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Factors Underlying Invasive Grass Fire Regimes in the Mojave Desert and its Consequences on Plant and Animal Communities

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ABSTRACT

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Climate change and exotic plant invasions are significant anthropogenic threats to desert community structure and resilience . In the Mojave Desert, the invasive grass red brome (*Bromus rubens* L) is increasing fire frequency and extent in response to climatic factors. The resilience of this ecosystem will be affected by how plant and animal communities respond to fire. To better understand these dynamics, we studied the environmental factors underlying changes in invasive grass fire regimes in the Mojave Desert and its structural and functional effects on plant and animal communities.

Following fire, reestablishment of native vegetation can be preempted by repeated burning associated with the abundant exotic grass red brome. Red brome density is correlated with various climate and landscape variables, but to establish causality, we experimentally assessed germination and growth of red brome. Red brome responded positively to fall precipitation, finer-textured soils, fertile-islands soils, and soils from burned landscapes. Red brome germination is maximized in wet fall periods when adequate water and optimal temperatures overlap . To evaluate landscape responses of pre- and post-fire plant communities and the potential for repeated burning we analyzed vegetation greenness (NDVI) data from 1985-2011 in response to temperature and precipitation. Landscape analysis indicated that the dominance of exotic grasses increases on post-fire landscapes. Following wet fall and winter seasons, high red brome productivity increases fire potential. Without mitigation, the establishment of an invasive-plant-driven fire regime is likely and may drive state transitions from arid shrublands to arid annual grasslands.

Potential revegetation of post-fire landscapes will depend at least in part upon the physiological response of surviving vegetation to post-fire landscapes. Plant physiological responses to post-fire landscapes were generally neutral or positive, suggesting that revegetation of post-fire landscapes is not precluded by resource loss associated with fire and may even be enhanced by post-fire conditions. This will likely translate to increased reproductive potential of surviving plants.

Alterations to small mammal populations will likely play a role in the reestablishment of vegetation (both native and exotics) as small mammals have strong top-down effects in arid ecosystems. Diversity and species richness responded negatively to burned landscapes as Merriam's kangaroo rat (*Dipodomys merriami*) increased in abundance while other species practically disappeared from burned landscapes. Merriam's kangaroo rat affects propagule sources through direct consumption, and seed dispersal. Increases in abundance and dominance of Merriam's kangaroo rat will likely alter plant recruitment.

Keywords: kangaroo rat, top-down effects, invasive-grass fire regime, bottom-up effects, fire, microhabitat, Mojave Desert, blackbrush, Joshua tree, creosote bush

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Chapter 1: Germination responses to temperature and moisture to predict temporal and spatial distributions of the invasive grass red brome and fire

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Chapter 1: Abstract

Exotic grass invasions have led to novel disturbance regimes across Earth's biomes. The annual grasses red brome (*Bromus rubens* L.) and cheatgrass (*Bromus tectorum* L.) are associated with shortened fire-return intervals and increased fire extent in the Great Basin and Mojave Desert of North America. Invasion success of these exotic grasses appears to be influenced in part by germination responses to climate fluctuations. Understanding how climate conditions influences germination characteristics of the exotic grasses is key in predicting red bromes invasion success and subsequent fire potential in the Mojave Desert. Herein we characterize germination of a red brome population through hydrothermal-time modeling. The hydrothermal-time requirements were then matched with historic climate data to estimate periods of maximal red brome germination and whether it was positively associated with fire. The optimal temperature for germination of a population of red brome was 19.6 °C with a hydrothermal-time constant of 44.5 MPa*°C*days and a mean base water potential of -1.31 MPa. This suggest that early fall precipitation events when temperatures are optimal for germination maximize red brome germination potential. The largest fire events occurred in summer 2005 and were preceded by optimal germination conditions in October of 2004. Climate models predicted intensification of fall and winter precipitation events that will likely drive further increases in red brome abundance and subsequently further increase widespread fire in the Mojave Desert.

Chapter 1: Introduction

Invasion of exotic plants can fundamentally alter plant communities by competing for resources and altering disturbance regimes (Chapin III et al. 2000). In arid ecosystems the invasion of exotic grasses is associated changing fire regimes (D'Antonio and Vitousek 1992). Exotic grasses produce continuous fine fuels which can carry fire from shrub to shrub enlarging the spatial extent and increasing temporal frequency of fires (Brooks 1999, D'Antonio and Vitousek 1992). Emergence of an invasive grass fire cycles in arid shrublands is of great concern as many desert plant species are not adapted to fire, but exotic grasses tend to respond positively to fire, which may drive the transition of desert shublands to exotic grasslands (Callison et al. 1985, Zouhar et al. 2008, Vamstad and Rotenberry 2010, Engel and Abella 2011, Brooks 2012). Due to the extent that invasive grasses negatively impact the structure and productivity of arid shrublands through fire, understanding the drivers of exotic grass expansion is critical for mitigation efforts.

The annual grasses, red brome (*Bromus rubens* L.) and cheatgrass (*Bromus tectorum* L.) have invaded vast areas of western North America (Reid et al. 2008). Success of *Bromus* spp. invasion is driven by functional strategies that include rapid growth rates, drought avoidance, high propagule pressure, positive responses to disturbance including fire (Wu and Jain, 1979) and low moisture requirements for germination (Beatley 1966; Salo 2004). This is in contrast to the native vegetation which generally has slow growth rates, are drought resistant, have low resilience to fire (Angert et al., 2007), and have specific germination requirements (Wallace 1972, Reynolds et al. 2012). The presence of these exotic grasses can reduce fire return intervals

in the Mojave and Great Basin Deserts from centuries to less than a decades and dramatically increased fire size (Brooks et al., 2004; Reid et al., 2008; Brooks, 2012).

The growth and expansion of red brome and cheatgrass is strongly controlled by climatic conditions (Salo 2005, Chambers et al. 2007, Reid et al. 2008) that are highly variable in arid and semi-arid deserts (Hereford et al. 2006, Snyder and Tartowski 2006). Historically, expansions of red brome have coincided with 'warm' PDO (Pacific Decadal Oscillation) regimes and future expansions may be influenced by anthropogenic changes to global climate patterns (Loik et al. 2004; Salo 2005). As a result of its evolutionary history in the Mediterranean region, growth of red brome is strongly responsive to fall and winter precipitation patterns (Salo 2004, 2005). Specifically, fall precipitation events, which are associated with El Nino Southern Oscillation (ENSO) cycles, are positively associated with relatively high abundances of red brome (Beatley, 1976; Abella et al., 2012). Early fall precipitation events may promote brome germination (Abella et al. 2012) since summer and winter temperatures extremes may inhibit seed germination (Alvarado and Bradford 2002).

Germination can be restricted by high temperatures (Alvarado and Bradford 2002). Sensitivity to high temperatures prevents seeds from germinating during the summer season when precipitation arrives stochastically and soil moisture does not persist (Huxman et al. 2004, Potts et al. 2006). Additionally, summer temperatures are also necessary to overcome primary dormancy referred to as thermal after-ripening (Bradford 2002, Meyer and Allen 2009). Prolonged exposure to high temperatures gradually decrease the level of dormancy in seeds of *Bromus* species by decreasing sensitivity to temperature and increasing sensitivity to available moisture (Allen et al. 1995). In the field, thermal after-ripening occurs during the summer

months; priming the seeds to germinate when moisture arrives in the fall or winter (Meyer and Allen 2009).

The interplay between temperature and surface soil moisture are the primary drivers for seed germination in many species and can be described using hydrothermal-time models (Gummerson 1986). Investigation of germination characteristics using hydrothermal-time models has led to accurate predictions of germination in the field of onions, carrots (Rowse and Finch-Savage 2003), and cheatgrass (Roundy et al. 2007). In turn, being able to predict large germination events can be useful in predicting invasive grass expansion, and in mitigating invasive-grass fire cycles. The germination requirements for red brome, an alien grass linked to increased fire in the Mojave Desert (Beatley, 1966; Brooks, 1999; Hunter, 1991), can be used to predict germination under different climate scenarios and identify those scenarios that are likely to promote red brome growth and fire risk.

The objective of this study is to produce a hydrothermal-time model that accurately characterizes germination conditions for fully after-ripened seeds of red brome and identify regional climate factors that influence germination. We predict that red brome germination rates will be optimal at temperatures and water potentials observed during wet fall periods in the Mojave Desert. We examine whether fires that have occurred in this region were preceded by favorable conditions for red brome germination as defined by the hydrothermal-time model.

Chapter 1: Methods

Chapter 1: Site description

The Beaver Dam Wash (37.15°N, 114.01°W) is located in the northeastern corner of the Mojave Desert. The Mojave Desert is classified as a warm desert and receives most of its precipitation in the winter. Vegetation is typical of Mojave Desert mid-elevation (~1000 m) shrubland dominated by creosote bush (*Larrea tridentata* (DC) Cov.), blackbrush (*Coleogyne ramosissima* Torr.), and white bursage (*Ambrosia dumosa* (A. Gray) Payne) with frequent Joshua trees (*Yucca brevifolia* (Engelm.)). The exotic annuals, red brome (*Bromus rubens*) and red-stem filaree (*Erodium cicutarium* (L.) L'Hér. ex Aiton) are ubiquitous on the landscape. The region has experienced several fires since 1984, but the fires of 2005 burned more area than all previous fires combined (Brooks and Matchett 2006).

Seed collection and incubation

Mature and senescent red brome stems with attached seeds were collected from Beaver Dam Wash in May of 2011. Seeds were stored at room temperature until October at which time they were stripped from stems and counted. Seeds were then incubated at 40°C for 48 hours. Subsequent germination indicated that the seeds had lost their dormancy.

To observe germination responses in red brome, twenty five seeds were incubated in petri dishes on germination paper (Anchor Paper, St. Paul, MN) under a factorial combination of five different water potentials (0.0, -0.5, -1.0, -1.5, and -2.0 MPa) and six different temperatures (0, 5, 10, 20, 25, 30°C) replicated four times. Water potentials were obtained using various concentrations of polyethylene glycol (PEG 8000 Sigma Aldrich) based on the equation of

Michel and Kaufman (1973) including corrections for temperatures. Germination paper was saturated in concentrations of PEG specific to water potential and temperature combinations. Petri dishes were placed in stacks by temperature treatment and enclosed in a clear plastic bag with a moist paper towel at the top and bottom of each stack to prevent evaporation (Christensen et al. 1996). Stacks were slightly tilted to prevent pooling of PEG solution around seeds. Temperatures were maintained with 12/12 h light cycles in 818 Low Temperature Illumination Incubators (Precision Scientific). Germinated seeds were counted at days 1, 2, 4, 7, 11, 14, 21, and 28 then removed from blotters.

Hydrothermal-time modeling

We used hydrothermal-time models to characterize germination requirements of a population of red brome. A population of seeds will progress towards germination by accumulating time ($t_{(g)}$) at temperatures (T) and water potentials (ψ) above a base temperature (T_b) and base water potential ($\psi_{b(g)}$) (Gummerson 1986) that are specific to the population and dormancy condition (Beckstead et al. 1996). The required amount of time spent above base temperature and water potential is called hydrothermal-time (θ_{HT}) and is a constant value for each population of seeds (eq. 1).

$$\theta_{HT} = \left(\psi - \psi_{b(g)}\right)\left(T - T_b\right)t_{(g)} \qquad \text{eq. 1}$$

As both temperature and soil moisture increase beyond minimum values, the rate of germination ($t_{(g)}^{-1}$), and fraction of germinated seeds (g), also increase until the optimal temperature (T_o) for germination is reached (Gummerson 1986). Above the optimal temperature (T_o) the rate of germination decreases and the base water potential ($\psi_{b(g)}$ - the lowest water potential for germination) increases until reaching zero (eq. 2) (Alvarado and Bradford 2002).

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$$\theta_{HT} = \left[\psi - \left(\psi_{b(g)} + k_t \left(T - T_o \right) \right) \right] \left(T_o - T_b \right) t_{(g)}$$ eq. 2

Where k_T is the coefficient for the linear increase in base water potential with temperature. The

temperature at which the base water potential ($\psi_{b(g)}$) equals zero is known as the critical

temperature ($T_{c(g)}$), above which germination will not proceed. The values for base water

potential vary with population fraction and are normally distributed about a mean base water

potential ($\psi_{b(50)}$) whose standard deviation is denoted by $\sigma_{\psi b}$.

To calculate the hydrothermal-time parameters (θ_{HT}, k_T, T_o, T_b, $\psi_{b(50)}$, and $\sigma_{\psi b}$) for red

brome we used repeated linear regression after the methods of Christensen et al. (1996). The

inverse cumulative distribution of the germination fraction (PROBIT[g]) is linearly related to the

distribution of the base water potentials (eq. 3).

$$\text{PROBIT}(g) = m\psi_{b(g)} + b$$ eq. 3

where

$$\psi_{b(50)} = \frac{-b}{m}$$ eq. 4

and

$$\sigma_{\psi b} = \frac{1}{m}$$ eq. 5

Substituting in the full hydrothermal-time equation for $\psi_{b(g)}$ we are able to determine the base

water potential ($\psi_{b(g)}$) across both sub-optimal (eq.6) and supra-optimal (eq.7) temperatures.

$$\text{PROBIT}(g) = m \left(\psi - \frac{\theta_{HT}}{\left(T - T_b \right) t_{(g)}} \right) + b$$ eq. 6

$$\text{PROBIT}(g) = m \left(\psi - k_t \left(T - T_o \right) - \frac{\theta_{HT}}{\left(T_o - T_b \right) t_{(g)}} \right) + b$$ eq. 7

Optimal R^2 values were obtained by manually substituting in values for θ_{HT}, k_T, T_o, and T_b within a spreadsheet application. Input data consisted of data points that had germination fractions greater than 0.05 and less than 0.96.

Climate and fire analysis

To assess climate conditions for optimal germination at Beaver Dam Wash 23 years of temperature data was summarized to means, maxima, and minima by month and precipitation to totals and means for each month. Climate data was measured at Badger Springs meteorological station (BADU1 37.1506° N, 113.9539° W, elev: 1216 m) and Brigham Young University's Lytle Ranch Preserve and obtained from University of Utah MesoWest station interface (mesowest.utah.edu). Historic fire boundaries were obtained from Monitoring Trend in Burn Severity on-line database (Eidenshink et al. 2007).

Chapter 1: Results

Germination responses

Germination rates appeared to increase above 0 °C, decline above 20 °C, and responded positively to high water potentials. Seeds incubated at 20 °C / 0 MPa germinated quickest showing 45% germination by day 2 with all seeds having germinated by day 4 (Fig. 1). For the 10 °C / 0 MPa treatment conditions, 100% germination was also achieved by day four but no seeds had germinated until after day 2. Complete germination was reached under four other treatments conditions (5 °C / 0 MPa, 5 °C / -0.5 MPa, 10 °C / -0.5 MPa, and 20 °C / -0.5 MPa) but required significantly more time (between days 14 and 28). Temperatures above 20 °C

regardless of water potential resulted in both prolonged and partial germination. At 30 °C no germination occurred below -0.5 MPa and never achieved more than 60% germination at 0 MPa. All treatments below -0.5 MPa never reached 100% germination within the 28 day period for all temperatures. Only four seeds germinated at the lowest water potential tested (-2 MPa). No seeds germinated at 0 °C.

Hydrothermal parameters

The most accurate hydrothermal-time model accounted for 83% of the variation observed in the rate of germination and fraction of germinated seeds (Table 1). The hydrothermal-time requirement (θ_{HT}) for this population of red brome was 44.5 °C*MPa*days. Germination progressed towards the hydrothermal-time requirement at temperatures above 0 °C (T_b). Rate of germination increased until reaching the optimal temperature (T_o) of 19.6 °C (Fig. 2 and 3). Above T_o germination rate declined towards critical temperatures ($T_{c(g)}$) at which progress towards germination ceased. Mean base water potential ($\psi_{b(50)}$) increased from -1.31 MPa at temperatures above T_o at a rate (k_T) of 0.12 MPa °C^{-1} until reaching 0 MPa at the mean critical temperature ($T_{c(50)}$) of 30.8 °C. Standard deviation of the base water potential ($\sigma_{\psi b}$) was 0.41 MPa.

Beaver Dam Wash climate data

Average monthly temperature in Beaver Dam Wash, where the seeds were collected, was normally distributed while precipitation was skewed and highly variable. Mean monthly minimum and mean monthly maximum temperatures ranged from -11.7 °C in January to 45 °C in August (Fig. 4). The majority of precipitation received was between the months of October

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through April but was inconsistent from year to year (Fig. 4). The optimal temperature (T_o) for red brome germination was reached in the months of October and April (Fig. 4). However, the mean critical temperature ($T_{c(50)}$) was exceeded from April to October. Average precipitation level did not exceeded 5 cm month^{-1}; however, individual months within the past 23 years have accumulated as much as 21 cm precipitation (Dec. 2010). Winter precipitation (Oct.-Apr.) accounted for 75% of the precipitation received. October of 2004 exceeded 13 cm of precipitation for the month; twice the amount received in any other year.

Chapter 1: Discussion

The observed germination responses (Fig. 1), and derived hydrothermal-time model (Table 1 and Fig. 2 and 3), indicated that red brome germination is maximized when 1) appreciable moisture is received; 2) at times when maximum temperatures do not exceed mean critical temperature ($T_{c(50)}$); and 3) as daily temperature averages near the optimal temperature (T_o) for germination. For the northeast region of the Mojave Desert, the temperature requirements are met during the months of April and October (Fig. 4). Both October and April have mean temperatures around the optimal temperature (T_o) and mean maximum temperatures less than the mean critical temperature ($T_{c(50)}$; Fig. 4). However, in April, seeds in the seedbank from the previous spring are mostly non-viable (Jurand et al. 2013) and red brome plants from the current year are not likely to have senesced and shattered seeds (personal observation). Any seeds that have recently shattered would likely have a high degree of dormancy (Corbineau et al. 1992, Finch-Savage and Leubner-Metzger 2006). Requirements for dormancy and germination indicate October as the most favorable month in the northeastern region of the Mojave Desert for

successful germination pending precipitation. Temperature requirements for germination vary across regions and seed populations since successful invaders of other regions would have been selected by local climate conditions, and other biotic and abiotic factors (Beckstead et al. 1996, Scott et al. 2010).

Germination requirements of red brome indicate that wet fall periods can promote high densities. The large fires of 2005 were preceded by the wettest October on record; exceeding any other year by twice the amount (Fig. 4). The probability of all viable red brome seeds germinating in response to the October 2004 precipitation pulses would have been high (Salo 2004). A 28 year time series of satellite images of the northeast Mojave revealed vegetation greenness was the most intense in spring of 2005 and red brome was likely a principal component of the vegetation (Horn, unpublished data). October 2010, the second wettest October recorded, also produced increased vegetation greenness and high red brome abundance on the landscape (Horn, unpublished data and personal observation). In June 2011 the abundance of dried red brome on the landscape made possible experimental burns that would have easily spread uninhibited if measures had not been taken to control it (St. Clair, personal observation).

Germination responses of red brome show that seeds can germination under a wide range of temperatures (Fig. 1); however, when germination rates are not maximized (at sub- and supra-optimal temperatures) neither are the odds for germinated plants to survive. One of the risks of germinating at sub-optimal temperatures during the late fall and winter is an increased chance of pathogen infection due to slower germination rates (Beckstead et al. 2007). Slower germination rates also occur at supra-optimal temperatures and prevent precocious germination when soil

moisture would typically be insufficient to sustain developing seedlings (Huxman et al. 2004, Potts et al. 2006).

Variability observed in germination requirements (Fig. 1) has important ecological consequences as plant populations respond to variation in inter-annual precipitation. Red brome does not reliably maintain an appreciable seedbank for more than a year (Jurand et al. 2013; Salo 2004); thus successive populations of red brome are largely dependent on viable seed production from the previous growing season. However, optimal conditions for germination and subsequent growth may not exist for extended periods of time due to the high inter-annual variability in precipitation (Hereford et al. 2006). Seeds that do germinate at non-optimal conditions, when temperature exceeds or is below the optimal temperature (T_o) (see Fig. 1), potentially generate propagules for the next generation but do so at increased risk of pathogen infection and insufficient moisture for seedling development (Salo 2004, Meyer et al. 2010). Even with the increased risk of plant mortality some plants will potentially reach maturity and set seed. Thus, in the event optimal conditions for germination are not reached during the year, variability in germination increases the odds that the presence of red brome may be maintained on the landscape.

Invading grasses experience strong selection pressures on germination traits. Populations of exotic grasses invade and undergo further selection in part by how germination characteristics respond to local environmental conditions (Beckstead et al. 1996). This selection is not only evident at the species level, where genotypes of cheatgrass are specific to different invaded regions (Scott et al. 2010), but is also demonstrated in niche sorting across the *Bromus* genus. The northern extent of red brome overlaps the southern extent of cheatgrass and coincides with

the boundary between the 'cool' Great Basin Desert and the 'warm' Mojave Desert in western

North America (Beatley 1966). The germination requirements of each species generally reflects

the climate conditions of the environments they have invaded. Specifically, red brome from the

Mojave had a lower mean base water potential ($\psi_{b(50)}$; Fig. 2 and Table 1; -1.3 vs -0.81 to

-1.27 MPa) and lower germination rate (t^{-1}; Fig. 2) than cheatgrass populations from the Great

Basin (Bauer et al. 1998, Bair et al. 2006, Meyer and Allen 2009). Lower mean base water

potential of red brome indicates that this population of red brome is capable of germination in

more arid conditions than cheatgrass populations reported in Meyer and Allen (2009). Higher

germination rates for cheatgrass means it is capable of germinating at the same rate as red brome

but does so at a lower temperature (Great Basin vs. Mojave). Environmental selection, based in

part on the different germination rates and base water potentials characteristics between red

brome and cheatgrass, has likely led to the current distribution of these *Bromus* species at the

boundaries of the Mojave and Great Basin deserts (Beatley 1966, Reid et al. 2008).(Reid et al.

2008)

Recent increases in widespread desert fire appear to result from a combination of plant

invasion and climate patterns (Abella et al. 2012; Brooks and Chambers 2011; Hereford et al.

2006). Early fall and sustained winter precipitation generated favorable moisture conditions for

germination and growth of exotic grasses (Fig. 4). Germination response of red brome in

particular is highly responsive to early fall precipitation events which help to maximize

abundance of red brome on the landscape (Abella et al. 2012); Horn et al., unpublished data).

Early fall rain events occur when temperatures are optimal for red brome germination (Fig. 2)

and pending sufficient moisture nearly all viable seeds are likely to germinate (Fig. 1). However,

fall and winter precipitation has fluctuated widely from year to year where some months received little to no precipitation (Fig. 4).

Predicted changes in climate will likely favor increased germination and growth in red brome. Climate models for southwestern North America predict an increase of intense fall and winter precipitation events followed by increases in drought duration and intensity (IPCC 2007, Jentsch and Beierkuhnlein 2008). Based on our data, greater fall precipitation will increase the proportion of red brome seed that germinate (Fig. 1 and 2) as fall temperatures maximize germination rates (Fig. 4). Increased average temperature with climate warming, will likely shift the timing of germination with temperature as germination is temperature dependent (Fig. 2). This will likely have cascading effect on red brome abundance and extent as more seed is produced. Years of drought on the other hand could result in population crashes (Salo 2004).

Increased germination in red brome can result in larger and more frequent fires for the Mojave Desert. The spatial extent of fires will likely fluctuate as populations of red brome germinate and grow in response to the fluctuating climate (Agnew 1997, Westerling et al. 2003). Years of intense fall and winter rainfall will maximize germination and growth of red brome. This will allow the exotic grass to fill shrub interspaces with fine fuels to carry fire greater distances (Brooks 1999, Brooks et al. 2004).

