusion and burn on the percentage of seeds left remaining in the dishes, after being left seven days in the field, of individual seed species that were used in our experiment in the summer of 2018.

<table>
<thead>
<tr>
<th>Species</th>
<th>Status</th>
<th>RODENTS</th>
<th>BURN</th>
<th>RODENTS x BURN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Status</td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>BRRU</td>
<td>Invasive</td>
<td>68</td>
<td>&lt; 0.001</td>
<td>1.52</td>
</tr>
<tr>
<td>BRTE</td>
<td>Invasive</td>
<td>286</td>
<td>&lt; 0.001</td>
<td>0.72</td>
</tr>
<tr>
<td>ERCI</td>
<td>Invasive</td>
<td>59</td>
<td>&lt; 0.001</td>
<td>1.99</td>
</tr>
<tr>
<td>AMDU</td>
<td>Native</td>
<td>6.11</td>
<td>0.02</td>
<td>0.65</td>
</tr>
<tr>
<td>BAMU</td>
<td>Native</td>
<td>31</td>
<td>&lt; 0.001</td>
<td>1.13</td>
</tr>
<tr>
<td>CORA</td>
<td>Native</td>
<td>12</td>
<td>0.002</td>
<td>1.34</td>
</tr>
<tr>
<td>LATR</td>
<td>Native</td>
<td>100</td>
<td>&lt; 0.001</td>
<td>0.12</td>
</tr>
<tr>
<td>SPAM</td>
<td>Native</td>
<td>3.72</td>
<td>0.07</td>
<td>0.79</td>
</tr>
<tr>
<td>KRLA</td>
<td>Native</td>
<td>55</td>
<td>&lt; 0.001</td>
<td>0.38</td>
</tr>
<tr>
<td>YUBR</td>
<td>Native</td>
<td>9.21</td>
<td>0.006</td>
<td>0.97</td>
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</table>