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Chapter 1: Tables

Table 1. Hydrothermal-time parameters for germination of a red brome population

parameter	value
hydrothermal time θ_{HT}	44.5 °C MPa days
base temperature T_b	0.0 °C
optimal temperature T_o	19.6 °C
mean critical temperature $T_{c(50)}$	30.8 °C
mean base water potential $\psi_{b(50)}$	-1.31 MPa
standard deviation of mean base water potential $\sigma_{\psi b}$	0.41 MPa
supra-optimal temperature coefficient k_T	0.12 MPa °C^{-1}
r^2	0.83

Chapter 1: Figures
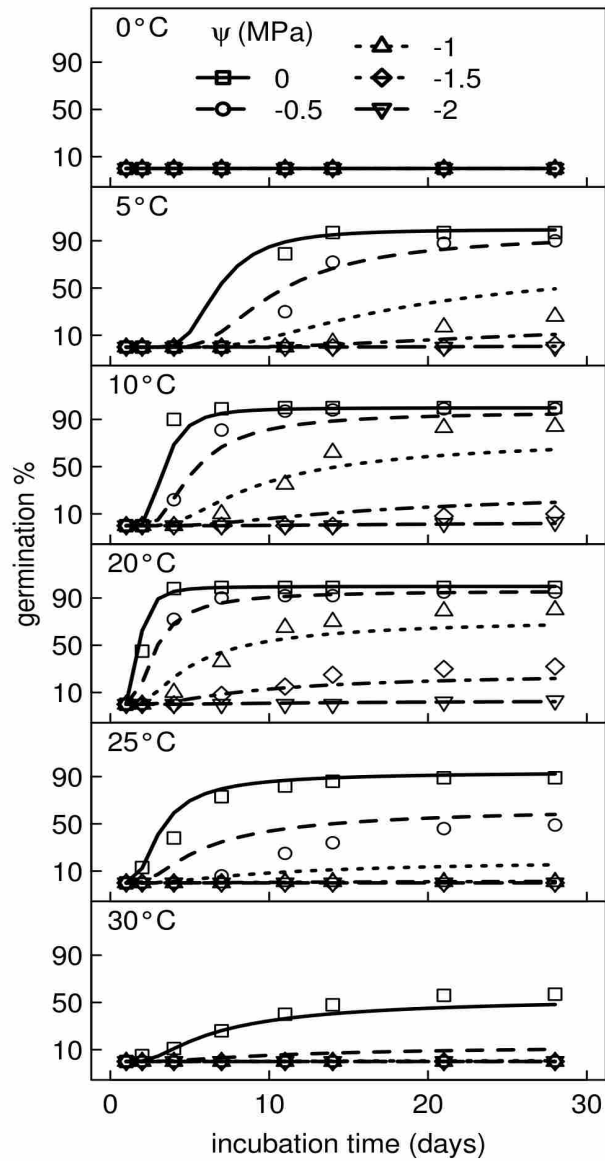
Fig. 1. Germination time courses for a red brome population at 0, 5, 10, 20, 25, and 30 °C. Water potentials shown are 0.0 (solid line, squares), -0.5 (short dashed line, circles), -1.0 (dotted line, triangles), -1.5 (dashed and dotted line, diamonds), and -2.0 MPa (long dashed line, inverted triangles). Modeled time courses are represented as lines with observed means as points.
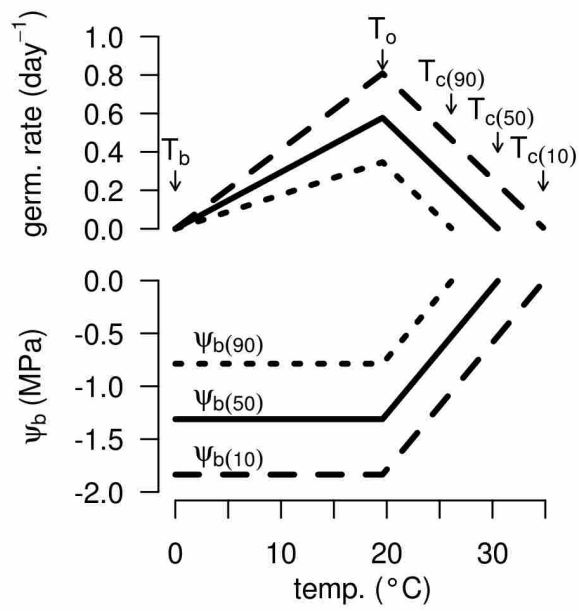
Fig. 2. Germination rates and base water potentials for the 10th, 50th, and 90th percentile of a red brome population. Base (T_b), optimal (T_o), and critical ($T_{c(g)}$) temperatures are denoted with arrows.
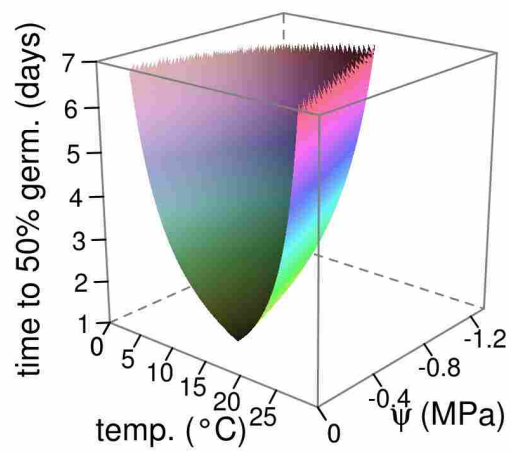
Fig. 3. Time to 50% germination for red brome population in response to temperature and available moisture
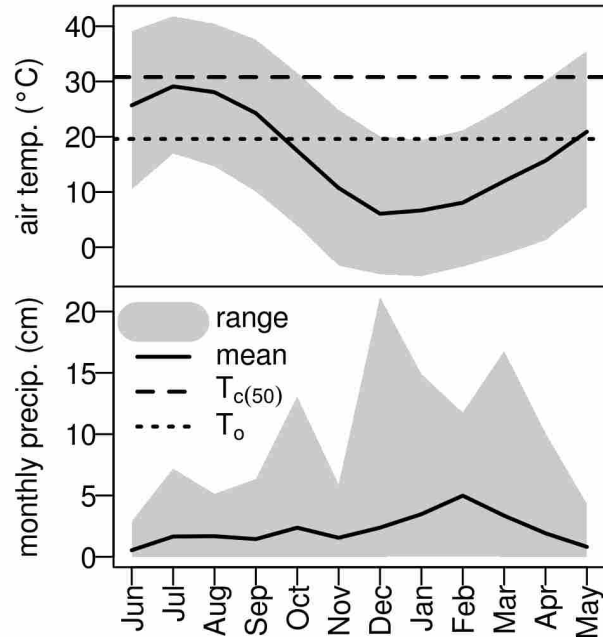
Fig. 4. Monthly range and means for temperature and precipitation for the growing season (June-May) at Beaver Dam Wash between 1989 and 2012. Optimal (T_o - dotted line) and mean critical ($T_{c(50)}$ - dashed line) temperatures for a red brome population are indicated.

Chapter 2: Temporal and spatial distributions of exotic invasive grasses in arid shrublands are controlled by precipitation timing, soil heterogeneity, and fire history

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Chapter 2: Abstract

Invasions of exotic grasses are increasing the spatial extent and temporal frequency of fire. Effective mitigation efforts to prevent further fire and improve restoration efforts depends on understanding the biophysical agents that drive spatial and temporal distributions of exotic grasses.

We examined seedling emergence, growth, and reproduction of the exotic grass red brome based on three different soil factors (soil texture, fertile-island topography, and burn history) and precipitation timing in a full-factorial experiment. Seedling emergence, biomass, stem and root lengths, inflorescence, and seed production were measured.

Red brome had greater seedling emergence, biomass, height, inflorescence, and seed production on soils that were finer-textured and from fertile-islands. Plants grown on fire-affected soils had greater seed production, plant height, and shoot biomass. Early fall precipitation advanced the time of stem growth and flowering and increased the number of emerged seedlings and seeds produced.

This data in conjunction with climate forecasting and soil and vegetation maps can be used to identify areas with high potential for red brome growth for fire mitigation planning. Our data suggests that areas with finer-textured soil will be more prone to high red brome density and biomass particularly in years with significant fall moisture. Coarser-textured soils are at less risk of burning due to lower abundance and growth potential of exotic grasses and may create natural fire breaks providing refugia for native woody plants. Fertile islands soils in both unburned and burned areas support higher densities of red brome and increase seed production that likely contributes to the expansion of red brome populations. Management planning for fire

intervention should consider early-fall precipitation patterns, soil texture and fire history as important determinants of red brome growth and fire potential..

Key-words: ecosystem transition, fire regime, invasive species, Mojave, red brome, novel disturbance,

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Chapter 2: Introduction

The introduction of non-native species to new ecosystems has been one of the most significant anthropogenic alterations on planet earth (Vitousek et al. 1997). Introduced species, alter biogeochemical cycles, reduce native biological diversity and negatively impact human finances and health (Vitousek et al. 1997). Among the most widespread and ecologically problematic invasions is the introduction and expansion of exotic grasses in arid ecosystems (D'Antonio and Vitousek 1992, Reid et al. 2008).

The major deserts of North America are heavily invaded by the exotic grasses red brome (*Bromus rubens* L.) and cheatgrass (*Bromus tectorum* L.) (Beatley 1966, D'Antonio and Vitousek 1992, Salo 2005, Reid et al. 2008). These Mediterranean species are associated with increased fire extent and frequency in the Great Basin and Mojave Deserts (Brooks 1999a, Brooks et al. 2004, Bukowski and Baker 2012). Exotic grasses often fill the interspaces between the shrubs creating a continuous fuel load that can cause large-scale fire. By altering the disturbance regime these exotic grasses remove long-lived native species, which has cascading effects that degrade the structure and function of arid shrublands (Huenneke and Noble 1996). Many desert shrubs show limited resilience to fire due to prolonged and historically episodic recruitment of native perennials (Callison et al. 1985, Lei 1999, Haubensak et al. 2009). The loss of native perennial shrubs following fire is further exacerbated by the positive response exotic grasses have to burned landscapes that can lead to invasive grass fire cycles (Brooks and Berry 2006, Brooks 2012, Abella et al. 2012). There is concern that the emergence of invasive grass-fire regimes with more frequent fire may promote state changes in vegetation that can fundamentally alter functional interactions within the biological community with unknown

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ecological consequences. The ability of invasive grass-fire-regimes to transform entire landscapes makes understanding the mechanisms driving the growth and expansion exotic grasses a high priority for management intervention (Huenneke and Noble 1996, Vitousek et al. 1997, Rice et al. 2008).

Both the magnitude and distribution of precipitation are critical factors in the germination and growth potential of invasive grasses (Beatley 1974, Salo 2004). *Bromus* spp. typically germinate in fall and winter when temperatures are optimal for germination (Horn et al. unpublished data, (Beatley 1966, Roundy et al. 2007). However, Red brome does not undergo secondary dormancy as cheatgrass which results in more uniform germination in fall and winter seasons (Salo 2004). High productivity of *Bromus* spp. appear to be correlated with episodic wet periods associated with ENSO (El Niño–Southern Oscillation) and PDO (Pacific Decadal Oscillation) cycles in which optimal temperatures overlap with high moisture resulting in a longer growing season (Horn et al. unpublished data, (Mack and Pyke 1983, Salo 2004, Abella et al. 2012). Furthermore, future climate projections predict higher amounts of fall/winter precipitation, and greater frequency of extreme weather events in deserts of North America (Westerling et al. 2006, IPCC 2007). Lacking in scientific literature is a mechanistic understanding of how fall precipitation timing influences germination, growth and reproductive potential of exotic grasses and its potential for altering fire behavior. With the continued expansion of invasive plants across desert systems and impending shifts in precipitation and temperature with climate change, it is critical that we understand the influence of precipitation timing with greater precision.

Spatial distribution of exotic grasses are strongly controlled by soil properties that can be highly heterogeneous across desert landscapes (Schlesinger and Pilmanis 1998, Brooks 2009, Miller et al. 2009). Through its influence on water and nutrient availability, soil texture strongly influences plant function and plant community development in deserts (Noy-Meir 1973, Schlesinger and Pilmanis 1998, Austin et al. 2004). Exotic grasses tend to respond positively to increases in soil moisture and nutrients particularly nitrogen (Brooks and Berry 2006, Hunter and Omi 2006, Abella et al. 2011). Specifics of how soil texture affects the development and reproduction of red brome and its interactions with precipitation timing are not well characterized.

Soil resource availability in desert shrublands is spatially variable based on fertile-island topography created by shrubs (Schlesinger and Pilmanis 1998). Fertile-island topography is developed as shrub canopies enrich underlying soils with plant-accumulated organic matter, finer-textured soil, and improved moisture conditions through shading (Ewing et al. 2007). Many plants preferentially establish within fertile-islands beneath shrub canopies and exotic grasses are no exception (Brooks 1999b, Walker et al. 2001, Drezner 2006). Fertile-islands have substantially higher concentrations of nutrients than shrub interspaces which contribute to the positive associates with establishing plants (Brooks 1999a, 1999b). Disturbance such as fire can remove shrub canopies but legacy effects on soil can persist (Ravi and D'Odorico 2009). While it is generally understood that fertile islands have positive effects on plant establishment and growth, it is poorly understood how soil conditions in fertile islands affect red brome growth independent from shade effects.

Fire can have important influences on soil processes that feedback on plant growth. Brome densities tend to increase following fire (Shinneman and Baker 2009, Brooks 2012, Abella et al. 2012). Fire can increase plant available nutrients by modifying soil structure and texture through secondary effects such as increased erosion (Lei 1999, Esque et al. 2010, Allen et al. 2011). Additionally the removal of shrub canopies decreases competition for soil resources (Phillips and MacMahon 1981). However, the effects of fire on desert soil processes are inconsistent (Allen et al. 2011) and its feedbacks on exotic grass emergence, growth and reproduction are not well understood.

Our study was aimed at experimentally isolating biophysical variables and their interactions that influence the growth and reproduction potential of red brome. We examined growth and reproductive responses of red brome to precipitation timing (presence or absence of fall precipitation pulse) and soil heterogeneity (soil texture and fertile islands vs. interspaces) and burn history (soils from burned vs. unburned landscapes) in the northeast region of the Mojave Desert that has recently experienced widespread wildfires. We predict that: 1) early fall precipitation stimulates successful emergence of red brome seedlings; and 2) finer-textured soils, fertile-islands effects, and fire-disturbed soils will independently and additively increase red brome productivity and reproduction.

Chapter 2: Materials and methods

Site description and seed collection

The focus of this study was in the Beaver Dam Wash (37.15 °N, 114.01 °W) located in the northeastern region of the Mojave Desert. Soils are classified as a very gravely sandy loam

(Soil Survey Staff 2011). Vegetation is typical of mid-elevation (~1000 m) shrubland dominated by creosote bush (*Larrea tridentata* (DC) Cov.), blackbrush (*Coleogyne ramosissima* Torr.), and white bursage (*Ambrosia dumosa* (A. Gray) Payne) with frequent Joshua trees (*Yucca brevifolia* Engelm.). The exotic annuals red brome and red-stem filaree (*Erodium cicutarium* L.) are ubiquitous. The prevalence of red brome likely contributed to the 2005 fires which burned more area than all previous fires since 1984 (Horn et al. unpublished data, Brooks and Minnich 2006). From within one of the remaining unburned areas, mature and senescent red brome stems with mature seeds were collected in May 2011 and stored at room temperature until October at which time seeds were cleaned from stems and counted.

Experimental design

To test emergence, growth, and reproductive responses of red brome to precipitation timing and soil characteristics the experiment was randomized in a 2 x 2 x 2 x 2 full-factorial design with seven replicates per treatment combination. The factor combinations included presence or absences of a fall precipitation pulse (late October), two general soil textures (finer vs. coarser), fertile-island topography (fertile-island vs. interspace) and burn history (soils from recently burned landscapes vs. unburned landscapes). Sites chosen for soil collection were nested by characteristics based first on general soil texture, then (within soil texture) on burn history, and then (within burn history) on fertile-island topography. The finer-textured soils were located on the west side of Beaver Dam Wash (37.141 °N, 114.039 °W, 962 m) with the coarser-textured soils on the east side of Beaver Dam Wash (37.097 °N, 113.965 °W, 1061 m). On each side of the wash soil cores were collected from adjacent burned and unburned areas along burn

boundaries of two independent fires that occurred in the summer of 2005. Soil cores were collected from beneath current (unburned) or former (burned) creosote bush canopies and in adjacent interspaces.

Soil cores were extracted using PVC tubing (8.8 cm diameter, 17.6 cm length, and 2.75 mm thick). PVC cylinders were driven into the soil with a wooden block and a rubber mallet. Soil surrounding the cylinders was excavated and cores were retrieved with the soil column intact. The bottom of the cores were sealed with drain caps that had been drilled with three 6.3 mm diameter holes to allow water to drain.

To test the effects of an early fall precipitation pulse in combination with soil characteristics all cores were watered based on the relatively wet 2004-05 growing season (preceding the 2005 fires) (Fig. 1). The large precipitation pulse was applied October 24, 2011, two weeks before all soil cores were placed on the same watering schedule. This precipitation pulse saturated the soil cores resulting in a large portion of the water draining from the soil cores. Subsequent precipitation additions as little as 1 cm were observed to quickly drain from the soil cores as well. Rapid saturation of soil cores indicated low water holding capacity of the soils and the primary effect of the fall precipitation addition being timing of precipitation and not volume. Pots were then watered on the same schedule starting November 7th. Soil cores were watered by hand with perforated plastic cups to simulate rain. By January 9th the grasses were well established within the soil cores and watering was done by slowly pouring precipitation amount onto the soil without pitting the soil surface.

To control for temperature and precipitation intact soil cores were placed within a climate-controlled greenhouse (40.24 °N, 111.64 °W) at Brigham Young University in Provo

Utah on October 21, 2011 for growing red brome. Before adding red brome seeds any plants visibly growing within soil cores were carefully removed to maintain integrity of soil structure. In each pot 100 red brome seeds were placed on the soil surface prior to water treatments. Temperatures were set to mimic monthly maximum and minimum temperatures at Beaver Dam Wash that occurred in 2004-05 however temperatures were significantly higher in the greenhouse.

Growth measurements

To quantify the effects of precipitation timing and soil properties several metrics involving red brome growth and reproduction were taken. Fifty-nine days after initial watering the number of emerged plants were counted. Shoot height was measured weekly beginning in November along with number of flowing heads starting in January. The experiment was terminated on May 1, 2012, 190 days after initial watering. Average plant height was measured from the soil surface to mean height of all grasses and inflorescences were counted. The above ground plant biomass was then harvested, stored in paper sacks in greenhouse to dry for two weeks, and weighed. Seeds where then cleaned from the inflorescence, counted, and weighed. All count data and mass measurements were standardized against the surface area of the soil core (60.8 cm^2).

Root analysis

Once above-ground biomass was removed root systems were extracted from soil cores. Soil cores were placed in sieves and rinsed with water until roots were free from soil particles

and other debris. Clean roots were transferred to 50 ml conical tubes, suspended in 10% ethanol, and stored at 4 °C.

To obtain total root length, roots were imaged with WinRHIZO Pro V 2009c software (Regent Instruments Inc., Canada) coupled with a flatbed scanner (Epson Expression 10000XL, Epson America Inc., USA) and attached transparency unit. Prior to scanning, root bundles were spread out and flattened on a 30x40 cm transparent tray with a small volume of water to allow maximum separation and least overlap of roots. Of the 112 soil cores 54 were used for root analysis with a minimum of three from every combination of precipitation and soil factors. After roots were imaged all 112 root samples were dried at 60 °C for two days and measured for dry biomass.

Soils analysis

Soils from Beaver Dam Wash were analyzed for soil texture, organic carbon, and total nitrogen. Coarser-textured soils came from the east side (37.087 °N, 113.976 °W) of Beaver Dam Wash while finer-textured soils came from the west side (37.143 °N, 114.030 °W). Within each soil-texture area samples were then taken from beneath current and former creosote bush canopies and adjacent interspaces within burned and unburned areas. Gravel and larger aggregates were removed from soils prior to analysis. Total nitrogen of the soil was determined using a nitrogen analyzer (C and N Determinator, LECO Cooperation, St. Joseph, Michigan, USA). Organic matter was measured using the dichromate oxidation method (Walkley and Black 1934). Soil texture was determined using a hydrometer.

Chapter 2: Statistical analysis

Analysis of variance (ANOVA) was used to test the main effects and interactions of precipitation timing and soil factors on red brome responses. All effects of precipitation timing, general soil texture, fertile island topography, and burn history were treated as fixed effects. All response variables were normally distributed. Soil organic matter, total nitrogen and texture analysis were examined with a full-factorial two-way ANOVA. Statistics were performed in Program R version 2.14.1 (R Foundation for Statistical Computing, Vienna, Austria).

Chapter 2: Results

Soil organic matter, total nitrogen, and texture

Soil organic matter and nitrogen were greater on fertile island soils but did not differ with general soil texture or burn history (Table 1). Fertile-island soils had 100% more organic matter (OM) than interspace soils. Total N was three times more concentrated on fertile-island soils than interspaces soils.

Sand, silt, and clay components varied with general soil-texture and burn condition but not with fertile-island topography (Table 1). Finer-textured soils had 17% less sand and 54% more clay than coarser-textured soils. Silt content did not differ with general soil texture, fertile-island topography, or burn condition. Soils from burned areas averaged 7% less sand and 21% more clay than soils from unburned areas.

Summary of main effects of early fall precipitation pulse, soil texture, fertile-island topography, and fire-affected soils on plant emergence, growth and reproduction

All four main effects (early fall precipitation pulse, soil texture, fertile-island topography, and fire affected soils) significantly affected the growth and reproduction of red brome (Table2). Early fall precipitation increased seed production, seedling emergence, stem growth rates and hastened flowering. Soils that were finer-textured and soils from fertile-islands independently enhanced number of emerged seedlings and seeds produced. Finer-textured soils produced red brome with greater stem heights, number of stems, flowering heads, root length, and biomass of both roots and shoots. Fire-affected soils increased seeds produced, plant height, and shoot mass.

Seedling emergence and stem density

Early fall precipitation pulse, and finer-texture and fertile-island soils positively affected seedling emergence and stem densities. Fire-affected soils also had greater stem densities. Seedling emergence increased in response to early fall precipitation pulse (12%), finer soil texture (25%), and fertile-island soils (20%) but not fire-affected soils (Fig. 3*a*). Stem counts were greater with finer-textured (28%) and fertile-island (25%) soils but not with fire-affected soils or early fall precipitation (Table 4). Fertile-island soil resulted in greater stem counts on finer-textured soils but had no effect on stems counts on coarser-textured soils (soil-texture x fertile-island topography interaction) (Fig. 3*a*). Finer-textured soil increased stems on fire-affected soils but not on unburned soils (soil-texture x burn history interaction) (Fig. 3*b*)

Shoot growth

Soil texture, fertile-island soils, and fire-affected soils affected final shoot height but precipitation timing did not. Shoot height and mass responded positively to finer-textured, fertile-island, and fire-affected soils (Fig. 2 *b* and *c*). Early fall precipitation initiated early increases in plant height, but by mid December plants that had not received an October precipitation pulse were equal in height (Fig. 4*a*). Differences in height due to soil properties (texture, fertile-island, and fire-affected) increased as the growing season progressed (Fig. 4 *b*, *c*, and *d*). Final shoot height and mass was greater on finer-textured (13% and 33%), fertile-island (17% and 51%), and fire-affected (10% and 14%) soils (Fig. 2 *b* and *c*). Soils from fertile islands enhanced shoot height indpendent of soil texture. Shoot height was greatest on finer-textured soils from fertile islands and shortest on coarser textured soils from shrub interspaces (soil-texture x fertile-island topography interaction) (Fig. 5).

Root growth

Soil texture, fertile-island soils, and fire-affected soils impacted root growth. Roots were longer and had more mass on finer textured (32% and 46%) and fertile-island (18% and 17%) soils (Table 3). Fertile island topography did not affect root mass on soils that were fire-altered (Fig. 6*a*); however, soils from fertile-islands within burned areas did increased shoot mass (Fig. 6*b*) (burn condition x fertile-island topography interaction). This caused root:shoot ratios to be higher on interspace soils from burned areas (Fig. 6*c*).

Reproductive output

Inflorescence count and seed count increased in response to early fall precipitation, and finer-textured and fertile-island soils but not to fire-affected soils. While early fall precipitation did not increase the final number of flowing heads (Table 3) it did cause flowers to develop earlier (starting in January) (Fig. 7*a*). The difference in number of flowering heads increased between soil textures with more inflorescence on finer-textured soils (Fig. 7*b*). Similarly, more flowering head developed on fertile-island soils as the growing season progressed (Fig. 7*c*). Final number of flowering heads were greater on finer-textured (57%) and fertile-island (30%) soils (Table 3). Seeds numbers were greater with an early fall precipitation pulse (13%) and on finer-textured (47%), fertile-island (18%), and fire-affected (19%) soils (Fig. 2*d*).

Chapter 2: Discussion

The objective of this study was to identify biophysical agents that influence the growth and reproduction of red brome. We found that early fall precipitation promoted the growth and reproduction of red brome and advanced the timing of flowering and plant height (Table 2 and 3 and Fig. 2, 4 and 7). Growth and reproduction of red brome increased with soils that were finer-textured, from fertile-islands, and were fire-affected (Tables 2 and 3). Prior to this study, identification of factors influencing the temporal and spatial distributions of red brome were limited to observational studies (Brooks 2012, Abella et al. 2012). Early fall precipitation pulse did not alter red brome biomass (Tables 2 and 3) but did increase the reproductive output (Fig. 2*d*) and timing of flowering (Fig. 7*a*). The increased reproductive output will likely increase the number of red brome plants in successive generations (Salo 2004). The positive

influence that finer-textured and fertile-island soils had on red brome growth (Table 2) indicate

these as soil factors which are more likely to support higher densities of red brome and are

subsequently at increased fire risk (Brooks 1999a, 1999b). Lastly, increased height and biomass

of red brome in response to fire-affected soils (Fig. 2 *b* and *c*) would also increase the potential

for secondary fires and influence the persistence of an invasive-plant-driven fire regime (Brooks

et al. 2004, Brooks 2012).

Precipitation timing

The sensitivity of red brome to the timing of fall precipitation is likely driven by red

brome germination requirements. The simulated early fall precipitation pulse occurred only two

weeks prior to the standardized watering regime but was sufficient to initiate greater seedling

emergence (Fig. 2*a*), earlier flowering (Fig. 7*a*), and increased number of seeds produced

(Fig. 2*d*). Optimal temperatures for red brome germination (~20 °C) are reached in the early fall

(Horn et. al. unpublished data). Fall and winter precipitation events that could initiate red brome

germination are expected to increase even though a more arid climate is predicted for

southwestern North America (Thomson et al. 2005, IPCC 2007, Seager et al. 2007). This

increase in fall and winter precipitation events will likely further the spread and heighten

densities of red brome as it increases seed production (Fig. 2*d*).

Soil texture

Soil texture appears to be a dominant factor controlling the spatial distribution and

abundance of exotic grasses. On finer-textured soils red brome had greater number of emerged

seedlings (Fig. 2*a*), taller shoots (Fig. 5*a*), more roots and stems (Table 3 and Fig. 2*c*) and reproductive output (Fig. 2*d* and 7) than on coarser-textured soils. The positive response of red brome to finer-textured soils is likely the result of greater available nutrients and most importantly, accessible water (Noy-Meir 1973, Austin et al. 2004). However, nutrient pools did not differ with general soil-texture (Table 1) suggesting that the increase in red brome productivity may simply be a product of more plant available moisture (Noy-Meir 1973, Abella et al. 2011).   Differences in soil texture across the landscape are subtle and can significantly affect the plant communities (Hamerlynck et al. 2000, Brooks 2009, Stevenson et al. 2009). The *finer-textured* soils and the *coarser-textured* soils chosen for this experiment are both classified as "very gravelly sandy loam" (Soil Survey Staff 2011), but closer examination revealed that the finer-textured soil contained more clay and less sand than the coarser-textured soil (Table 1). This difference in soil texture was enough to invoke increases in shoot height, biomass, and seeds produced (Fig. 2 *b-d*) and has been shown to affect the emergence of red brome seedlings (Abella et al. 2011). Indicated by the strong responses of red brome to soil texture (Table 2), subtle changes in soil texture across landscapes likely influence the distribution and abundance of red brome (Brooks 2009, Abella et al. 2012).

Fertile-island topography

The positive response of red brome to fertile-island soils is likely associated with several attributes of fertile islands including both increased available nutrients and water relations (Noy-Meir 1973, Ewing et al. 2007). Red brome productivity was significantly greater when grown on soil cores collected from fertile islands (Table 2 and Fig. 2). Fertile islands often have greater

organic matter, microbial activity, and finer surface soil texture than interspaces (Schlesinger and Pilmanis 1998, Walker et al. 2001, Drezner 2006, Ewing et al. 2007) which can increase plant productivity (Noy-Meir 1973). We did detect significant increases in soil organic matter and total nitrogen (Table 1) which likely increased red brome's access to nutrients; particularly nitrogen which red brome responds positively to and can be limiting in desert systems (Hooper and Johnson 1999, Brooks 2003).

Fertile island topography and general soil texture together appear to influence the spatial distribution of red brome (Noy-Meir 1973, Ewing et al. 2007, Brooks 2009). Fertile-islands on coarser-textured soils can increase growth in red brome similar to that of finer-textured soils as we observed shoot height from coarser-textured soils within fertile-islands (12.9 cm) to be similar to stem heights on finer-textured soils from fertile-islands (13.7 cm) and interspaces (12.5 cm) (Fig. 5). However, stem densities only increased on finer-textured soils from fertile islands (18908 m^{-2}) than on than on coarser-textured soils from fertile-islands (13294 m^{-2}) and shrub interspaces from either soil texture (13635 m^{-2} and 12055 m^{-2}) (Fig. 3a). These responses of red brome to general soil texture, fertile-islands topography, and their interactive effects indicate that they are dominant factors controlling the spatial distribution of red brome populations and the continuity of potential fuel loads for fire.

Fire history

Results from this study suggests that fire generates positive feedbacks in promoting growth and abundance of exotic grasses. Soils from burned landscapes enhanced shoot height, mass and seed production (Fig. 2b-d), and no negative effects on red brome growth from fire-

affected soils were observed. Increases in red brome densities after an initial fire have been confirmed in the field but densities do not increase again with secondary fires (Brooks 2012). The positive response of red brome to burned soils may be associated with nutrient pulses from combusted biomass (Esque et al. 2010), but the long term persistence of fire-induced nutrient pulses is uncertain (Allen et al. 2011) and increases were not detected in our soils analysis (Fig. 2). Nonetheless red brome productivity did increase on fire-affected soils indicating that some soil attribute is associated with fire.

Alternative to the hypothesis that positive feedbacks of soils from burned areas are caused by fire is the potential that differences soil conditions existed previous to the fire and influenced the spread of fire. Soils from burned areas had more clay and less sand than soils from unburned areas (Table 1). This is counterintuitive since the removal of shrub canopies is expected to have increase wind erosion removing reduced the finer-textured particles and associated nutrients (Okin et al. 2001). As mentioned earlier, soil texture has strong influence on red brome growth (see Table 2). Pre-fire soil conditions likely influenced the patchiness of the fire by affecting the continuity of red brome fuels and post-fire growth on these soils could be perceived as an effect of fire (personal observation, Brooks 1999a).

Fire does alter soil properties to which exotic grasses would be responsive (Lei 1999, Okin et al. 2001). The effects of fire can homogenize the resource distribution of fertile-island topography (Okin et al. 2001, Ravi and D'Odorico 2009) which would reduce the effect fertile-island soils have on red brome growth. Root mass of red brome differed with fertile-island topography on unburned soils but did not differ on burned soils (Fig. 6*a*) however, (Okin et al. 2001, Ravi and D'Odorico 2009) shoot mass results did not change with fire history (Fig. 6*b*).

These same responses did not exist for fertile-island x soil-texture interaction (Table 2) and indicates that effects of fire did alter soils but not to complete homogenization since some effects of fertile-islands are still present. Additionally, soils from burned areas had more clay (Table 1) and other studies have found fire in arid systems to decrease soil moisture, bulk density, and soil organic matter (Lei 1999, Allen et al. 2011). These fire-altered soil characteristics likely contributed to differences in red brome growth in response to soils from burned and unburned areas.

Conceptual model: How precipitation timing soil heterogeneity, and fire-affected soils influence invasive-plant-driven fire regimes

The invasion of exotic grasses into arid and semi-arid shrublands has brought with it an invasive-plant-driven fire regime (Fig. 8) (D'Antonio and Vitousek 1992, Brooks et al. 2004). Factors of precipitation timing and soil properties of texture, fertile-island topography, and fire history are influential in the colonization and spread of the exotic grass red brome (see Table 2); and therefore influence the establishment and the persistence of an invasive-plant-driven fire regime (Brooks et al. 2004). Initially, introduced exotic grasses primarily colonize on finer-textured soils and within fertile-islands (Fig. 8*a.1-3*). During years of high and early fall precipitation grasses expand onto coarser-textured soils and into shrub interspaces (Fig. 8*b.1-4,* see Fig. *2a* and *c*) generating continuous fuel loads (Brooks 1999a). Pending ignition, initial fires burn intensely due to woody fuels (Brooks 2002, Esque et al. 2010b) and results in low-productivity landscapes (Fig. 8*c.1-2*). Following initial fire exotic grasses respond positively to burned landscapes (see Fig. 2*b-d*). Pending sufficient moisture and ignition, low-intensity fires

(Fig. 8*d.1-6*) will further reduce any surviving shrubs and establish an invasive-plant-driven fire regime (Brooks et al. 2004, Brooks 2012). Under this fire regime many native plants, particularly woody perennials, are unable to reestablish and even disappear entirely from the landscape (Callison et al. 1985, Lei 1999, Engel and Abella 2011). Productivity and ecosystem function of these systems remains degraded as long as exotic grasses continue to drive extensive fires (Huenneke and Noble 1996). Temporal variation of invasive grass biomass is of particular concern since climate scenarios predict increases in intense precipitation events and lengths in intervening drought (IPCC 2007).

Management Recommendations

The emergence of an invasive-plant-driven fire regime and the long-term negative impacts it brings has made the need for management mitigation imperative in order to preserve and restore native plant communities of arid and ecosystems. The positive effects of fire on red brome growth and reproduction (see Fig. 2), the negative effects of fire on native plant community dynamics (Callison et al. 1985, Lei 1999, Engel and Abella 2011), and the prolonged recovery rates of native perennials make prevention of initial fire the primary step in preventing the establishment of an invasive-plant-driven fire regime. As finer-textured soils are more capable of generating high densities of exotic grasses (see Fig. 2*c* and 3) the potential for burning is also high (Brooks 1999a) and management efforts to limit spread of fire by disturbing fuel continuity would require greater intensity on finer-textured soils. Coarser-textured soils are at less risk of burning due to lower abundance of exotic grasses (Fig. 2*c*) and may create natural fire breaks providing refuge locations for native woody plants. Fire risk in arid shrublands

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increases when moisture arrives early in the fall, is sustained throughout the winter, and where the soil texture of shrub interspaces is fine enough to maintain growth and increase biomass of fine fuels. As precipitation increases the potential for coarser-textured soils to have fire-carrying fuel loads increases as well. Additionally, previously burned areas can be at increased risk for subsequent burning (Brooks 2012). In order for restoration and preservation efforts to succeed fire must be completely inhibited for century long intervals (Webb et al. 2009, Brooks 2012). Therefore, manual disruption of fuel continuities will need to be increased during years of high and early fall precipitation.

Chapter 2: Acknowledgements

Chapter 2: References

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Chapter 2: Tables

Table 1. Sand, silt, clay, organic matter (OM), and total nitrogen (N) content of Beaver Dam Wash soils with regard to general soil-texture, fertile-island topography, and burn history. means ± standard error. F-values are given for differences in within main effect categories and are denoted as *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$.

soil component	general soil texture			fertile-island topography			burn history		
	finer	coarser	$F_{1,32}=$	fertile-island	interspace	$F_{1,32}=$	burned	unburned	$F_{1,32}=$
sand (%)	46.6±1.2	56.2±1	54***	51.1±1.4	51.7±1.7	0.2	49.4±1.7	53.4±1.3	9.1**
silt (%)	30.4±0.6	28.8±0.8	3.6	30.2±0.8	29±0.7	1.9	29.8±0.8	29.4±0.6	0.2
clay (%)	23±0.7	15±0.6	136***	18.7±1	19.3±1.2	0.6	20.8±1	17.2±1.1	26***
OM (%)	0.658±0.066	0.673±0.073	0.05	0.887±0.057	0.444±0.035	39***	0.656±0.064	0.675±0.075	0.08
N (%)	0.039±0.006	0.044±0.007	0.6	0.062±0.005	0.021±0.004	38***	0.046±0.006	0.038±0.007	1.4

Table 2. F-table of growth and reproductive responses of red brome to early fall precipitation pulse (precip) and soil properties of texture (soil text), fertile-island topography (fertile-is.), and fire-affected soils (burn hist). Response variable include emerged seedlings , stem count, inflorescence count (seed heads), seed count (seeds), mean shoot height, total length of roots (root length), shoot mass, root mass, and root to shoot ratio (root:shoot). Differences in treatments are denoted as *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$.

source of variance	seedlings $F_{1,96}=$	stems $F_{1,96}=$	inflorescence $F_{1,96}=$	seeds $F_{1,96}=$	height $F_{1,96}=$	root length $F_{1,36}=$	shoot mass $F_{1,96}=$	root mass $F_{1,96}=$	root:shoot $F_{1,36}=$
precip	4.38*	1.759	0.46	5.64*	1.734	0.875	1.629	1.598	0.472
soil text	17.67***	18.38***	59.951***	51.783***	22.26***	14.251***	44.637***	33.001***	0.91
fertile-is	11.309**	15.064***	21.06***	9.907**	37.084***	4.773*	92.693***	5.932*	12.18***
burn hist	0.039	0.08	1.227	10.51**	13.917***	0.013	9.464**	1.211	0.002
soil text:precip	2.366	0.168	0.018	1.209	0.003	0.091	0.669	0.347	0.716
fertile-is:precip	1.613	0.006	0.022	1.214	0.193	0.158	0.329	0.331	1.082
burn histt:precip	0.619	0.052	0.022	0.135	0.509	0.749	0.006	0.001	0.007
soil text:fertile-is	1.191	5.781*	3.19	1.597	5.309*	0.059	0.644	0.007	0.255
soil text:burn hist	0.37	4.877*	0.345	0.29	0.027	0.208	0.021	0.39	0.146
fertile-is:burn hist	0.269	0.631	2.686	0.119	0.193	1.38	0.702	5.163*	5.864*
soil text:fertile-is:precip	0.104	0	0.003	0.154	0.147	0.101	0.011	0.126	0.243
soil text:burn hist:precip	0.307	1.911	0.068	0.02	1.204	0.08	2.163	0.356	0.379
fertile-is:burn hist:precip	0.082	0.342	1.081	0.754	2.194	0.29	8.536**	2.224	0.125
soil text:fertile-is:burn hist	2.827	7.319**	1.933	2.586	0.147	1.648	3.704	3.703	0.448
soil text:fertile-is:burn hist:precip	4.232*	5.096*	0.626	0.019	1.204	1.37	0	1.002	1.268

Table 3. Means and differences of plant stems, root length, root mass, root:shoot ratio, total biomass, and inflorescence (seed heads) in response to the main effect in differences in fall precipitation pulse , soil texture, fertile-island soils, and burn condition (± SE). Differences in treatments are denoted as *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, N.S.= not significant.

	fall precip. pulse			general soil texture			fertile-island topography			burn history		
	fall pulse	no pulse	difference	finer	coarser	difference	fertile is.	interspace	difference	burned	unburned	difference
stem density (stems m^{-2})x100	139 ± 7	150 ± 9	-7%N.S.	163 ± 9	127 ± 8	28%***	161 ± 10	128 ± 7	25%***	146 ± 9	144 ± 9	2%N.S.
Inflorescence (seed heads m^{-2})x100	92 ± 4	88 ± 5	4%N.S.	110 ± 6	70 ± 4	57%***	102 ± 6	78 ± 5	30%***	93 ± 6	87 ± 4	7%N.S.
total root length (m root m^{-2} soil)x100	227 ± 15	243 ± 16	-6%N.S.	269 ± 18	204 ± 14	32%***	256 ± 13	217 ± 18	18%*	236 ± 20	234 ± 12	1%N.S.
root mass (g m^{-2} soil)	122.02 ± 7	132.47 ± 9	-8%N.S.	151 ± 9	103.49 ± 7	46%***	137.32 ± 8	117.18 ± 9	17%*	131.8 ± 10	122.7 ± 6	7%N.S.
root:shoot	0.23 ± 0.01	0.24 ± 0.01	-4%N.S.	0.24 ± 0.01	0.23 ± 0.02	6%N.S.	0.21 ± 0.01	0.26 ± 0.02	-20%***	0.24 ± 0.02	0.24 ± 0.01	0%N.S.
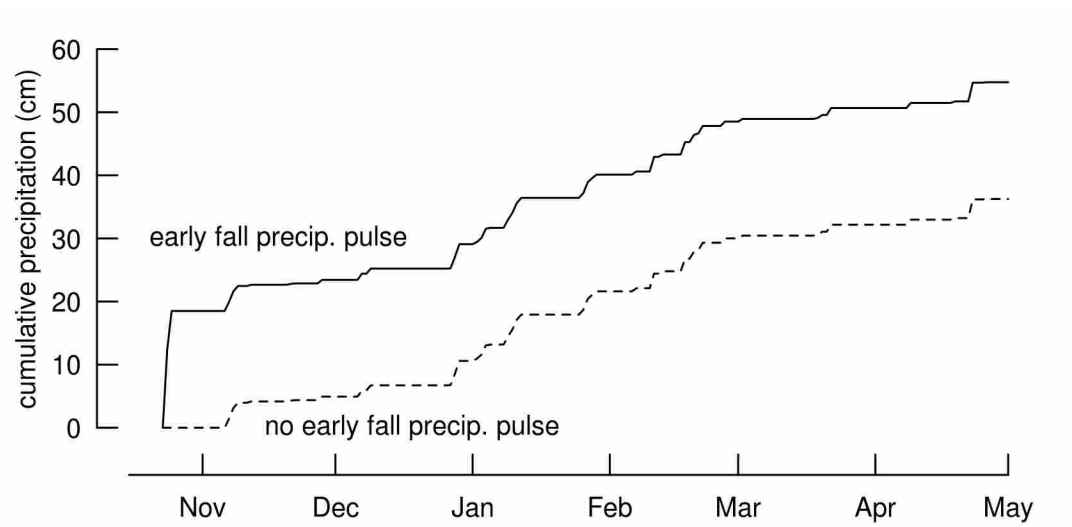
Fig. 1. Watering regime for greenhouse experiment starting at day 0, October 24, 2011.
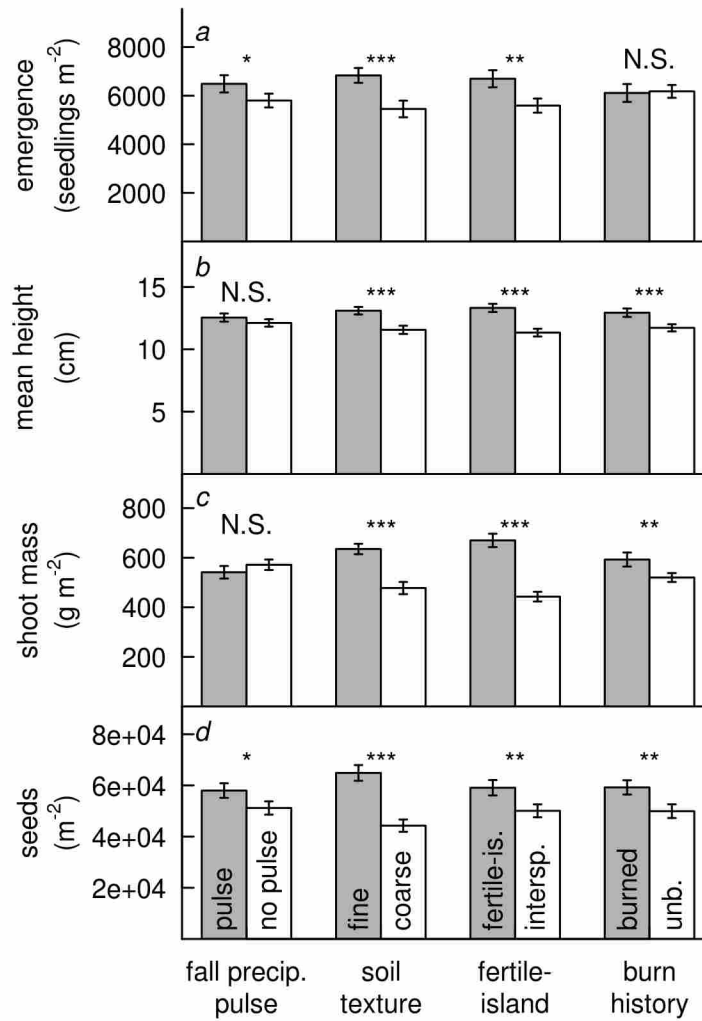
Fig. 2. Response in *a*) emerged seedlings, *b*) mean shoot height, *c*) shoot mass, and seed count to early fall precipitation pulse (fall precip. pulse), soil texture, fertile-island soils, and fire-affected soils (burn history). Error bar = SE. Differences in treatments are denoted as *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, N.S. = not significant at $\alpha=0.05$.
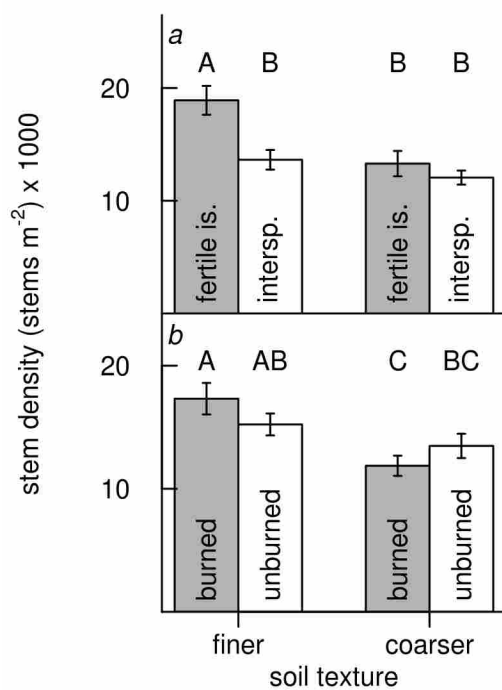
Fig. 3. Response of stem densities to the two-way interactive effects of *a*) soil texture x fertile-island soils and *b*) soil texture x burn history. Capital letters indicate significant differences at α=0.05. Error bars = SE.
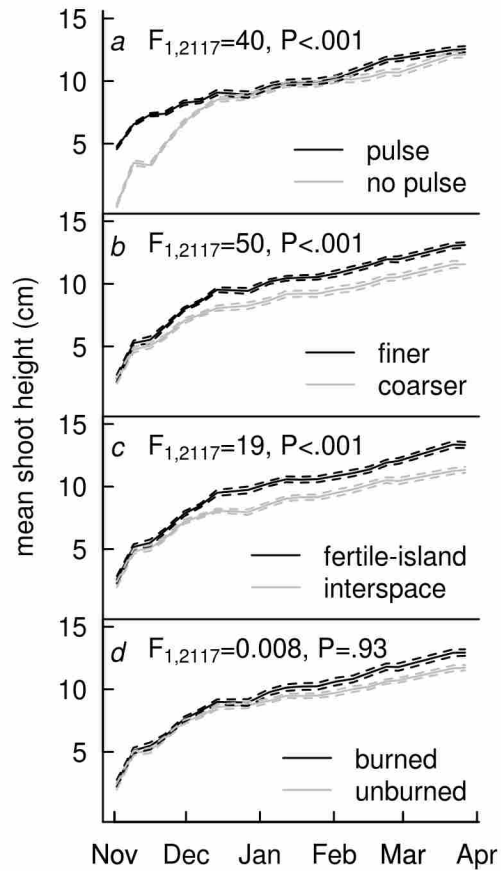
Fig. 4. Mean shoot height response to *a*) early fall precipitation pulse, *b*) soil texture, *c*) fertile-island soils, and *d*) soils from burned and unburned areas throughout the growing season. Dashed lines represent ± standard error.
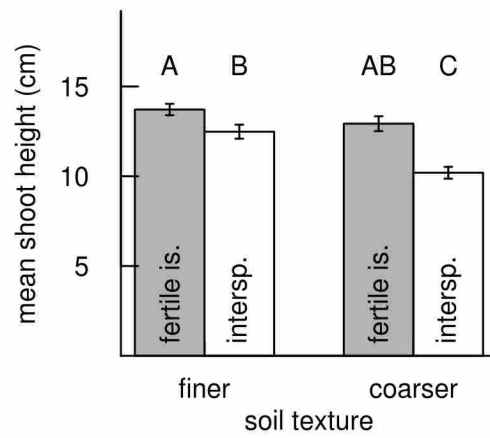
Fig. 5. Mean shoot height responses to two-way interactive effects of soil texture and fertile-island soils. Capital letters indicate significant differences at α=0.05. Error bars = SE.
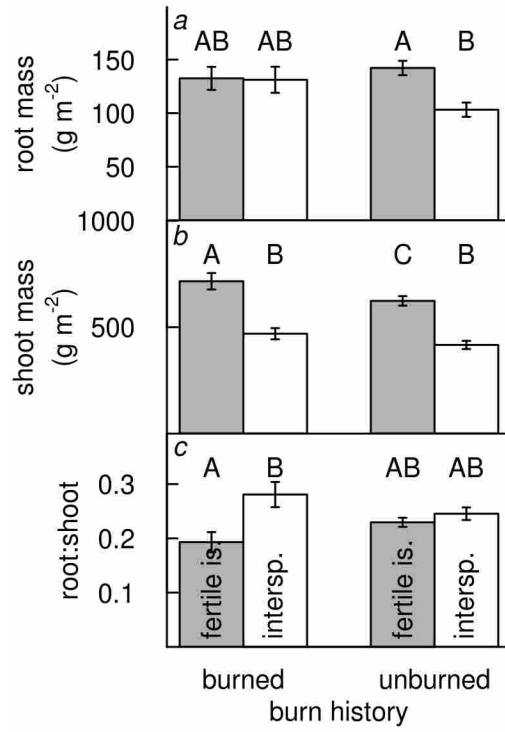
Fig. 6. Response of *a*) root mass, *b*) shoot mass, and *c*) root:shoot ratios to two-way interaction of fire-affected and fertile-island soils. Capital letters indicate significant differences at α=0.05. Error bars = SE.
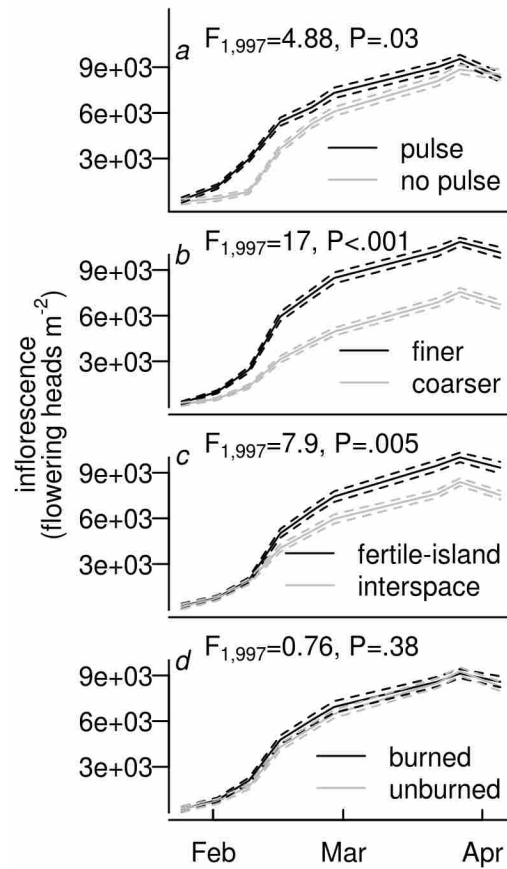
Fig. 7. Number of flowering heads (inflorescence) produced with respect to *a*) early fall precipitation pulse, *b*) soil texture, *c*) fertile-island soils, and *d*) fire-affected soils (burn history) throughout the growing season. Dotted lines represent ± standard error.

Fig. 8. Conceptual model of how biophysical variables alter fire regimes in arid shrubland though promoting growth of exotic grasses. *a.1-3*) Exotic grasses invade onto semi-arid shrublands preferentially on fine-textured soils and within fertile-islands. *b.1-4*) Early fall precipitation promotes grass expansion onto coarser soils and into shrub interspaces, creating continuous fuel loads for widespread fire. *c.1-2*) Initial fires are relatively intense due to woody fuels and results in low-productivity landscapes. *d.1-6*) Invasive-plant-driven fire regime: invasive grasses respond positively to burned landscapes and are dominate when moisture is sufficient, creating potential for subsequent low-intensity fires. *e*) Potential reestablishment of native perennial shrubs only occurs in the absence of fire; however, revegetated areas maintain altered community structure compared to undisturbed communities. *f*) prolonged drought can potentially reduce abundance of exotic grasses.
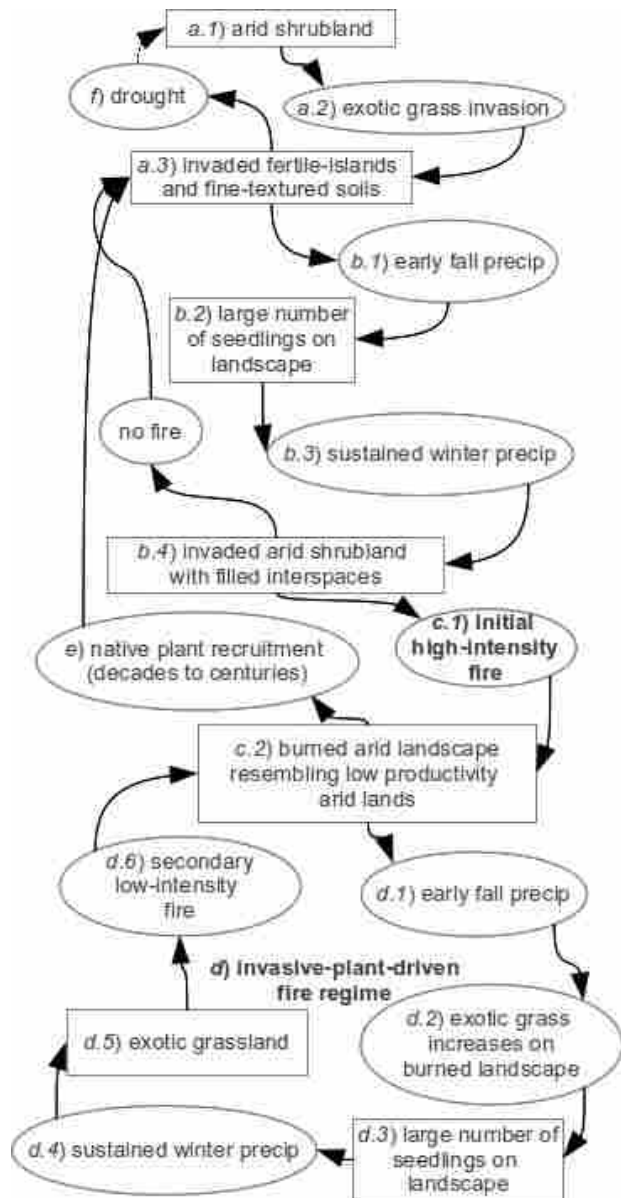
Chapter 3: Landscape-scale evidence for the emergence of climate driven invasive-grass fire regimes in the Mojave Desert

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Chapter 3: Abstract

Anthropogenic perturbations to climate and vegetation are expected to alter wildfire regimes globally. Invasion of exotic plants into arid systems of North America have altered fuel load characteristics resulting in large fires with shorter fire return intervals (< a decade) where fire historically occurred on a limited spatial extent and infrequently (> centuries). Understanding how climate patterns and burn conditions influence the spread and growth of invasive grasses is necessary for mitigating the spread of invasive plants and desert wildfire. The objective of this study was to characterize how exotic grass invasion and and the effects of wildfire change plant productivity of a desert shrubland at the landscape scale and discuss the potential for future recurrent fires. Vegetation response to antecedent precipitation and temperature was assessed using a vegetation index (NDVI) time-series derived from 403 moderate-resolution satellite images via linear regression analysis. Vegetation greenness was particularly responsive to precipitation received in the months of February, April, September, October, and December and was likely related to growth requirements of red brome (*Bromus rubens* L) a dominant invasive annual of the Mojave Desert. Vegetation greenness (NDVI) of burned landscapes increased in sensitivity to precipitation events within a few years after burning. Maximum and minimum NDVI values for post-fire landscapes were respectively higher and lower than pre-fire landscapes. This is indicative of dominant vegetation that has transitioned from perennial shrubs to annual grasses. Patterns of NDVI on post-fire desert landscapes resemble grassland landscapes where fire is naturally frequent and drives plant community structure. The heightened response of post-fire landscapes to projected increases in extreme

weather events will likely increase the extent of wildfire on invaded arid shrublands and drive

native shrublands to exotic grasslands.

Chapter 3: Introduction

Fire is a key driver in the development of many terrestrial ecosystems. Many plant communities have evolved with fire and depend on natural fire regimes to maintain proper ecological function (Bond and Keeley 2005, Chapin III et al. 2011). Fire dynamics such as intensity, frequency, and duration are governed in part by vegetation structure, plant productivity, and biomass accumulation (Keeley 2009). Plant productivity responds to antecedent moisture, promoting biomass accumulation over wet periods (Westerling et al. 2003). This links wildfire patterns with climate oscillations, producing periods of high and low fire activity from annual to millennial scales (Kitzberger et al. 2007). Anthropogenic perturbations to climate and vegetation are predicted to alter wildfire regimes globally (Westerling et al. 2003, IPCC 2007, Marlon et al. 2009) with strong potential feedbacks on plant community development and resilience (D'Antonio and Vitousek 1992, Huenneke et al. 2002, Haubensak et al. 2009).

Introduction of exotic invasive species is a principal mechanism by which human activity alters the ecological effects of fire (Vitousek et al. 1997). By changing the quantity, quality, and connectivity of fuels plant invasions can alter fire regimes (D'Antonio and Vitousek 1992, Brooks et al. 2004a, 2004b). Changes in fire behavior can have deleterious effects on native plants and may increase the expansion and growth potential of invasive species (Hobbs and Huenneke 1992, Haubensak et al. 2009, Brooks 2012), leading to the emergence of invasive plant-fire cycles. There is concern that invasive plant-fire regimes with shorter fire intervals will promote state changes (from shrublands to grasslands) in vegetation that permanently alters plant community composition and function. Mitigating the negative effects of plant invasions and

altered fire regimes on ecosystem function requires a mechanistic understanding of climate and fire effects on invasive plant growth.

Understanding the relationship between climate and plant growth is paramount to identifying the behavior and consequences of fire (Rao and Allen 2010). Precipitation patterns largely control the temporal and spatial distributions of plants (Hamerlynck et al. 2000, Bedford et al. 2009, Brooks 2009, Miller et al. 2009, Schwinning et al. 2011). Soil moisture is the primary limiting factor for germination and growth of plants including invasive grasses that carry fire (Beatley 1967, 1969). While the quantity of precipitation is an important driver of plant productivity and function; equally important that the distribution of precipitation (frequency, timing) (Knapp et al. 2002, St. Clair et al. 2009). Precipitation patterns are highly variable but have some predictability based on natural cycles such as the Pacific Decadal Oscillation (PDO), and El Nino Southern Oscillation (ENSO) (Hereford et al. 2006, Mo et al. 2009). Furthermore, climate change is expected to increase variability in precipitation by altering the frequency and intensity of rain and drought events (Easterling et al. 2000, Sun et al. 2007). Lacking in current literature is an understanding of how changing precipitation patterns can alter plant growth that fuels fire. With the continued expansion of invasive plants across earth's ecosystems and impending shifts in precipitation and temperature with climate change, it is critical that we understand these relationships with greater precision as they influence our ability to find solutions for improved management.

Deserts, which account for approximately 33% of the earth's terrestrial surface, are particularly sensitive to disturbance. In the last 100 years, the major deserts of North America have experienced widespread plant invasions and fire (Brooks 1999, Brooks et al. 2004a, Reid et

al. 2008, Bukowski and Baker 2012). Recent analyses shows that these desert systems may be at a "tipping point" in which fires that historically were rare and patchy are increasing in frequency, size and intensity (Brooks and Matchett 2006). Expansive fires have the potential to destabilize desert ecosystems as native desert biota are generally not fire adapted and are slow to recover following disturbance (Lei 1999, Abella 2009, Engel and Abella 2011). Because large-scale fire in deserts appears to be a relatively new phenomenon, its underlying causes and consequences are still poorly understood. The Mojave and Great Basin Deserts of North America are currently experiencing unprecedented increases in wildfires that appear closely linked to the expansion of red brome (*Bromus rubens* L.) and cheatgrass (*Bromus tectorum* L.) (Brooks and Matchett 2006, Bukowski and Baker 2012). Arid ecosystems that once had fire return intervals of centuries are now experiencing multiple burns on decadal time scales (D'Antonio and Vitousek 1992, Brooks and Pyke 2000, Brooks 2012). In the presence of a shortened fire-return interval many native plants are unable to become reestablished resulting in permanent changes to desert plant communities (Abella 2009, Engel and Abella 2011, Brooks 2012). Fuel structures on landscapes that have previously burned have been altered from pre-fire conditions due to the loss of woody vegetation; changing fire attributes such as severity and duration (Brooks 2002). There is a need for a clearer understanding of how invasive grasses respond to burned desert environments and how burned landscapes change their sensitivity to precipitation and temperature.

The objective of this study was to characterize how exotic grass invasion and fire changes plant productivity of a desert shrubland (measured remotely through NDVI) and discuss what implications there are for potential recurrent fires. We address the following questions: 1) How does fire change plant productivity in response to precipitation and temperature at a landscape

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scale, and 2) what precipitation timing is most influential on total vegetation? We predict 1)

vegetation greenness of post-fire landscapes will demonstrate greater sensitivity (with more

extreme maxima and minima) to precipitation and temperature than pre-fire landscapes, and 2)

vegetation greenness will be particularly sensitive and consistently respond to fall and winter

precipitation events.

Chapter 3: Methods

Chapter 3: Study area

  We focused our study on the Beaver Dam Wash (37.15 °N, 114.01 °W) in the

northeastern region of the Mojave Desert due to its association with the invasion of exotic

grasses and recent increases in extensive fires (Fig. 1). The vegetation is typical of Mojave

Desert mid-elevation (~1000 m) shrublands; dominated by creosote bush (*Larrea tridentata* DC

Cov.), blackbrush (*Coleogyne ramosissima* Torr.), and white bursage (*Ambrosia dumosa* A. Gray

Payne) with abundant Joshua trees (*Yucca brevifolia* Engelm.). The exotic annuals, red brome

and red-stem filaree (*Erodium cicutarium* L.) are ubiquitous on the landscape. Burned areas are

visually distinctive by severely reduced abundance of shrubs and large abundances of exotic

annuals during moist years (Fig. 2) (see Horn et al. unpublished data).

  Since 1984 over 550,000 hectares have burned in the Mojave Desert (Brooks and

Matchett 2006). The majority of this occurred in the unprecedented fire year of 2005 (385,357

ha) in which approximately 1% of the Mojave Desert was burned. These fires were highly

concentrated in the northeastern region of the Mojave (Fig. 1). Within the past three decades

nearly the entire watershed of Beaver Dam Wash has burned at least once. Our analysis includes

a pre- and post-fire time-series reconstruction of the Bird Refuge fire (ignition 27 June 1995, 496

ha) and Westside fire (ignition 23 June 2005, 23,784 ha) which reburned the Bird Refuge fire

area (Fig. 1).

Landsat image processing

To obtain a historic record of plant productivity we calculated vegetation greenness

(Normalized Difference Vegetation Index - NDVI) from 403 Landsat images archived over 26

years. All available Landsat 5 Thematic Mapper (TM) and Landsat 7 Enhanced Thematic

Mapper (ETM+) images from 1985 through 2011 in path 39 row 34 were obtained from the U. S.

Geological Survey (USGS) Earth Resources Observation and Science (EROS) center

(eros.usgs.gov). Digital numbers of individual band rasters were corrected to surface reflectance

values using Landsat Ecosystems Disturbance Adaptive Processing System (LEDAPS) (Masek

2005) on a Optiplex 720 (Dell Inc. Round Rock, TX, USA) (Intel core i7-2600 processor with 4

GB ram) running Ubuntu OS 12.04 LTS Precise Pangolin (Canonical London, UK). Images with

excessive cloud cover or distortion in the region of interest were removed from the analysis

resulting in a final number of 403 images retained for analysis. Bands 4 (near infra-red) and 3

(red) of each Landsat images were then used to generate normalized difference vegetation index

(NDVI) [(B4-B3)/(B4+B3)] using Raster math function in ArcGIS 10.0 (ESRI). Average NDVI

signals were obtained by averaging 50 randomly sampled pixels in each fire area (Bird Refuge

and Westside) for each NDVI raster layer. Fire areas were delineated from burn boundaries

available from Monitoring Trend in Burn Severity (Eidenshink et al. 2007). Only NDVI pixel

values greater than zero were retained for regression analysis as NDVI values less than zero typically represent cloud cover or other image distortions (Jensen 1996).

Chapter 3: Climate data

Weather data was compiled from two separate data sources within the Beaver Dam Wash and summarized to daily values of precipitation, and daily maximum and minimum temperatures. Precipitation and temperature data recorded at Badger Springs meteorological station (BADU1 37.1506 °N, 113.9539 °W, elev: 1216 m) was obtained from University of Utah MesoWest station interface (mesowest.utah.edu) and data recorded at Brigham Young University's Lytle Ranch Preserve (37.143 °N, 114.021 °W, elev: 849 m) was obtained from Utah Climate Center (climate.usurf.usu.edu). Days for which values were absent from BADU1 weather data were filled with values from Lytle Ranch Preserve.

Comparison of burned and unburned landscapes

Fire effects on vegetation greenness were examined by comparing NDVI signals from Bird Refuge and Westside fire boundaries between 1985-2011 during which time both areas burned. Vegetation greenness was compared by a temporal moving ratio between the average NDVI signals from Bird Refuge area vs. the average NDVI signal from Westside area. NDVI values previous to 27 June 1995 compare the two areas before either burned. NDVI values between 27 June 1995 and 23 June 2005 compare the post-fire Bird Refuge area to the pre-fire Westside area. NDVI values after 23 June 2005 compare Bird Refuge and Westside areas after both have burned.

Regression analysis

To determine the influence of temperature and precipitation on vegetation greenness response of pre- and post-fire Mojave Desert shrublands we used linear regression between measured vegetation greenness and climate variables. We focused the analysis on the time period (27 June 1995 to 23 June 2005) when the Bird Refuge area had burned (post-fire) and the Westside area had not (pre-fire) in order to examine vegetation greenness of pre- and post-fire landscapes under identical precipitation regimes. Vegetation greenness values at time t ($NDVI_t$) were regressed with the average maximum temperature (*Tmax*) of the previous 30 days (eq. 1) and separately with antecedent precipitation (*Precip*) received within the previous 360 days (eq. 2). Pre- and post-fire landscape responses were contrasted by the interaction of fire history (*Fire* – pre-fire or post-fire) with average maximum temperature and antecedent precipitation.

$$NDVI_t = Fire * \left(\beta_0 + \beta_{Tmax} * \frac{1}{30} \sum_{days=1}^{30} Tmax_{t\text{-}days} \right) \qquad \text{eq. 1}$$

$$NDVI_t = Fire * \left(\beta_0 + \beta_{Precip} * \sum_{days=1}^{360} Precip_{t\text{-}days} \right) \qquad \text{eq. 2}$$

Regression analysis was performed in Program R version 2.14.1 (R Foundation for Statistical Computing, Vienna, Austria).

To examine the effect of precipitation timing on vegetation greenness for pre- and post-fire landscapes we expanded the regression equation to accommodate for precipitation lagged in 30 day increments. For each of the 403 Landsat images the average maximum temperature of the previous 30 days was determined along with the accumulated antecedent moisture. Antecedent

moisture (*Precip*) was binned in twelve 30 day interval sums (*i*) previous to each image

acquisition date (i.e. precipitation received days 1-30, days 31-60, days 61-90... before image

acquisition date - *t*) (eq. 3).

$$NDVI_t = Fire * \left(\beta_0 + \beta_{Tmax} * \frac{1}{30} \sum_{days=1}^{30} Tmax_{t-days} + \sum_{i=1}^{12} \beta_{t-i} * Precip_{t-i} \right) \qquad \text{eq. 3}$$

The coefficient of each explanatory variables (β_{Tmax} and β_{t-i}, in units of NDVI*°C^{-1} or NDVI*cm

precip.$^{-1}$) indicates relative influence of temperature or moisture on vegetation greenness for the

given lag-time interval (*t-i*). Similar regressions of precipitation to vegetation indices have been

used before however, these have required the use of a seasonal dummy variable which were

replaced in our model by lagged temperature (Kawabata et al. 2001; Lotsch et al. 2003).

The effects of precipitation seasonality on vegetation greenness were examined using

linear regression similar to above but with antecedent precipitation binned by calendar months

previous to image acquisition date. NDVI values were also binned to maximum values for each

calendar month between 27 June 1995 and 23 June 2005. Antecedent moisture (*Precip*$_i$) was

binned by the 12 calendar months (*months* = Jan., Feb., Mar., etc.) that preceded the month of

each Landsat image acquisition (eq. 4). Antecedent average maximum temperature was not

included in eq. 4 as it co-varies with season.

$$NDVI_t = Fire * \left(\beta_0 + \sum_{months=1}^{12} \beta_{t-months} * Precip_{t-months} \right) \qquad \text{eq. 4}$$

Fire effects on the response of vegetation to precipitation and temperature were examined

by generating separate regression models for burned and unburned landscapes. Input data for

regression models was temporally separated to before 27 June 1995 (where both areas were

unburned) and to the time between 27 June 1995 and 23 June 200 (when Bird Refuge area had

burned and Westside remained unburned). Variable coefficients were compared across models

using standard z-test. Comparison of explanatory variables coefficients across burn conditions

indicates changes in vegetation sensitivity to both seasonality and magnitude of precipitation.

Models were extrapolated across all available weather data and compared to observed vegetation

greenness values.

Chapter 3: Results

Vegetation response to precipitation and temperature

Vegetation greenness of post-fire desert landscapes had greater positive response to

antecedent precipitation (P = .0012) and more negative response to temperature (P = .014) than

unburned areas (Fig. 3). Total precipitation of the previous 360 days increased NDVI on average

0.0032 ($\pm$0.0003) cm^{-1} for post-fire Bird Refuge area and 0.0020 ($\pm$0.0002) cm^{-1} for pre-fire

Westside area (Fig. 3a). Average maximum temperature of the previous 30 days decreased NDVI

on average by -0.0032 ($\pm$0.0005) °C^{-1} for post-fire Bird Refuge area and by -0.0017 ($\pm$0.0003)

°C^{-1} for pre-fire Westside area (Fig 3b). Precipitation-NDVI relationship had adjusted r^2 values of

.36 and and .50 for the post-fire and the pre-fire areas respectively. Temperature-NDVI

relationship had lower adjusted r^2 values of .18 and .19 for post-fire and pre-fire areas

respectively.

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Satellite image time-series analysis:fire effects on vegetation greenness

Vegetation patterns were visually distinctive between pre- and post-fire landscapes. Clear vegetation contrasts were seen between the 1995 fire area (Bird Refuge burned 27 June 1995) and the surrounding 2005 fire area (Westside burned 23 June 2005) that change from a dry year (2004), wet year (2005) and after burning a second time (2006) (Fig. 4). Compared to the surrounding vegetation, Bird refuge had equal or lower levels of greenness in spring of 2004 but was visually greener during the springs of 2005 and 2006.

Time-lines of vegetation greenness indicated local maximum values were achieved immediately preceding fires, with significantly greater fluctuations (i.e. higher late winter/early spring maximums and lower summer minimums) in vegetation greenness following initial fire (Fig. 5). NDVI values ranged from 0.11 to 0.32 in unburned areas and 0.10 to 0.44 for burned areas (Fig. 5). Annual maximum NDVI typically occurred in the month of March and were most intense following wet fall and winter seasons. Vegetation greenness peaked in spring of 2005, which was preceded by a precipitation pulse in October 2004. The total precipitation received in October 2004 was more than double the precipitation received in any other fall period in the 22 year record. Prior to either area burning the ratio of Bird Refuge and Westside areas averaged 1.1 with maximum and minimum values of 1.2 and 0.9 (Fig. 5). However, after the 1995 fire and before 2005 fire, ration maximums of vegetation greenness between post-fire and pre-fire areas were as high as 1.5and as low as 0.63. The drought years of 2002 and 2003 saw low vegetation greenness, little fluctuation in the signal, and the ratio between post- and pre-fire areas was approximately 1. After the 2005 fire, the post-fire to post-fire ratio peaked at 1.7 in the spring of 2006 and then abruptly dropped back to ratios near 1. After 2006, vegetation greenness values

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between the post-fire Bird Refuge and post-fire Westside areas were similar even though NDVI values fluctuate with greater magnitude than before fire.

Relationship between vegetation greenness and antecedent precipitation and temperature

The effects of fire resulted in increased responsiveness of vegetation greenness to precipitation received within 90 days (Fig. 6). Between 1995 and 2005 the post-fire area responded to precipitation received within the previous 1 to 30, 31 to 60, and 61 to 90 days by 2.9 ($P = 0.003$), 2.0 ($P = 0.001$), and 1.6 ($P = 0.049$) times that of the pre-fire area respectively (Fig. 6). However, NDVI responses to temperature did not differ between post- and pre-fire areas ($P = 0.19$) .

The effects of fire intensified seasonal influences of precipitation on vegetation greenness (Fig. 7). Vegetation greenness responded positively to precipitation received in the months of February, September, October and December and negatively to precipitation received in April for the time period of 1995-2005. Of these months, fire resulted in increased sensitivity to precipitation received in February ($P = 0.009$) and October ($P = 0.006$).

Chapter 3: Discussion

Our data indicates fire in Mojave Desert shrublands results in increased sensitivity of landscape vegetation to precipitation. Vegetation on post-fire landscapes had greater response to antecedent precipitation than pre-fire landscapes (Fig. 3). This resulted in post-fire landscapes that fluctuated to higher and lower levels of NDVI values (Fig. 5) that were positively correlated with antecedent precipitation (Fig. 6). The post-fire change in vegetation greenness responses

appears to be the result of a transition from dominant cover of native shrubs to invasive annual grasses as fire has removed most perennial shrubs from the landscape (Lei 1999, Vamstad and Rotenberry 2010, Steers and Allen 2011). Exotic grasses have been observed to increase on desert landscapes after initial fire and are likely the dominant component of burned landscapes (Fig. 2*b*) (Brooks 2012).

Fall and winter precipitation events drive vegetation greenness of exotic annuals

Fall and winter precipitation events were indicated as primary drivers in vegetation greenness for both pre-fire and post-fire landscapes. In particular, precipitation received in the months of September, October, December, and February was positively correlated with vegetation greenness (Fig. 7). The seasonal influence of precipitation events on vegetation greenness was likely linked to precipitation patterns in the Mojave where the majority of precipitation arrives in the winter season (Hereford et al. 2006, Redmond 2009). The uneven distribution of precipitation throughout the year may bias these months as significant drivers in vegetation greenness; however, for every calendar month there was at least one instance in the 22 year record when little to no rainfall was received. Precipitation received in February, September, October, and December regularly produced positive responses in vegetation greenness while other months did not.

The significant correlation of fall and winter precipitation events to vegetation greenness and seasonality of maximum vegetation greenness likely deals with the life history of the dominant plant species. Fall and winter precipitation provides the Mediterranean winter annual red brome with a longer growing season and more growth potential (Beatley 1966, Salo 2004,

Brooks and Berry 2006). Maximum NDVI values were regularly reached in March when red brome typically reaches its maximum vegetative growth state (Fig. 5; personal observation). Consistent with our results, heavy fall precipitation has been positively correlated with high red brome abundance in the field (Abella et al. 2012). While ground reference data is lacking for previous vegetation years, red brome was observed to be the dominant vegetation of burned areas in 2011 (Fig. 2) and was likely the principal contributer to vegetation greenness in previous years.

The strong response of vegetation greenness to early fall precipitation is likely a function of germination characteristic of red brome., Seeds of *Brome* spp. are released in spring and remain dormant throughout the summer to prevent precocious germination when moisture is limiting (Allen et al. 1995, Salo 2004, Hereford et al. 2006). By fall, most seeds will have become non-dormant when temperatures are optimal for red brome germination pending adequate moisture (Horn et al unpublished data; (Salo 2004). Early successful germination of red brome primes the system for high fine fuel loads if moisture remains adequate through the winter months.

Fire effects intensifies seasonal fluctuations in vegetation greenness

Patterns in Post-fire vegetation greenness indicate a transition in the dominant vegetation type. The time-series analysis demonstrates a post-fire shift from relatively stable NDVI values to strong seasonal fluctuations in NDVI (Fig. 5). This is presumably associated with the loss of perennial shrub communities and a transition to annual grass dominance. Post-fire fluctuation in NDVI are likely driven by high productivity of annual grasses during the winter and early spring

period followed by senescence in late spring and summer (Beatley 1966, 1976). Annual grass productivity is more responsive to precipitation than perennial shrubs (Agnew 1997) and drought is likely the reason for low NDVI values in 2002 and 2003 (Fig. 5). Even before 2005 the vegetation greenness peak in March of 2005 in the fire pre-fire area (Westside) was likely driven by red brome germination and growth in response to high fall and winter precipitation (Fig. 5). After fire fluctuations in vegetation greenness are even stronger likely due to post-fire increases in exotic grasses (Brooks 2012). Similarly, cheatgrass (*Bromus tectorum*) invasions have increased inter-annual variability of vegetation greenness on post-fire landscapes (Bradley and Mustard 2005). Increased seasonal variability in vegetation greenness likely represents at least a temporary transition in dominant vegetation type from a perennial shrubland to an annual grassland.

Initial fire negatively impacts annual seedbank

Lag time of vegetation greenness following fire is likely associated with dynamics in the seedbank. Following the 1995 fire of Bird Refuge and the 2005 fire of Westside there was a 1 to 2 year period in which the NDVI signal remained low and lagged in response to precipitation (Fig. 5). Time may be required to build up the exotic grass seedbank and could delay green-up response to precipitation. However, since red brome was likely a principle component of the initial fuels, there would also have been a large amount of seed generated pre-fire. During fire, seedbanks can be drastically reduced depending on the intensity, duration and seasonality of fire (Esque et al. 2010). Potentially, plant propagules of some species can be effectively eliminated by fire (Cave and Patten 1984). However, with the 2005 fires there was no lag in NDVI for

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reburned Bird refuge area while there was in the newly burned Westside area (Fig. 5 see peak at 2006 in the Bird Refuge:Westside ratio). We suggest that fire temperatures in the 2005 were likely cooler for already burned Bird Refuge area than previously unburned Westside area due to reduced shrub cover. Native shrub cover adds significant fuel to fires contributing to the mortality of the seed bank (Brooks 2002). With secondary fires the contribution of native shrubs to fuel load is not significant (Brooks 2002); resulting in lower temperatures and shorter residence time of fire and likely leaves more of the seedbank intact for germination the following growing season.

Predicted climate patterns will increase risk of fires

Landscape scale responses of invasive exotic grasses will likely continue to intensify with projected climate scenarios. Our data clearly indicates that post-fire landscapes can have increased sensitivity to precipitation events and are capable of generating abundant vegetation in wet fall and winter seasons. Under projected climate scenarios, fall and winter precipitation events are predicted to increase for the arid systems of North America (Westerling et al. 2003, IPCC 2007). These precipitation events will likely favor expansion of exotic grasses, increasing the risk of initial fires, and perpetuate exotic-plant-driven fire regimes (Brooks et al. 2004a).

Conclusions/management recommendations:

Frequent fire will represents a transition in vegetation communities for the Mojave Desert. Our analysis clearly indicates that vegetation on post-fire landscapes increases in sensitivity and magnitude to precipitation events that will likely promote recurrent fire. As exotic

grasses invade, fuel load and continuity can increase in desert shrub communities promoting expansive fires (Brooks 1999, Brooks et al. 2004a) and can be detected by significant increases in landscape vegetation greenness (Fig. 5). After an initial fire, vegetation responds with greater sensitivity to precipitation (Fig. 6 and 7) as burned landscapes are dominated by exotic annuals that senesce in early spring (Beatley 1966, Brooks 2012). Exotic grass dominance creates the potential for subsequent fire in burned areas which further reduces native survivorship but has limited effect on the seedbank of the exotic annuals (Brooks 2002, 2012). The survived seedbank then has the potential for generating biomass that could fuel another fire pending precipitation of adequate seasonality and magnitude. Frequent fire would preclude the recruitment of native perennials and the reestablishment of native plant community function whether autogenic or otherwise (Brooks 2012).

Our models for vegetation greenness can be used in conjunction with predicted climate scenarios to assess the potential of future fuel loads that can carry expansive and frequent fires. Our analysis indicates desert landscapes can have a predictable response to precipitation patterns and is also indicative of the dominance of annual grasses vs shrubs. The models generated for these regions of the Mojave Desert indicate vegetation responses to precipitation can be consistent based on fire history (eq. 3 and 4 and Fig. 6 and 7). This relationship can be applied to predicting vegetation greenness in invaded landscapes and assess the potential for initial and repeated fires in response to forecasted climate patterns. Our vegetation greenness models are sensitive to both the volume and timing of precipitation which, for the arid southwest North America, are predicted to intensify with specific seasonality in fall and winter seasons followed by increased intensities of drought (Knapp et al. 2002, IPCC 2007). Additionally, these models

can be applied to identify areas that have become dominated by annual grasses, track exotic grass invasions, and isolate areas that may be at increased risk of fire. The ability to predict the spatial and temporal distribution of exotic grasses and fuels can help land managers more effectively allocate resources to areas at greatest risk when mitigating the effects of fire.

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Chapter 3: Figures
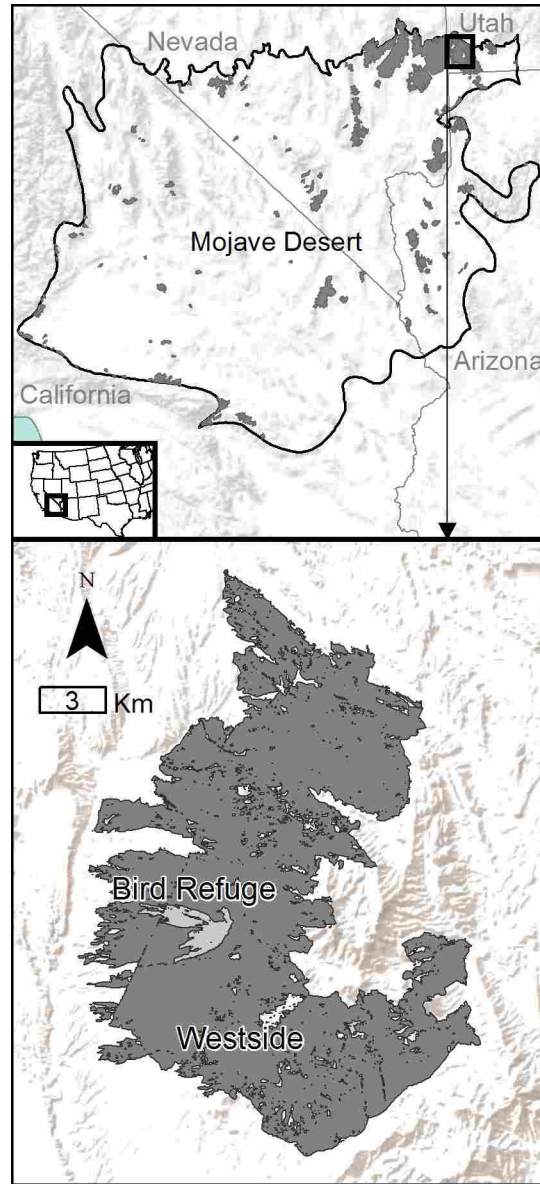
Fig. 1. Fires in the Mojave Desert from 1984 to 2010 (top) highlighting Bird Refuge (light gray) and Westside fires (dark gray) (bottom). One percent of the Mojave Desert burned in 2005 and was concentrated in the northeastern region. When the Westside fire burned 23 June 2005 it reburned the Bird Refuge fire that initially burned on 27 June 1995.
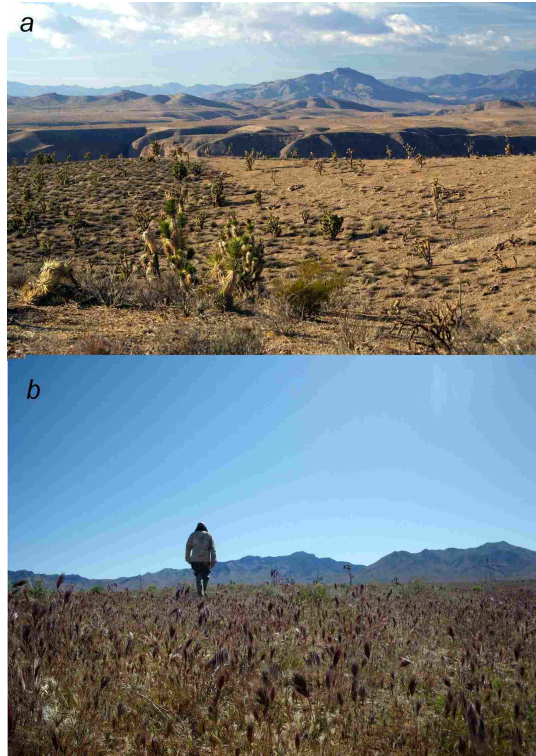
Fig. 2. Photographs of *a*) burned and unburned Mojave Desert landscape within Beaver Dam Wash and *b*) Westside burned terrain. Foreground in *a*) is a boundary in the the 2005 Westside fire with a portion of the 2005 Duzak fire in the background. Dominant plants in unburned area are blackbrush (*Coleogyne ramosissima*), creosote bush (*Larrea tridentata*), and Joshua tree (*Yucca brevifolia*). Westside burned terrain (*b*) in May 2011 following a relatively wet fall and winter (39 cm of precipitation from October 2010 through February 2011). High density red brome (*Bromus rubens*) is seen in the foreground.
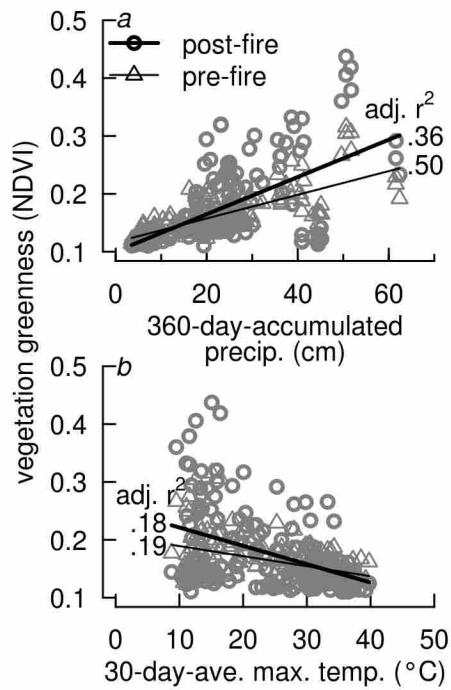
Fig. 3. Vegetation greenness (NDVI) vs. *a*) total precipitation received within the preceding 360 days of image acquisition and *b*) average maximum temperature over the previous 30 days for burned Bird-Refuge (burned – thick line and circles) and unburned Westside (unburned – thin line and triangles) areas from June 27, 1995 to June 23, 2005.
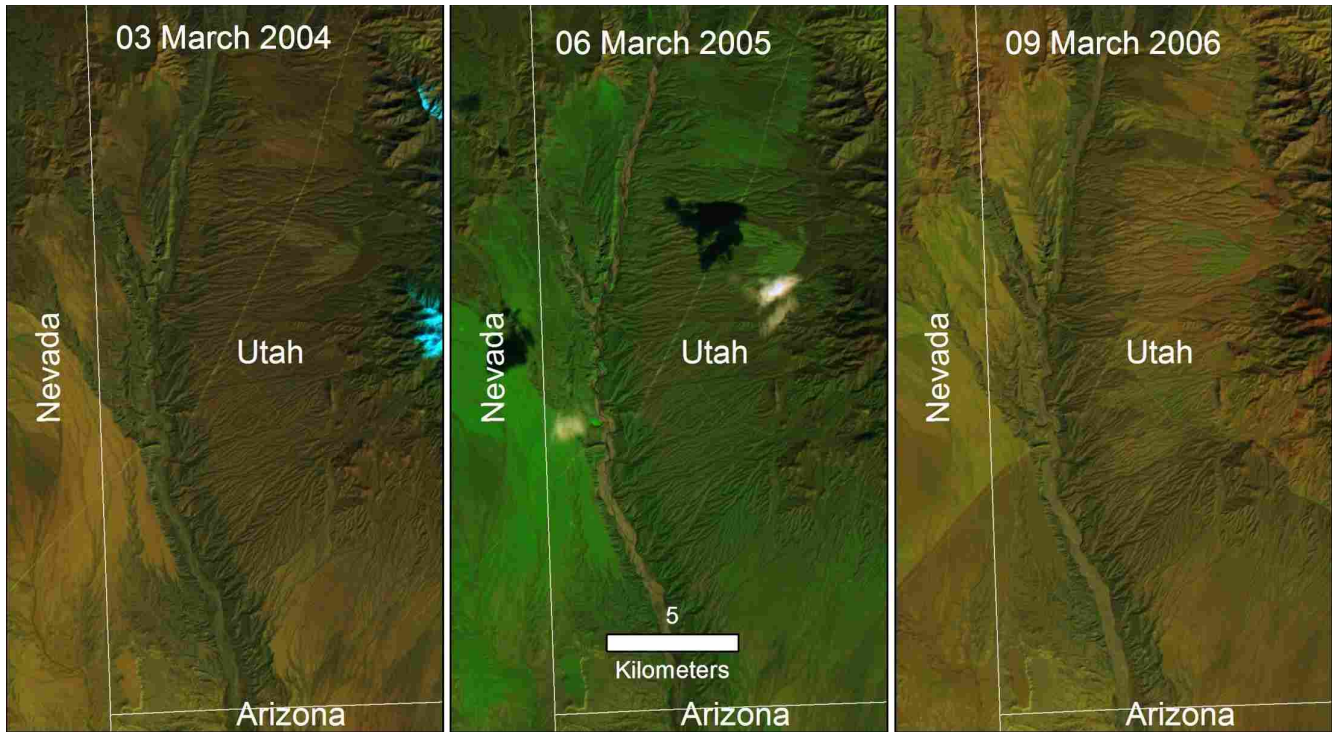
Fig. 4. Beaver Dam Wash in the northeastern Mojave Desert on March of 2004, 2005, and 2006 via 741 Landsat 5 during maximum yearly green-up. Bands are displayed as red (band 7 2.08-2.35 µm short-wave infra-red), green (band 4 0.76-0.90 µm near infra-red), and blue (band 1 0.45-0.52 µm blue). More green indicates more vegetation. Burn boundary of the 1995 Bird Refuge fire is clearly visible in all three images and appears a greater intensity green in both 2005 and 2006 image. Burn boundary of the 2005 Westside fire is visible in the 2006 image along with other fires that burned in 2005.
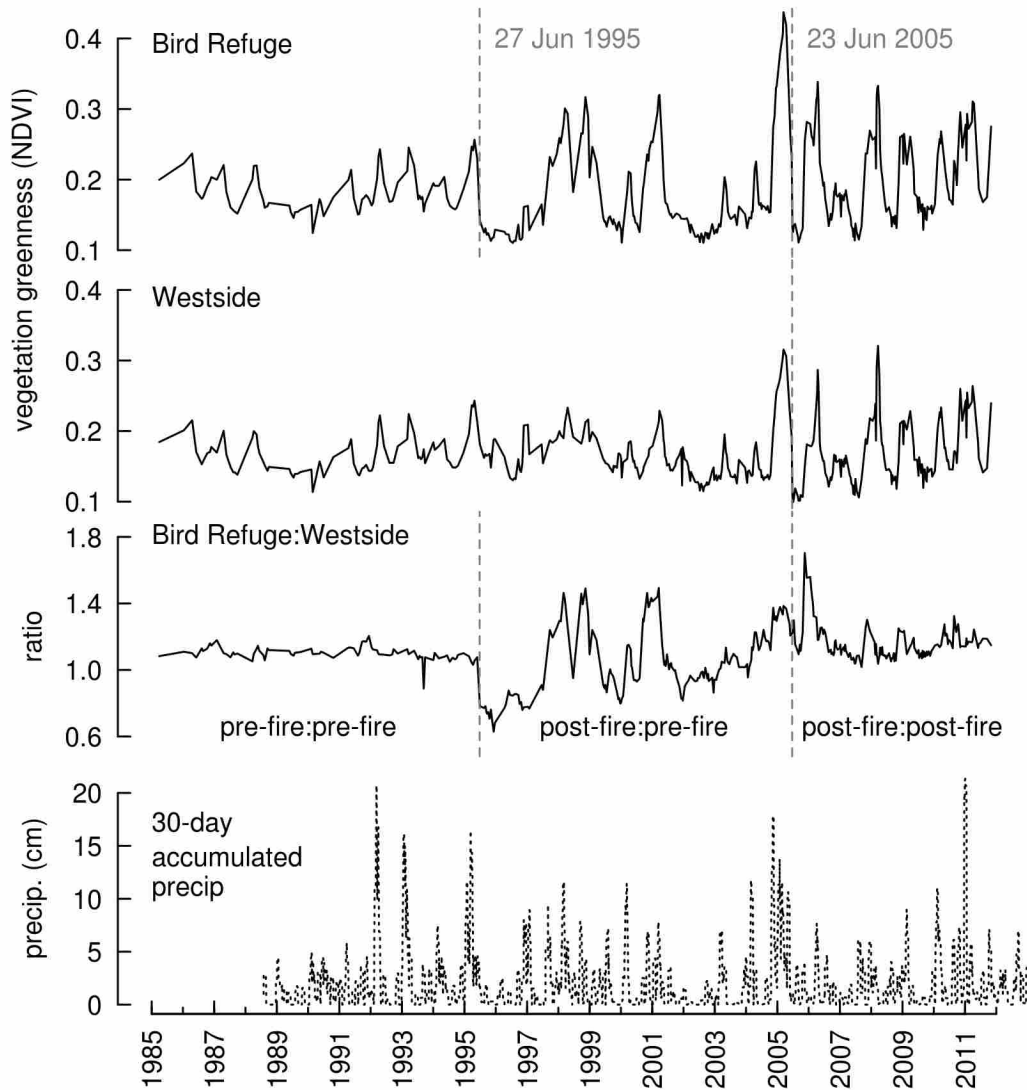
Fig. 5. Comparison of Bird Refuge and Westside vegetation greenness time-lines showing spatial differences and similarities between the two based on pre- and post-fire periods. Vertical dashed lines indicate times of fire occurrence for each area. Bird refuge area burned on 27 June 1995 then again with the Westside fire on 23 June 2005. The ratio compares relative differences in NDVI over the 27 year time-line for pre-fire vs. pre-fire, post-fire vs. pre-fire, and post-fire:post-fire.
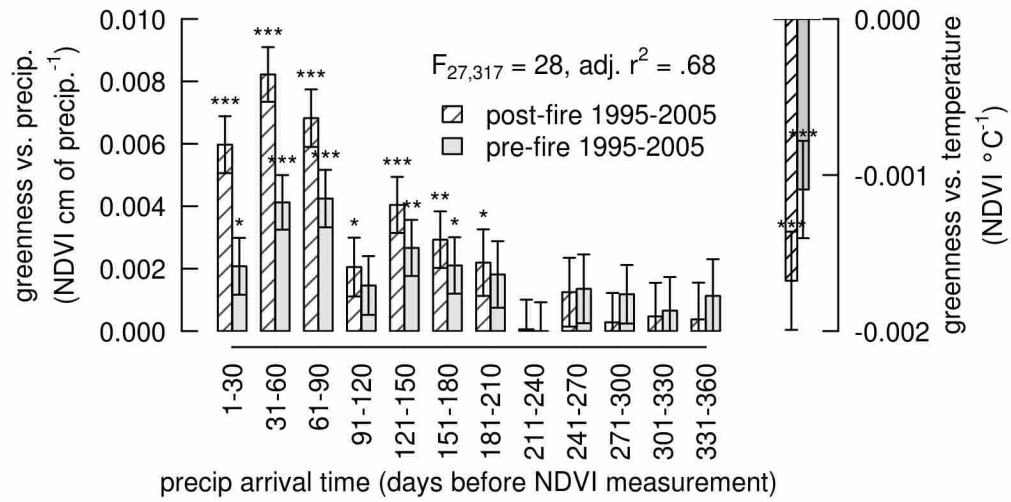
Fig. 6. Comparison of modeled precipitation and temperature coefficients for post-fire (Bird Refuge) and pre-fire (Westside) areas between 1995 to 2005. Significant coefficients at α=0.05 are denoted as *** = P<0.001, ** = P<0.01, * = P<0.05.

Fig. 7. Coefficients of modeled vegetation greenness throughout 1995 and 2005 in response to precipitation received in the 12 calendar months previous to image acquisition between post-fire (Bird Refuge) and the pre-fire (Westside) areas. Significant coefficients at $\alpha=0.05$ are denoted as *** = P<0.001, ** = P<0.01, * = P<0.05.

Chapter 4: Invasive grass driven wildfires reduce desert plant community diversity but stimulate plant function

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Chapter 4: Abstract

Invasions of exotic grasses have increased the frequency and size of wildfires in arid ecosystems in recent decades. Because this is a relatively new phenomenon, fire effects on plant community structure and functional responses of surviving or re-establishing desert vegetation are largely unknown. The objectives of this study were to examine changes in plant community structure and diversity and characterize plant functional responses in post-fire desert landscapes.

Plant community characteristics and functional responses were characterized from 2009-2011 along paired transects of multiple independent fires that occurred in 2005. To examine the range of potential functional responses of desert plants to fire, we selected two dominant perennial species that vary markedly in their functional traits and resource acquisition strategies: Joshua tree (*Yucca brevifolia* Engelm.) and creosote-bush (*Larrea tridentata* D.C. Cov.).

The fires were severe as evidenced by a 73% and 86% decrease in shrub abundance and cover and reductions in plant diversity (42%) and richness (56%). Plant-functional responses to burned landscapes were generally positive. Burn effects on xylem water potential were neutral to positive, more pronounced for creosote than Joshua tree, and were greatest during periods of water deficit. Both species maintained higher foliar nitrogen and phosphorus concentrations in burned areas across seasons. Post-fire conditions had no effect on foliar sucrose and starch levels in Joshua tree but stimulated the accumulation of carbohydrates in creosote during the summer and fall periods. Creosote shrubs in burned areas had 50% greater leaf area than shrubs in unburned locations.

Positive responses of surviving desert shrubs to burned landscapes is most likely associated with competition release from neighboring plants that were removed by fire and may contribute to increased reproductive output.

These results indicate that while desert wildfires drastically alter plant community structure and diversity they increase soil resource availability and plant function, which may facilitate the re-establishment potential of the perennial plant community.

Keywords: creosote, fire, Joshua tree, Mojave, photosynthesis, plant nutrients, post-fire recovery, water potential

Chapter 4: Introduction

Plant invasions have the capacity to fundamentally change native plant communities by increasing competition for resources, and altering disturbance regimes (Chapin III et al. 2000). In arid and semi-arid ecosystems the introduction of exotic grasses are driving novel fire regimes (D'Antonio and Vitousek 1992). Deserts generally experience less fire than other biomes because water deficits and nutrient limitations to plant growth result in low and discontinuous plant fuels (Humphrey 1974, Brooks and Chambers 2011). However, the size and frequency of wildfires are increasing drastically in arid ecosystems (Brooks and Matchett 2006, Keeley 2009, Haubensak et al. 2009, Epanchin-Niell et al. 2009). Increased fire activity is being driven by invasion of exotic annual grasses (*Bromus* and *Schismus* spp.) that increase the connectivity and quantity of plant fuels resulting in larger, more intense fires (Brooks et al. 2004). These large-scale fires appear to be unprecedented or extremely rare over the last several millennia (Brown and Minnich 1986) suggesting that the biological community may exhibit limited resilience.

Plant community response to disturbance varies markedly across ecosystems. In fire adapted systems, plant community cover and diversity often increase drastically following fire through vegetative regeneration and stimulation of seed bank germination (Keeley et al. 2003). Desert flora often demonstrates limited capacity for vegetative regeneration and desert plant species vary widely in their sensitivity to fire (Callison et al. 1985, Lei 1999, Webb et al. 2009). This suggest that deserts are generally poorly adapted to fire and raises questions about the long-term impacts of invasive grass wildfires on desert plant communities and their potential for recovery (Engel and Abella 2011). Recent studies suggest that re-establishment of desert plant community structure and diversity following wildfire is possible but post-fire communities do

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not resemble pre-fire communities or adjacent unburned areas (Abella 2010, Vamstad and Rotenberry 2010). The ecological interactions that shape post-disturbance plant community assembly in arid ecosystems remain poorly understood.

High intensity desert wildfires can limit plant community regeneration by scorching root crowns and causing native seed bank near the soil surface to lose viability (Brooks 2002, Esque et al. 2010). These effects of fire can limit plant community regeneration in the short term. Longer term recovery is at least partially dependent on the survivorship and functional responses of vegetation to burned landscapes and how it translates to reproductive success and recruitment.

Surviving plants on burned landscapes experience drastic shifts in environmental conditions. These can include changes in soil hydrology, physical structure, and nutrient content (Webb et al. 2009). Soils can decrease in pore space, soil water content, and soil organic matter while increasing in surface temperature and pH (Lei 1999). Fire can affect soil nitrogen through altering the structure and activity of biogenic soil crusts (Lei 1999, Belnap and Lange 2002). The loss of plant cover following fire increases both wind and water erosion changing the surface geology and chemistry to which some desert plants are sensitive (Hamerlynck et al. 2002, Stevenson et al. 2009). Additionally, competition for soil resources is likely altered with the reduction in plant density following fire (Mahall and Callaway 1992, Brisson and Reynolds 1994, Holzapfel and Mahall 1999). While recent studies have shed light on the structural effects of desert fire on plant communities, (Abella 2009, 2010) desert wildfire impacts on biodiversity need further elucidation and the functional response of surviving or regenerating perennial vegetation are unknown.

With the emergence of large-scale fires in deserts and their predicted expansion under future climate scenarios (Lenihan et al. 2003, IPCC 2007), there is a critical need to better understand fire effects on plant community diversity and the functional responses of desert plants to fire-altered landscapes. Herein we characterize post-fire changes in the structure, composition and functional responses of a desert plant community several years after large-scale desert fires that occurred in the Mojave Desert. The following questions were addressed: 1) How is plant community structure and diversity modified following fire? 2) Does soil resource acquisition and carbon metabolism of plants change in burned desert landscapes? 3) Do plant functional responses to fire-altered landscapes vary by species with different resource acquisition strategies? 4) How do functional responses to fire-altered landscapes fluctuate with changes in soil resource availability across seasons?

To examine the range of potential functional responses of desert plants to burned landscapes, we selected two dominant, perennial species that vary markedly in their functional traits and resource acquisition strategies; Joshua tree (*Yucca brevifolia* Engelm.) and creosote-bush (*Larrea tridentata* D.C. Cov.). Joshua tree, with shallow root structure, acquires water and nutrients from near-surface soil and stores reserves in its stem and semi-succulent leaves. In contrast, creosote, with deep roots (up to 5 meters), depends on deeper water sources to maintain year round function (Smith et al. 1983, Schwinning and Hooten 2009, Stevenson et al. 2009). Both can resprout following disturbance but mortality and post-fire regeneration failure are common with high fire severity (Humphrey 1974, Brown and Smith 2000, Loik et al. 2000).

Chapter 4: Materials and Methods

Chapter 4: Site Description

The study area was located in the Beaver Dam Wash in northeaster region of the Mojave Desert. Vegetation present is typical of mid-elevation (850-1080 m) Mojave Desert shrubland dominated by blackbrush (*Coleogyne ramosissima* Torr.)*,* creosote-bush*,* white bursage (*Ambrosia dumosa* (A. Gray) Payne)*,* and Joshua tree. Much of the area is covered with exotic plant species including red-stem filaree (*Erodium cicutarium* (L.) L'Hér. ex Aiton) and the winter annual red brome (*Bromus rubens* L.)*.* The soil is a young alluvium with a sandy loam texture. The study area experienced extensive fires in 2005 and 2006. We sampled plants in burned areas caused by four separate fires that occurred in the spring/summer of 2005: *Westside* (ignition: June 23 – 23,782 ha), *Duzak* (ignition: June 22 – 132,395 ha), *Burgess 1* (July – 60 ha), and *Burgess 2* (ignition: July 23 – 543 ha) and in adjacent unburned areas. Fire boundaries were identified from Monitoring Trends in Burn Severity (MTBS) (Eidenshink et al. 2007) and verified in the field. Climate data was obtained from Badger Springs meteorological station located within Beaver Dam Wash study area (37.1506° N, 113.9539° W, elevation: 1216 m) through University of Utah MesoWest Station Interface (mesowest.utah.edu). The sum of precipitation received 90 days previous to sampling times was used as a proxy to estimate available moisture at the time of sampling.

Vegetation assessment

In May of 2011, vegetation surveys were conducted in circular plots (5 meter radius) at 100 m intervals along 1 km paired transects along fire boundaries in Beaver Dam Wash. On

average transect pairs were 210 m from burn boundaries or roads. Shrubs and forbs rooted within plots were counted by species to calculate species abundance and measurements of the major and minor axes of perennial shrubs was used to calculate shrub cover. We used species richness and Shannon's Diversity Index ($H = -\Sigma p_i \ln (p_i)$ where p_i is the proportion of the ith species) to describe the vegetation community. Species richness and Shannon's Diversity Index (H) was calculated based on the number of native shrubs and forbs rooted within plots.

Functional measurements

To assess functional responses of plants to fire-altered landscapes, 60 Joshua tree and 60 creosote plants were measured along the fire boundaries at six different sites for a total of 120 plants. Each site consisted of a burned area and a paired adjacent unburned area. Xylem water potential, photosynthesis, foliar nutrients (nitrogen and phosphorus), and carbohydrates were measured the weeks of February 9th, May 3rd, August 16th and October 29th 2010. Xylem water potential measurements were also made in August 2009 and August 2011. Measurement times were randomized across sites to avoid any diurnal bias.

Xylem Water Potential

To determine plant water relations, pre-dawn xylem water potentials (Ψ_{pd}) were measured between 00:00-06:00 local time using a pressure chamber (PMS Instrument Company, Albany, OR, USA). Mid-day (Ψ_{md}) water potentials taken in August 2011 were measured between the hours of 11:30 and 16:00 local time. Measurements were made on leaves (Joshua tree) and stems (creosote). For Joshua tree, fully expanded leaves were cut near the point of attachment on

rosettes appropriately 1.5 meters from the ground. Terminal creosote stems were haphazardly sampled from the canopy. Two measurements were obtained from every plant during each sampling period.

Photosynthesis

To examine response of photosynthetic activity to fire-altered landscapes we measured electron transport rates (ETR) using a leaf fluorometer (6400-40 Leaf Chamber Fluorometer, LI-COR Biosciences Lincoln, NE). ETR was measured between the hours of 10:00 and 17:00. Measurement times were randomized across sites to avoid any diurnal bias. For each plant, measurements were taken in triplicate (and then averaged) at three haphazardly selected canopy locations that were within arm's reach (up to 1.5 m for Joshua tree). Leaf chamber light levels were set at 1500 µmol m^{-2} s^{-1}. Leaves were allowed 30 seconds to acclimate in the leaf chamber before initializing the ETR measurement.

Foliar nutrient analysis

To examine post-fire effects on foliar chemistry (nitrogen and phosphorus), leaf tissue from Joshua tree and creosote used in the water potential measurement was retained for laboratory analysis to examine fire effects on foliar chemistry (nitrogen and phosphorus). Leaf tissue was dried at 60˚C for approximately 48 hours. Samples were then ground using a Wiley Mini-Mill (Thomas Scientific, Swedesboro, NJ, USA). Dried leaf tissue was analyzed with a nitrogen analyzer (TruSpec, CN Determinator, LECO Cooperation, St. Joseph, MI) using the combustion method (Campbell 1991). For phosphorus analysis, dried leaf tissue was ashed in

glass scintillation vials in a muffle furnace for 12 hours at 495˚C, dissolved in hydrochloric acid

and analyzed on a spectrophotometer (SpectraMax Plus 384, MDS, Toronto, Canada) according

to the methods of Murphy and Riley (1962).

Foliar sucrose and starch

Sucrose and starch concentrations were examined from Joshua tree and creosote leaf

tissue according to the methods of St.Clair et al. (2009) using a Megazyme total starch kit

(Wicklow, Ireland). Non-structural carbohydrates were extracted from 20 mg of ground leaf

tissue in three volumes of 0.67 ml of 80% ethanol (final extraction volume of 2 ml) in a shaking

incubator at 80°C. Aliquots of sample extract (20 μl) were placed in micro-plate wells in

triplicate for both glucose and sucrose analysis then evaporated in a drying oven for 20 minutes

at 55 °C. A volume of 200 μl GOPOD reagent (Megazyme kit) was added to each well. Invertase

was added to the wells being analyzed for sucrose. Absorbance was read at 510 nm. Sucrose

values were determined from the differences in absorbances between samples before and after

the addition of invertase. Standard curves were prepared using pure glucose and sucrose

standards.

Starch was extracted from tissue samples left after the ethanol extractions described

above. Deionized water (2 ml) was added to these samples and then autoclave at 135 °C for 1

hour. Aliquots of 40 μl of sample were hydrolyzed in an alpha-amylase solution and placed in a

shaking incubator for 20 minutes at 100˚C. Samples were cooled at room temperature for 10

minute and further hydrolyzed with the addition of amyloglucosidase and incubation with gentle

shaking at 50˚C for 45 minutes. Megazyme GOPOD reagent was added to the samples and the

reaction was allowed to develop for 15 minutes. Plates were read at a wavelength of 510 nm in the spectrophotometer. Starch standard curves were developed from purified corn starch (Sigma Aldrich) serially diluted in water. All standards and unknown samples were run in triplicate.

Creosote canopy structure

Canopy dimensions and leaf area index (LAI) of creosote was characterized in October 2011 for differential responses to burned landscapes. Canopy dimensions were measured horizontally along major and minor axes and vertically at the highest branch point on the same shrubs used for physiological measurements. Leaf area index (LAI) was averaged from 10 measurements on each creosote shrub using an AccuPAR LP-80 ceptometer (Decagon Devices Pullman, WA) placed at various angles horizontally at the base of the shrub canopy.

Statistical analysis

Fire effects on xylem water potential, foliar nutrients, carbohydrates and ETR across the four sampling periods during 2010 were analyzed using Proc Mixed Repeated Measures model in with burn conditions as fixed effect, sampling period as a repeated measure, and site as a random effect. Fire effects at each sampling period were tested using a student's t-test paired by site. Pearson's correlation coefficient was used to determine relationships between xylem water potential, foliar nutrients, ETR and foliar carbohydrates. One-way ANOVA models with fire as a fixed effect and site as a random effect were used to assess the effects of fire on plant abundance, cover, diversity, and richness and canopy architecture and LAI of creosote . Statistical analyses were conducted in SAS and JMP statistical software (SAS Institute, Cary North Carolina).

Chapter 4: Results

Plant community structure

Fire drastically altered plant community composition and structure. Abundance of common species (greater than one individual per plot) was reduced by more than 65% in burned areas (Table 1). Burned landscapes (six years post-fire) had 85% less shrub cover than adjacent unburned areas (Table 1 and Fig. 1). Blackbrush experienced the greatest reduction in cover (97%) followed by several other species that had greater than 78% cover reduction (Table 1). The most common species growing in burned areas were white bursage and desert marigold (*Baileya* Harv. & A. Gray ex A. Gray) (Table 1). Post-fire landscapes were reduced in species diversity (H) and richness by 42% ($P < 0.001$) and by 56% ($P < 0.001$) respectively.

Creosote canopy structure

Creosote canopies were structurally different in burned and unburned locations. In burned areas creosote shrubs were 18 % shorter (P < 0.001) with 50 % greater LAI (P < 0.001) than plants in unburned areas (Figs 2 and 3). The major and minor horizontal axes of creosote in burned and unburned areas were similar (P = 0.18 and 0.67, respectively).

Plant Water Potential

The effects of fire on plant water relations were mostly neutral to positive, but responses differed by species (Figs 4 and 5, and Table 2). In May 2010 Joshua tree Ψ_{pd} was 29% higher in burned than unburned locations (P < 0.001) but no other fire associated differences were observed. Creosote Ψ_{pd} were different between burned and unburned areas during periods of

greater water stress (Figs 4 and 5). Lowest average Ψ_{pd} (-4.8 ± 0.2 MPa) was observed in the summer of 2009 during which time Ψ_{pd} were 30% higher in burned areas (P < 0.001). These low Ψ_{pd} coincided with the lowest accumulated precipitation of all the sampling periods (Fig. 5). This is opposed to wetter times when water relations were substantially better, and Ψ_{pd} did not differ between unburned and burned landscapes (Figs 4 and 5). However, under the more water stressed conditions of mid-day, creosote Ψ_{md} was 10% higher in burned landscapes (P < .001) (Table 2).

Foliar nutrients

Foliar nutrients were consistently higher in burned landscapes. Both Joshua tree and creosote responded positively to burned condition with mean increases in foliar nitrogen of 17% ($P < 0.001$) and 22% ($P < 0.001$) respectively (Table 2 and Fig. 6 a and b). In both species responses of foliar nitrogen to fire-altered landscapes were consistent across time (Table 2) with higher levels from fall to spring and then a drop during the summer period (Fig. 6). Foliar phosphorus concentrations averaged across seasons were 8% and 21% greater on burned landscapes than on unburned areas for Joshua tree and creosote ($P = 0.060$ and $P < 0.001$) (Table 2 and Fig. 6 c and d).

Photosynthesis

Electron transport rates (ETR) for were not strongly affected by burn conditions but varied significantly across seasons (Fig. 7. a and b, and Table 2). The only significant response of ETR to fire-altered landscapes was a positive response of Joshua tree during August 2010 ($P =$

0.003) (Fig. 7a). Electron transport rates were greatest for creosote during the spring and summer periods in contrast to Joshua tree which had relatively depressed ETR values during the summer period.

Foliar non-structural carbohydrates

Burned landscapes had no effect on foliar sucrose and starch levels in Joshua tree but stimulated the accumulation of carbohydrates in creosote during the summer and fall periods (Fig. 7 d and f). For both species, foliar sucrose and starch levels varied significantly across seasons (Table 2). Foliar carbohydrates in Joshua tree tended to be higher in the fall and winter period (Fig. 7 c and e). For creosote , sucrose and starch peaked strongly during the spring and fall periods. Interestingly, Joshua tree had much higher levels of sucrose while creosote had much higher levels of starch. Non-structural carbohydrates were not significantly correlated with foliar nitrogen, foliar phosphorus, or water relations in either species (all r values < 0.22).

Chapter 4: Discussion

The Mojave Desert fires of 2005 were severe as evidenced by drastic reductions in the abundance, cover, diversity and richness of the native shrub community six years after the fire (Table 1). Other studies have shown shrub cover to return to values that met or exceeded pre-fire values within twenty years but only to be dominated by one or two species (Steers and Allen 2011b). Post-fire desert landscapes can persist with low shrub diversity for decades (Engel and Abella 2011). Shrub cover has the potential to return to pre-fire cover values however, diversity of plant communities would likely remain low and not resemble that of pre-fire or unburned

plant communities (Vamstad and Rotenberry 2010; Engel and Abella 2011; Steers and Allen 2011a). A few shrubs along with perennial and annual forbs including white bursage and brittlebush are known to be strong colonizers following desert fire (Steers and Allen 2011a). However, loss of shrub cover prolongs regeneration of long-lived perennials since many desert species depend upon nurse shrubs for establishment (Brittingham and Walker 2000, Walker et al. 2001, Drezner 2006). Long-term changes in plant community structure and diversity are likely to have cascading effects on the entire biological community through bottom-up forces (Horn et al. 2012).

Loss of native seed bank with high burn intensity (Brooks 2002) and excessive cost and frequent failure of re-seeding efforts are constraints to native plant community re-establishment in burned desert landscapes (Zouhar et al. 2008, Weigand and Rogers 2009). There is however, an intact (albeit modified) native shrub community that survived the 2005 fires (Table 1). How these surviving native shrubs function and reproduce in burned landscapes is likely an important determinant of the recovery potential of the native plant community. Surprisingly, the functional responses of surviving or regenerating perennial plants in burned desert landscapes are unexplored in the literature.

Growth patterns in some desert plants have been strongly linked to soil structure and hydrology (Stevenson et al. 2009). Whether fire positively or negatively influences soil hydrological properties in deserts remains ambiguous (Allen et al. 2011). Lei (1999) suggested that fire effects on soil hydrology tended to be negative. However, we found that fire-altered landscapes generally had neutral to positive effects on plant water relations (Fig. 4). These positive effects of fire on water relations were limited to dryer periods indicating interactions

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between burn condition and water availability, which varies significantly by season and year (Figs 4 and 5). When moisture is limited, plant competition can have a greater influence on water relations than soil characteristics; however, soil characteristics dominate under high moisture availability (Hamerlynck et al. 2002). Fonteyn and Mahall (1981) found that removal of neighboring vegetation improved water relations in creosote. This suggests that competition release stemming from reduced plant density is a primary reason for more favorable water potentials observed on burned landscapes under conditions of water deficits (Fig. 5).

Hydraulic responses to burn conditions and seasonality were species specific and likely a result of the different water acquisition strategies. Joshua tree acquires water from near-surface soils and stores water in its semi-succulent leaves. This water storage strategy enables Joshua tree to be less dependent than creosote on available soil moisture, especially during dry periods (Smith et al. 1983, Schwinning and Hooten 2009). High water potentials measured on the leaves of Joshua trees reflected their function as water storage structures (Fig. 4) and appears to mitigate competition for soil moisture in unburned areas during drought (Schwinning and Ehleringer 2001).

Fire can strongly alter soil nutrient status and nutrient acquisition by plants. In arid systems a significant amount of biological nitrogen is found in plant tissues (Esque et al. 2010, Allen et al. 2011). Much of this nitrogen is returned to the soil in the form of NH_4 and NO_3 along with other mineral nutrients following fire (Esque et al. 2010). However, soil nutrient pulses following fire can dissipate rather quickly (1-2 years) in desert systems (Allen et al. 2011). This may be related nutrient export via wind erosion and/or heavy leaching due to the poor nutrient holding capacity of desert soils (Steers and Allen 2011a, Allen et al. 2011). However, our results

demonstrate that burn conditions strongly stimulated foliar nitrogen and phosphorus acquisition in both Joshua tree and creosote six years post-fire (Fig. 6) indicating that factors other than a nutrient pulse immediately after fire are involved. Post-fire conditions could promote shifts in soil microbial community composition or activity that alters N-fixation rates in desert soil crusts. However, in the Colorado Plateau, N-fixation rates of soil crusts were observed to dramatically decrease with disturbance (grazing and fire) resulting in reduction in soil nitrogen availability (Evans and Belnap 1999). Within the Mojave Desert, soil nitrogen is tightly cycled between soil microbes and plants within "fertile-islands" that develop beneath shrub canopies (Ewing et al. 2007). High burn intensities within these fertile islands (Table 1), reduces microbial activity and N-fixation rates in the short term (Bahr et al. unpublished data). Much less is known about long term (> 2 years) soil microbial responses to fire. Competition release likely contributes to better nutrient relations as the tight nutrient cycling within fertile islands is disrupted, making those nutrients available to surviving plants. Death of competitors may also allow root expansion of surviving plants into rooting zones of burned plants (Fonteyn and Mahall 1981, Brisson and Reynolds 1994). While we see a clear signal of greater nutrient acquisition by surviving perennial plants in burned desert landscapes the underlying mechanisms are still poorly understood.

The effects of fire on plant carbon metabolism are largely uncharacterized in deserts. Our data indicates that burned desert environments have neutral to positive effects on photosynthesis and leaf carbohydrates and that these effects vary strongly by season (Fig. 6). Changes in nutrients (i.e. nitrogen and phosphorus) affect photosynthesis conjointly with plant-available water (Lajtha and Whitford 1989, Hooper and Johnson 1999) and may have contributed to the

positive effects that fire had on carbon metabolism. However, we saw no correlation between foliar starch accumulation and foliar nutrient (nitrogen and phosphorus) concentrations across burn conditions. Photosynthesis, sucrose, and starch were much more strongly influenced by seasonality than by burn condition. The highest carbohydrate accumulations for creosote were observed in spring and fall, which is consistent with other studies (Strain 1969, Oechel et al. 1972), and may be related to less stressful temperature and moisture conditions. The marked differences in ETR and carbohydrate accumulation between the two species in response to burn conditions and seasonality emphasizes that differences in plant strategies are also an important determinant of desert plant function.

Morphological enhancement was some of the clearest evidence that shrubs respond positively to burned landscapes. On burned landscapes creosote canopies were more dense and had larger leaves than creosote shrubs in unburned areas (Figs 2 and 3). Similar enhancements occur when creosote is grown on favorable soils (Hamerlynck et al. 2000) and are likely due to better water and nutrient relations (Lajtha and Whitford 1989). While photosynthesis on a leaf area basis did not vary strongly between creosote in burned and unburned landscapes, the significantly greater leaf area in creosote in burned areas suggest greater photosynthetic potential on a whole plant basis. Taken together, our data indicates that burned desert environments have no negative effects on surviving perennial vegetation and often have positive influences depending on species and season.

Autogenic recovery of native plant communities have been demonstrated following desert fire (Webb et al. 2009, Abella 2009, Vamstad and Rotenberry 2010, Steers and Allen 2011a). Our results suggest that improved water relations, foliar nutrient status and carbon metabolism of

surviving vegetation may contribute to regeneration success of the plant community. Recent assessments of plant reproduction along the same paired transects used in this study demonstrated that burned environments strongly stimulate flower and fruit production of surviving plants (Lybbert and St. Clair, unpublished data) suggesting a link between fire, greater soil resource acquisition by surviving plants, and higher reproductive capacity. Our data demonstrating increased resource acquisition and metabolism of plant in burned environments suggest that autogenic recovery is not precluded by the functional responses of plants to burned desert landscapes.

None of the above examples of autogenic recovery, nor our findings, consider multiple burns which would continue to reduce the number of surviving shrubs and may alter plant functional responses differently than single burns (Brooks 2012). Repeat fires on short time scales are occurring as the same exotic grasses that carried the initial fire are among the first to re-colonize the burned landscape (Brooks 2002, 2012). Grass invasion and shorter fire cycles alter nutrient availability in desert systems through erosion, volatilization and nutrient homogenization (Ravi and D'Odorico 2009, Allen et al. 2011). These changes could constrain native shrub recruitment and preclude re-establishment of native shrub communities.

Chapter 4: Acknowledgements

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Chapter 4: References

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Chapter 4: Tables

Table 1. Abundance and cover of the 14 most common native species (shrub or forb) in burned and unburned plots. Measurements were taken in May 2011, six years post-fire. Differences are the percent reduction of unburned minus burned plots. Means presented with standard error.

| species | common name | abundance | | | | | | cover | | | | | |
| | | unburned plot | | burned plot | | difference | | unburned plot | | burned plot | | difference | |
		plants plot^{-1}	error	plants plot^{-1}	error	% change	p-value	% cover	error	% cover	error	% change	p-value
all plants	all plants	37	1.49	10	1.49	-73%	<0.01	22%	0.58%	3.20%	0.58%	-86%	<0.01
Coleogyne ramosissima	backbrush	13	0.89	0.37	0.89	-97%	<0.01	7.42%	0.51%	0.22%	0.51%	-97%	<0.01
Ambrosia dumosa	white bursage	5.75	0.82	1.57	0.82	-73%	<0.01	1.82%	0.25%	0.40%	0.25%	-78%	<0.01
Larrea tridentata	creosote bush	2.95	0.25	0.63	0.25	-79%	<0.01	4.98%	0.48%	0.61%	0.48%	-88%	<0.01
Krameria spp.	ratany	2.82	0.27	0.37	0.27	-87%	<0.01	1.45%	0.13%	0.13%	0.13%	-91%	<0.01
Yucca baccata	banana yucca	2.37	0.73	0.73	0.73	-69%	0.12	0.85%	0.24%	0.30%	0.24%	-65%	0.10
Thamnosma montana	turpentine bush	2.65	0.30	0.40	0.30	-85%	<0.01	1.12%	0.13%	0.14%	0.13%	-88%	<0.01
Yucca brevifolia	Joshua tree	1.75	0.22	0.17	0.22	-90%	<0.01	1.93%	0.30%	0.31%	0.30%	-84%	<0.01
Ephedra nevadensis	ephedra	1.67	0.28	0.12	0.28	-93%	<0.01	0.29%	0.05%	0.02%	0.05%	-93%	<0.01
Encelia farinosa	brittlebrush	0.58	0.24	0.90	0.24	54%	0.36	0.33%	0.11%	0.37%	0.11%	11%	0.81
Baileya spp.	desert marigold	0.20	0.45	1.20	0.45	500%	0.12	-	-	-	-	-	-
Acamptopappus sphaerocephalus	rayless goldenhead	1.03	0.21	0.35	0.21	-66%	0.02	0.23%	0.05%	0.05%	0.05%	-77%	<0.01
Lycium andersonii	water jacket	0.45	0.14	0.87	0.14	93%	0.04	0.12%	0.03%	0.12%	0.03%	-0.17%	1.00
Cylindropuntia acanthocarpa	buckhorn cholla	1.03	0.14	0.20	0.14	-81%	<0.01	0.84%	0.13%	0.17%	0.13%	-80%	<0.01
Sphaeralcea ambigua	globe mallow	0.03	0.59	1.18	0.59	3450%	0.17	-	-	-	-	-	-
other	other	1.42	-	1.02	-	-	-	0.82%	-	0.37%	-	-	-

Table 2. F-values from repeated measures ANOVA examining effects of fire and time of sampling on foliar nitrogen (N), foliar phosphorus (P), photosynthesis by electron transport rate (ETR), foliar sucrose, and foliar starch of Joshua tree and creosote-bush. Significance designated as *$p < 0.1$, **$p < 0.01$, ***$p < 0.001$.

source of variance	Ψ_{pd}	N	P	ETR	sucrose	starch
Joshua tree						
fire	2.96	23***	3.55*	3.31*	0.71	0.4
sampling period	16***	72***	2.34*	20***	38***	342***
fire*sampling period	2.42	0.19	2.11*	1.92	0.24	0.69
creosote-bush						
fire	0.97	70***	40***	0.35	0.43	10.1**
sampling period	27***	19***	15***	317***	22***	119***
fire*sampling period	2.14	0.83	4.07**	0.75	2.14	3.1*

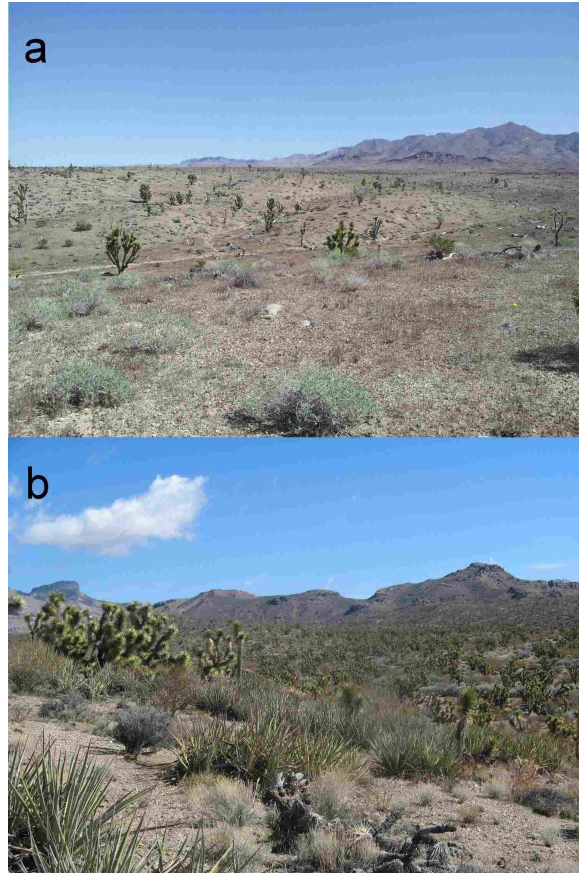Fig. 1. Examples of a) burned and b) unburned Mojave Desert landscapes.
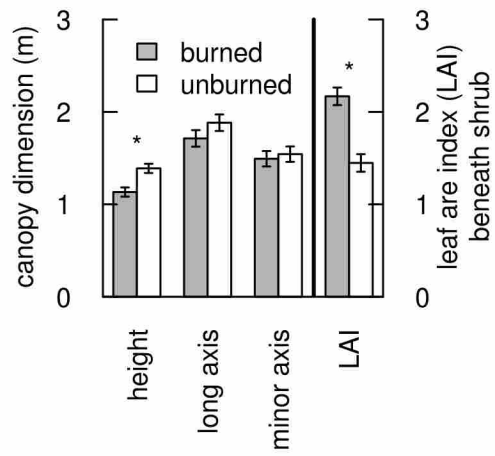
Fig. 2. Creosote canopy height, major-axis, minor-axis, and leaf area index (LAI) (mean ± SE) on burned (filled bars) and unburned (open bars) landscapes. Asterisk indicates *P* < .001. error bars ± 1 standard error.

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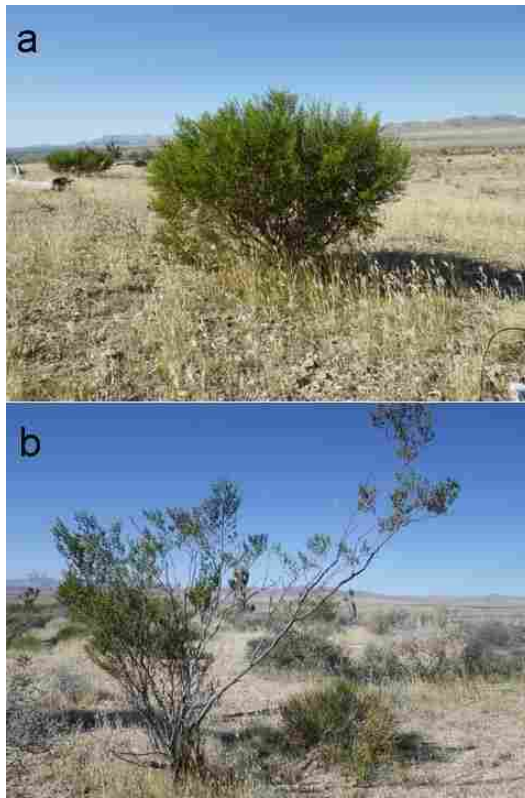
Fig. 3. Example creosote shrubs illustrating the differences in leaf density of canopies in a) burned and b) unburned areas.
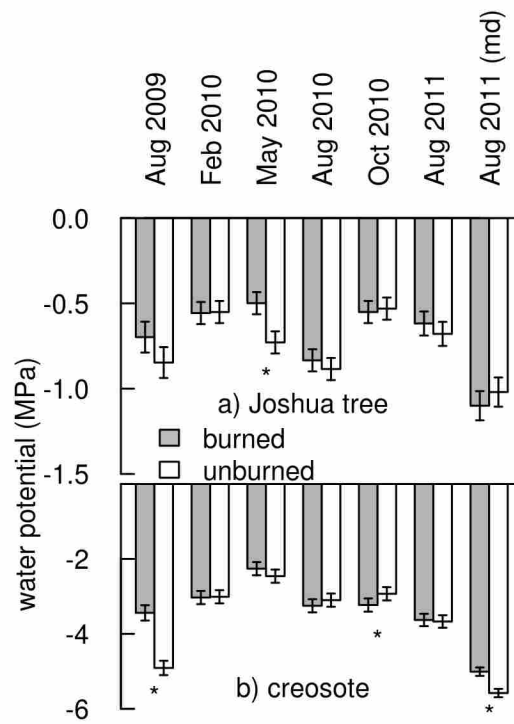
Fig. 4. a) Joshua tree and b) creosote *w*ater potentials (mean ± SE) along burned (filled bars) and unburned (open bars) transects across various seasons in 2009, 2010, and 2011. All values are from pre-dawn measurements except the last set of bars that present mid-day (md) values. Asterisk indicates *P* < 0.05
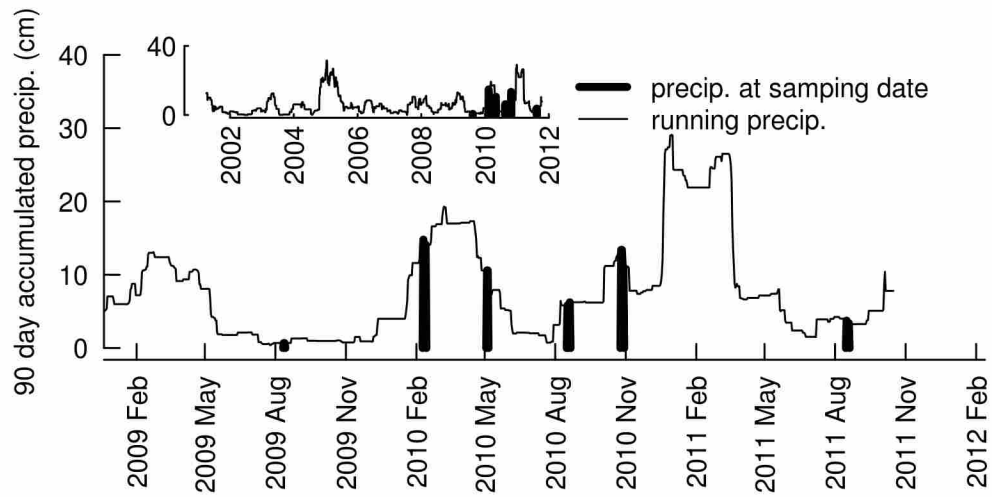
Fig. 5. Accumulated precipitation record for Beaver Dam Wash recorded at the Badger Springs meteorological station (37.1506 N, 113.9539 W). Ninety-day accumulated precipitation was lowest during the 2009 sampling period.
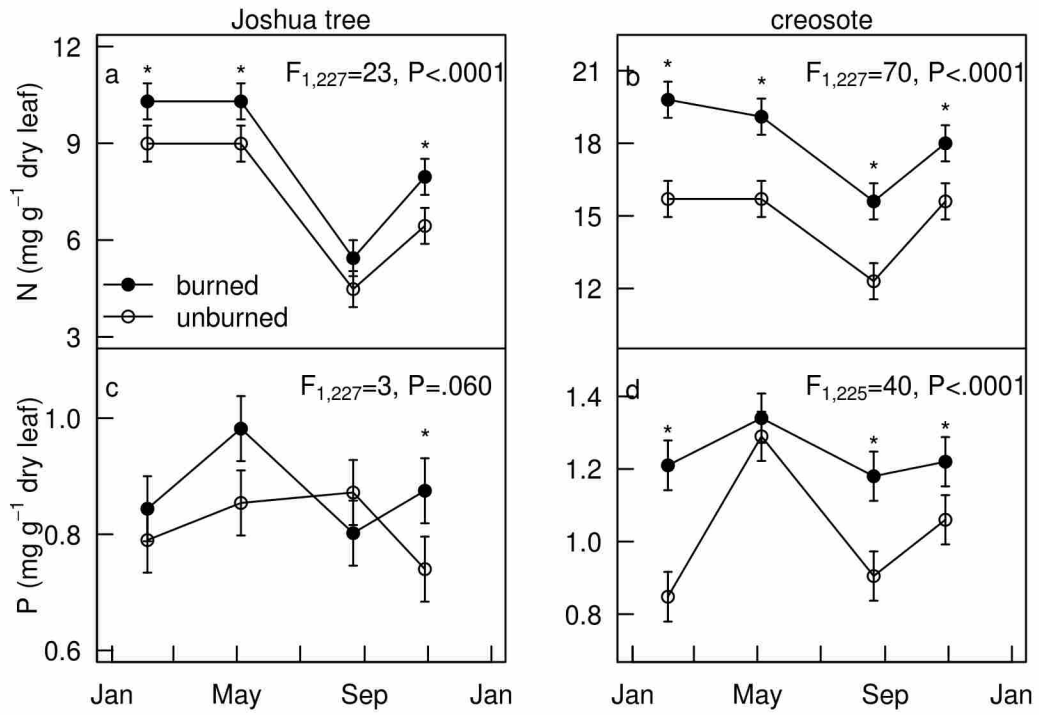
Fig. 6. a-b) Foliar nitrogen , and c-d) foliar phosphorus of Joshua tree and creosote (mean ± SE) on burned (filled circles) and unburned (open circles) transects across 2010. *P*-values for the main effect of fire across all time points are given in upper right corners of each graph. Asterisks indicate significant differences ($P \leq 0.05$) between paired comparisons.
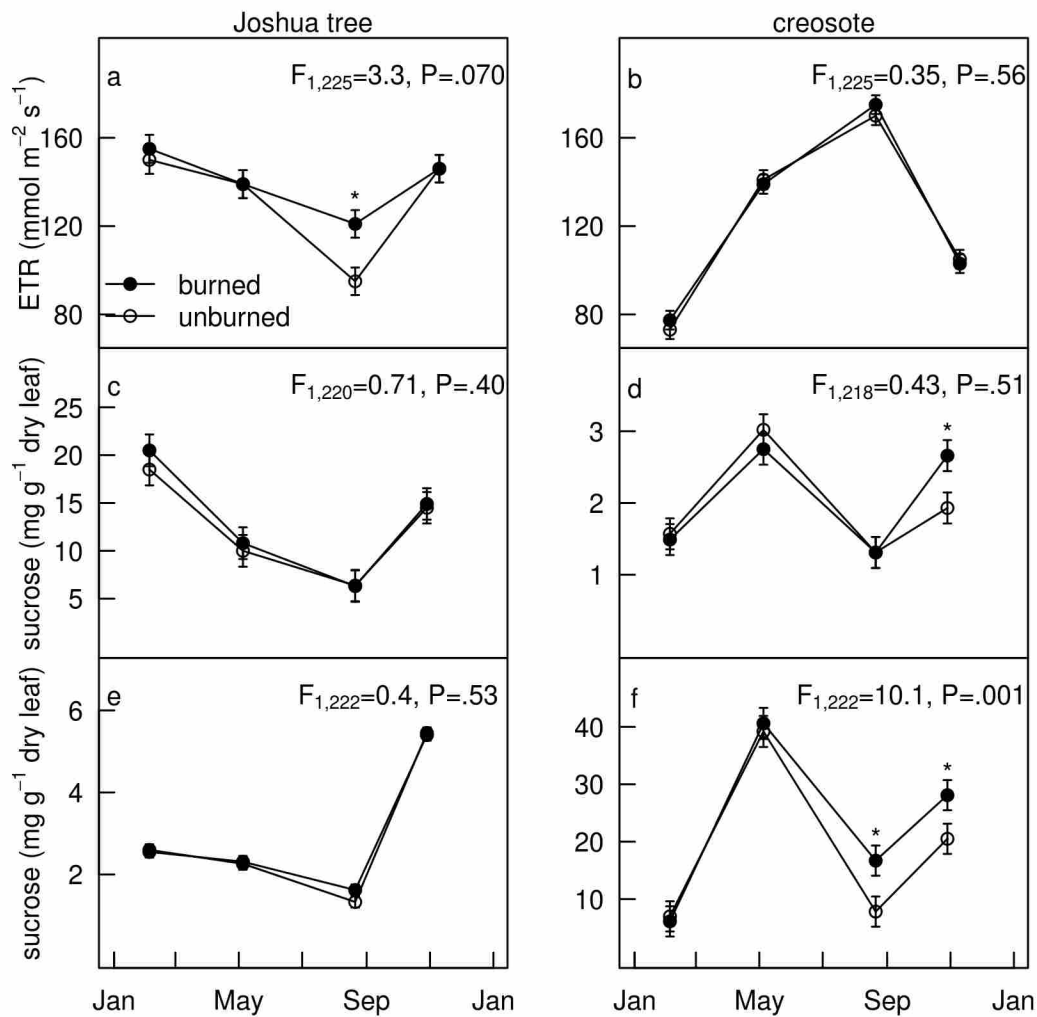
Fig. 7. a-b) Electron transport rates (ETR), c-d) foliar sucrose, and d-f) foliar starch of Joshua tree and creosote (mean ± SE) on burned (filled circles) and unburned (open circles) transects across the four major seasons of 2010. *P*-values for the main effect of fire across all time points are given in upper corners of each graph. Asterisks indicate significant response to fire-altered landscapes ($P \leq 0.05$) within single sampling times.

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Chapter 5: Expansive fire in Mojave Desert shrubland reduces abundance and species diversity of small mammals

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Chapter 5: Abstract

Changes in plant community structure and composition of the Mojave Desert in response to greater fire intensity and extent are likely to have strong bottom-up effects on the biological community. The objective of this study was to determine how expansive fire in Mojave Desert impacts small mammal communities across seasons. We sampled small mammals in paired burned (4e5 years post-fire) and unburned areas of Beaver Dam Wash in southwestern Utah. Fire reduced total abundance of small mammals, and species richness and species diversity of the small mammal community. Merriam's kangaroo rat (Dipodomys merriami) responded positively to fire (15% greater in burned areas). Longtailed pocket mouse (Chaetodipus formosus) and canyon mouse (Peromyscus crinitus) were 91% and 98% less abundant in burned versus unburned areas. The positive response of Merriam's kangaroo rat to fire is most likely correlated with their preference for open foraging microhabitat while other species captured prefer greater and more diverse cover. Because the small mammal community has been dramatically affected by fire, it is likely that top-down control of vegetation structure will be dominated by Merriam's kangaroo rat in burned areas, which may promote more open habitat by limiting the growth of annual and perennial grasses.

Keywords: kangaroo rat, top-down effects, bottom-up effects, fire, microhabitat

Chapter 5: Introduction

Desert ecosystems tend to experience less fire because water and nutrient limitations to plant growth result in low and discontinuous fuel loads (Kozlowski 1974). However, recent analysis shows that the Mojave Desert region may be at a "tipping point" between fire regimes of infrequent, patchy, small fires to continuous, large fires (Brooks and Matchett 2006). For example, fires burned 240,173 ha in the Mojave's mid elevation shrubland from 1980-2004, while in 2005 alone, a few fires burned more than 318,655 ha (Brooks and Matchett 2006). It is hypothesized that dramatic increases in non-native annual grasses (*Bromus* and *Schismus* spp.) under the right climatic conditions produce continuous fuel beds (Hunter 1991, Brooks 1999, Brooks et al. 2004) that appear to be driving an invasive plant/fire cycle in the Mojave Desert region (Brooks and Matchett 2006).

Small mammal communities are influenced directly by fire and also indirectly by burn effects on plant community structure. Research in tallgrass prairies has shown the direct effects of fire on small mammals includes burns, heat stress, asphyxiation, physiological stress, trampling, and predation during escape from fire (Kaufman et al. 1990). Some species that have aboveground nests, such as Neotoma spp., may perish directly from fire (Simons 1989, 1991). However, burrowing rodents such as Dipodomys spp., Perognathus spp., and Chaetodipus spp. are more likely to survive with greater burrow depth (Howard et al. 1959). Emigration can occur as small mammals flee their burrows/nest during the fire and do not return (Kaufman et al. 1990). Physiological stress induced by fire can impact small mammal populations through abortion of litters or abandonment of young. However, the primary influences fire has on the small mammal communities are indirect effects through changes in vegetation composition and

structure via bottom-up effects (Price 1978a). These changes in the plant community can alter the quantity or quality of food, availability of nest sites, alterations in predator-prey interactions and incidence of parasitism and disease (Kaufman et al. 1990).

Heteromyid rodents in the Mojave Desert possess unique attributes that cause them to interact with plant communities differently. For example, Kangaroo rats obtain the majority of their water through metabolism of carbohydrates leading to preferences for seeds high in carbohydrates (Zeng and Brown 1987). Both pocket mice and kangaroo rats have fur lined cheek pouches in which they transport preferred seeds to scatter and larder hordes (Pyare and Longland 2000, Beck and Vander Wall 2010) which is a dispersal mechanisms for plant propagules. Rodent species differ in foraging patterns based on microhabitat structure (Rosenzweig and Winakur 1969, Price 1978b, Hallett 1982). Changes in the structure of the small mammal community following fire can therefore alter top-down controls that small mammals have on plant community structure (Brown and Heske 1990, Kerley and Whitford 2009).

Because of the strong interactions and feedbacks between plant and small mammal communities, understanding how recent expansive fires in the Mojave Desert impacts small mammal communities is an important step in predicting how changing fire dynamics will alter the composition and function of Mojave Desert ecosystems. The objective of this study was to identify how recent fires in Mojave Desert mid-elevation shrubland, impacts the small mammal community. The following predictions were tested: 1) fire reduces small mammal abundance; and 2) small mammal species show differential sensitivity to fire-altered landscapes resulting in changes in small mammal community species richness and diversity.

Chapter 5: Methods

Chapter 5: Study location

The study area is located in the Beaver Dam Wash in southwest Utah (Fig. 1). Vegetation

present is typical of mid-elevation (850-1080 m) Mojave Desert shrubland dominated by

blackbrush (*Coleogyne ramosissima*), creosote bush (*Larrea tridentata*), white bursage

(*Ambrosia dumosa*), and Joshua tree (*Yucca brevifolia*). Much of the area is covered with exotic

plant species such as, filaree (*Erodium cicutarum*) and the winter annual red brome (*Bromus*

rubens). The soil is a young alluvium with sandy loam surface soils. The landscape has been

altered by extensive fires. From summer 2009 to spring 2010 we sampled small mammals in

existing burned areas caused by three separate fires that occurred in the spring/summer of 2005:

Westside (June, 27,059 ha), Duzak (July, 7,065 ha – within Utah), and Burgess 2 (July, 712 ha)

("Utah BLM On-line Data" n.d.).

Rodent survey

Four 1 kilometer long transects were established within previously burned areas and each

transect was paired with an adjacent transect in an unburned area (Fig. 1). Using digital

elevation models, transects were selected to generally follow ridge tops to minimize

topographical variations between burned and control sites. We sampled near burn boundaries to

minimize spatial effects on small mammal communities. Therefore differences that we observed

were likely due to fire. Burned sites were chosen based on adequate distance to comparable

unburned control sites as dictated by existing fire boundaries. Live-traps were geographically

distributed at 20 meter intervals along eight 1 kilometer long transects and baited with

commercially available wild birdseed mix. Traps were at minimum 50 meters (with an average of 211 meters) from any burn boundary, road or other distinct landscape transition.

One trapping session was conducted in each of the four seasons. A trapping session consisted of two consecutive nights of trapping the same site. Trapping sessions were held in August (summer) and October (fall) of 2009 and February (winter) and May (spring) of 2010. Sherman live traps were baited and set at dusk, and then checked after dawn. Small mammals were identified to species, weighed to the nearest 0.5 grams, checked for reproductive status, tagged with a small numbered ear tag and then released. Capture and handling procedures were approved by BYU Institutional Animal Care and Use Committee (Protocol # 09-0302).

Chapter 5: Statistics

Mean abundance of small mammals was calculated for the number of unique individuals of all species and for each individual species by site and by season from the trapping data obtained in August 2009 to May 2010. Tagged individuals that were captured in subsequent trapping seasons were counted as a unique individual for that season. We used species richness and Shannon's Diversity Index (SDI= $-\sum$pi ln(pi) where pi is the proportion of the i th species) to describe the small mammal community. Statistical significance for abundances, species diversity (SDI), and species richness was analyzed using Proc Mixed Repeated Measures model in SAS (SAS Institute, Cary North Carolina). Season was the repeated measure and data were grouped into 4 blocks of paired sites.

Information criterion methods (Akaike 1974, Burnham and Anderson 2002) were used to analyze five hypothetical models based on the effects of fire (fire) and two-way interactions of fire with

different seasons, and species (Table 1). Model 1 in Table 1 was used in the repeated measures ANOVA analysis.

Chapter 5: Results

Capture rate

We captured 383 individuals in 3,136 trap-nights between August 2009 and May 2010. 105 individuals were captured both first and second nights of trapping. 70 individuals were captured in more than one season. No individuals were recaptured on a different transect than where they were initially captured. Species captured included long-tailed pocket mouse (*Chaetodipus formosus*), Merriam's kangaroo rat (*Dipodomys merriami*), chisel-toothed kangaroo rat (*Dipodomys microps*), Ord's kangaroo rat (*Dipodomys ordii*), desert wood rat (*Neotoma lepida*), grasshopper mouse (*Onychomys leucogaster*), canyon mouse (*Peromyscus crinitus*), and deer mouse (*Peromyscus maniculatus*) (Fig. 2). White-tailed antelope squirrels (*Ammospermophilus leucurus*) were also common in Beaver Dam Wash but were excluded from analysis since over-night trapping did not provide an accurate measure of the abundance of this diurnally active small mammal.

Relative abundance of individuals by species

Merriam's kangaroo rat was the most frequently captured rodent averaging 10.8 ± 0.4 unique individuals per site per season (Fig. 2). The number of captures of long-tailed pocket mice and deer mice averaged 1.6 ± 0.4 and 1.3 ± 0.4 unique individuals per site per season,

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respectively. All other species cumulatively averaged fewer than 0.3 unique individuals per site per season.

Fire and seasonal effects on small mammal abundance

The mean number of unique small mammals captured along burned transects was less than unburned transects according to information theoretic analysis (Table 1). Unburned sites averaged 15.9 ± 1.6 unique individuals per season while burned sites averaged 12.1 ± 1.6 unique individuals per season. The presence of fire, season, and their interaction term in model 1, which had the lowest AICc value, emphasizes their important role in small mammal responses in our study (Table 1). In the ANOVA analysis season was significant ($p < 0.0001$) while fire ($p = 0.086$) and the interaction term ($p = 0.14$) were not. The Δi of 8.9 between models 2 and 1 indicates that seasonal fluctuation in small mammal activity was affected by fire (see section 3.5). Small mammal abundance ranged from 21.5 to 5.9 individuals per site and was greatest during the summer and winter periods (Fig. 3). In relation to unburned control sites, burned sites had lower small mammal abundance during summer and fall but not during the winter and spring periods (Fig. 3). Reproductive condition and sex ratios of small mammals were not significantly affected by fire ($p = 0.5$ and $p = 0.6$ respectively).

Fire effects on species richness and diversity

Species richness and diversity were significantly lower along burned transect compared to unburned controls ($p < 0.001$). Grasshopper mice, deer mice, chisel-toothed kangaroo rats, and Ord's kangaroo rats were never captured within the burned zones. The few desert wood rats

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that were caught within the burned sites were found near deadfall. Merriam's kangaroo rat, the most abundant small mammal year round, was dominant on both burned and unburned sites, and was often the only species captured on burned sites. This resulted in the average species richness for burned sites of 1.31 ± 0.15 species per site per season. Species richness for unburned sites averaged 2.4 ± 0.15 species per site per season. Shannon's diversity index (SDI) averaged 0.62 ± 0.06 for unburned sites and 0.13 ± 0.06 for burned sites.

Fire and seasonal effects on individual species

Small mammal species varied in their response to fire ($p < 0.01$, Table 2). More specifically, Merriam's kangaroo rat had greater abundances along burn transects ($p = 0.05$), whereas all other species had negative (e.g., long-tailed pocket mouse and canyon mouse) or undetectable responses to fire (Fig. 2). Long-tailed pocket mouse abundance only showed negatively responses to fire in the summer with captures too infrequent to demonstrate a response during other seasons (Fig. 3). Fire had a strongly negative effect on canyon mouse abundance in summer and fall but captures were too infrequent in winter and spring periods to document responses. Merriam's kangaroo rat abundance was positively affected by fire in the summer and winter seasons, showed negative fire responses in fall and no significant effect of fire in the spring.

Chapter 5: Discussion

Fire influences on abundance of small mammal

Consistent with our first prediction, burned sites had fewer small mammals than adjacent undisturbed sites. Reduction in total abundance of small mammals in burned sites was most strongly influenced by losses of long-tailed pocket mice and canyon mice. For heteromyid rodents, different species have been observed to specialized in different foraging microhabitats (i.e. large open spaces, small open spaces, large bushes, and trees) and interspecies competition increases heteromyid preferences to particular foraging microhabitats (Price 1978b). The elimination of shrub-covered microhabitats by fire in Beaver Dam Wash likely had negative effects on persistence of long-tailed pocket mice which prefer shrub cover (Price 1978b).

All species captured had negative or undetectable responses to fire with the exception of Merriam's kangaroo rat. Merriam's kangaroo rat dominated small mammal captures (>70%) and was the only species that was more abundant in the burned sites than the unburned controls (see Fig. 2). Merriam's kangaroo rat increase at burned sites is likely related to its foraging preference for open spaces (Price 1978b, Simons 1991, Vamstad and Rotenberry 2010). Bailey's pocket mouse (*Chaetodipus baileyi*) (similar to long-tailed pocket mouse in our study) has previously been observed to decrease in numbers after controlled fire in the Sonoran Desert (Simons 1991). Consistent with our findings canyon mice have also been observed to prefer unburned sites and old burned sites with greater vegetation cover than recently burned sites (Vamstad and Rotenberry 2010). Decreases in individuals of some species at burned sites has not previously been observed to decrease total small mammal numbers as increases in Merriam's kangaroo rat numbers at burned sites compensated for reductions of other species (Vamstad and Rotenberry

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2010). In contrast, we found that the positive response of Merriam's kangaroo rat to burned habitat was not sufficient to compensate for the severe losses of long-tailed pocket mice and canyon mice in burned sites.

The diet of Merriam's kangaroo rat includes up to 30% green vegetation by volume between February to May and again in August (Bradley and Mauer 1971). Limited green annual vegetation can limit reproduction of Merriam's kangaroo rat and effectively reduce the population (Beatley 1969, 1976). However, we found Merriam's kangaroo rat from burned sites in reproductive conditions throughout the trapping sessions except in October. Either Merriam's kangaroo rat is able to find sufficient green tissue for water from surviving native plants or exotic annuals in burn zones or they are capable of sustaining themselves on metabolic water (Soholt 1975, Walsberg 2000). A reliable food source is also necessary to maintain or increase Merriam's kangaroo rat populations whose diet consists primarily of seeds (Bradley and Mauer 1971). Merriam's kangaroo rat has been shown to be the primary consumers of creosote bush (*Larrea tridentata*) seeds (Boyd and Brum 1983). However, creosote bush mortality along our burned transects was greater than 90% (unpublished data). Merriam's kangaroo rat has been found to be capable of consuming 90% of the total filaree production (Soholt et al. 1973). Invasive vegetation like redstem filaree (*Erodium cicutarium*) is prevalent throughout the burned sites. Given the lack of native vegetation and the abundance of invasive annuals we hypothesize that Merriam's kangaroo rats are meeting their food and water needs by consuming exotic plant tissues and seeds.

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Fire reduced species richness and diversity

Burned sites had lower species richness and species diversity (SDI) than in adjacent undisturbed

sites as outlined in our second prediction. A study in Joshua Tree National Park (Vamstad and

Rotenberry 2010) also reported that fire decreased small mammal species diversity but not

species richness. Rosenzweig and Winakur (1969) observed that granivorous desert rodent

diversity increased with environmental heterogeneity. Lower species diversity and richness in

burned areas in our study may be linked to increased interspecies competition among rodents as

fire homogenizes the landscape (Rosenzweig and Winakur 1969). Our data are consistent with

the idea that more expansive and numerous open spaces left from large fires have provided

Merriam's kangaroo rat with its preferred foraging habitat. All other granivorous species in

burned sites deal with loss of preferred habitat (which is likely linked with predator evasion

strategies) and increased competition from Merriam's kangaroo rat.

Fire effects vary by season

Seasonal variances in small mammal populations (particularly for Merriam's kangaroo

rat) have been observed (Zeng and Brown 1987) and are linked with precipitation through plant

primary production (Beatley 1976, Thibault et al. 2010). However, we observed that seasonal

fluctuations in small mammal captures between burned and unburned areas (see Fig. 3 and

Table 1 models 1 and 3). The reductions in Merriam's kangaroo rat captures for autumn 2009

along burned transect compared to unburned controls may have been associated with exposure to

low temperature (0 ºC) and high winds (personal observation). Temperature and wind effects are

likely greatest at burned sites which lack vegetation cover resulting in temperature extremes to which rodents are sensitive (Reynolds 1958).

Implications for plant communities

Fire effects on small mammal community structure can have feedbacks on the plant community via top-down effects that includes consumption of primary production, seed predation and dispersal, and soil disturbance (Titus et al. 2002, Vander Wall et al. 2005, Stapp 2010). Our data show that burned Mojave Desert landscapes experience drastic changes in small mammal community structure characterized by increases in Merriam's kangaroo rat and losses of other species. A few studies provide insight on how a more dominant influence by Dipodomys spp. may feedback on the re-establishment of plant communities following fire. Kerley and Whitford (Kerley and Whitford 2009) found that Dipodomys spp. can promote shrub establishment by reducing the amount of tall grasses present through the consumption of grass tillers. In the Chihuahuan Desert, experimental exclusion of Dipodomys spp. resulted in an increase in tall perennial and annual grasses (Brown and Heske 1990, Curtin et al. 2000).

The interplay between plant and small mammal communities are strongly influenced by climate conditions (Beatley 1976). The disturbance to the small mammal community may affect their ability to limit the establishment of annual grasses which would result in higher fuel loads. Future studies should focus on identifying how patterns of future climate will influence small mammal-plant interactions particularly as it relates to shorter fire return intervals associated with invasive grass-fire cycles (Beatley 1966, Agnew 1997).

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Chapter 5: Tables

Table 1. AIC table for hypothetical models

Model	log(L)	*K (number of parameters)*	AICc	Δ_i	relative likelihood	w_i
1	-519.65	7	1043.3	0	1	0.988456
2	-524.1	6	1052.2	8.9	0.011678567	0.011544
3	-536.2	6	1076.4	33.1	6.49E-008	6.42E-008
4	-540.55	5	1085.1	41.8	8.38E-010	8.28E-010
5	-541.6	4	1087.3	44	2.79E-010	2.76E-010

Model	Model
1	count = fire + species + season + fire*species + fire*season + species*se
2	count = fire + species + season + fire*species + species*season
3	count = fire + species + season + fire*season + species*season
4	count = fire + species + season + species*season
5	count = species + season + species*season

Table 2. F-values from repeated measures ANOVA examining abundance, diversity, and richness of small mammals to fire (across burn boundaries), season (over the four different trapping periods), fire and season (effect of fire changing with season), and fire*season*species (species specific effects of fire in relation to season).

Source of variance	abundance	diversity	richness
fire	3.42	50.11***	23.62***
season	14.19***	10.51***	5.25
fire*season	2.09	5.16**	2.04**
fire*species	3.58**	n/a	n/a
fire*season*species	2.47***	n/a	n/a

Significance designated as *P < 0.05, **P < 0.01, ***P < 0.001
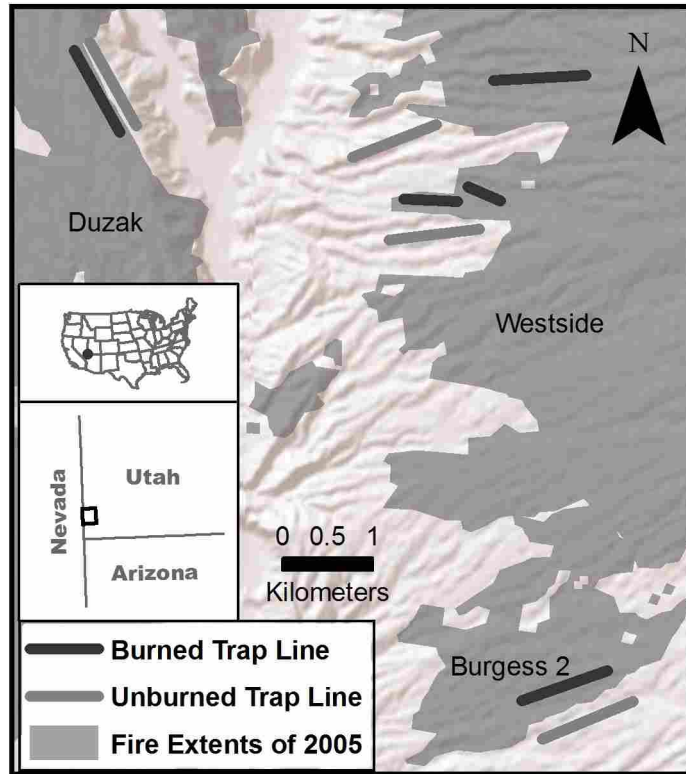
Chapter 5: Figures

Fig. 1. Map of Beaver Dam Wash (N37.14, W114.03) study site. Trap-lines in three independent burns (black) were paired with adjacent traplines in unburned sites (gray). Study area denoted by black rectangle in southwest corner of Utah.
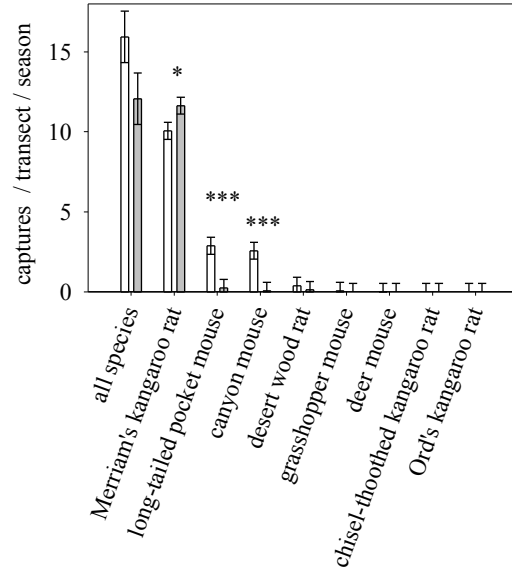
Fig. 2. Number of small mammals captured along unburned (white bars) and burned (gray bars) transects differentiated by species. Statistical significant defined as: * p < 0.05; ** p < 0.01; *** p < 0.001.
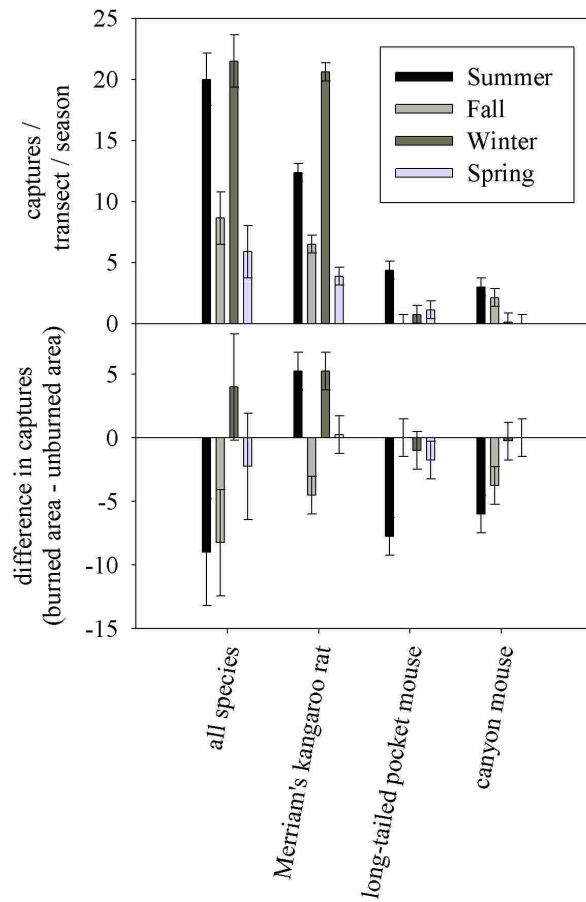
Fig. 3. Average abundance of small mammals (top) and difference in the number of small mammals between burned and unburned transects (bottom) for all species, Merriam's kangaroo rat, long-tailed pocket mouse, and canyon mouse for all four trapping sessions. Average values below '0' in bottom graph indicate fewer number of small mammals in burned vs. unburned areas. Error bars are ±1 standard error