IMPACTS OF CLIMATE AND DISTURBANCES ON VEGETATION DYNAMICS IN PIÑON-JUNIPER WOODLANDS

by

MIRANDA D. REDMOND

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written by Miranda D. Redmond
has been approved for the Department of Ecology and Evolutionary Biology

Dr. Nichole Barger

Dr. William Bowman

Dr. Jeffry Mitton

Dr. Tania Schoennagel

Dr. Thomas Veblen

Date______________

The final copy of this thesis has been examined by the signatories, and we
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Redmond, Miranda D. (Ph.D. Ecology and Evolutionary Biology)

IMPACTS OF CLIMATE AND DISTURBANCES ON VEGETATION DYNAMICS IN PIÑON-JUNIPER WOODLANDS

Thesis directed by Associate Professor Nichole N. Barger

ABSTRACT

Global climate change and altered disturbance regimes have already and are predicted to continue to cause significant shifts in vegetation distribution. Regional warming has increased tree mortality rates over the past several decades through increasing water deficits and insect outbreaks, which have dramatically changed forest and woodland structure and altered water and energy fluxes and carbon stocks. For the first part of my dissertation, I use field surveys and historical data to examine how changes in climate and recent piñon pine (*Pinus edulis*) mortality events may affect tree regeneration dynamics in the widely distribution piñon-juniper (*Juniperus osteosperma and J. monosperma*) woodlands of the southwestern USA. First, I show that piñon seed cone production declined by 40% from the 1974 decade (1969-1978) to the 2008 decade (2003-2012) in revisited stands throughout New Mexico and northwestern Oklahoma. Seed cone production was highly correlated with late summer temperatures at the time of cone initiation. Further, declines in seed cone production were greatest among populations that experienced the greatest increases in growing season temperatures, which were the populations located at the cooler, upper elevations. Second, I examine the effects of increasing temperatures and recent piñon mortality on tree recruitment and growth across the southwestern USA and determine how these effects are moderated by local climate, biotic interactions, and soil properties. In addition to changing climate and recent mortality events, large tracts of land across the western U.S. have been managed over the last century in an effort to increase forage production and timber harvesting yields, reduce the risk of wildland fires, and/or restore ecosystem structure, and these human disturbances can also dramatically alter these woodland ecosystems. The second part of my dissertation research documents the spatial extent and cost of past management treatments done within piñon-juniper woodlands of the Colorado Plateau. In addition, I determine the legacy effects of these past treatments on understory vegetation and woodland structure as well as the efficacy of current management practices at accomplishing management goals. Overall, my findings have provided important insights into how woodlands recover following disturbances under a warmer climate.

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CHAPTER 1

INTRODUCTION

Background

The effects of changing climate and altered disturbance regimes on vegetation dynamics is a pressing research concern. Global climate change has been predicted to increase the frequency and severity of drought events occurring under warmer temperatures (Meehl & Tebaldi, 2004; Seager et al., 2007), which may lead to substantial shifts in vegetation distribution (Choat et al., 2012). Extensive tree mortality has already occurred across the western USA (Breshears et al., 2005; van Mantgem & Stephenson, 2007; van Mantgem et al., 2009; Worrall et al., 2010) and globally (Allen et al., 2010; Carnicer et al., 2011) over the past decade as a result of a combination of drought, insect outbreaks and warmer temperatures. This has led to an increasing need to effectively manage ecosystems to both mitigate hazardous wildfires and maintain, and in some cases restore, the structure, function, diversity and dynamics of forest and woodland ecosystems. The overarching goal of my dissertation research is to better understand the effects of climate and disturbances on vegetation dynamics so that as a society we can make more informed management decisions. My research addresses this overarching goal by investigating questions such as: 1.) How do drought-induced tree mortality and climate affect tree regeneration dynamics and what are the bottlenecks to tree regeneration? [Chapters 2 and 3]; 2.) Do biotic interactions and soil properties moderate the effects of changing climate on tree regeneration? [Chapter 3]; 3.) What is the effect of forest management practices on understory vegetation and tree regeneration over both short (1-2 yr) and long (50 yr) time scales? [Chapters 4-6]

Study System

In this dissertation, I focus my research on woodlands co-dominated by piñon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma* and *J. monosperma*), a widespread vegetation type of the southwestern USA and one of the predominant vegetation types administered by federal land-management agencies in the US (Romme et al., 2009). There has already been an increase in water deficits throughout the southwestern USA over the past decade (Williams *et al.*, 2013), and future projections of climate change across this region suggest this trend will continue (Seager *et al.*, 2007; Williams *et al.*, 2013). Due to a combination of warmer temperatures, drought, and beetle infestations between 2002 and 2004 there was extensive piñon mortality, with upwards of 90% mortality in some stands (Breshears *et al.*, 2005; Mueller *et al.*, 2005; Clifford *et al.*, 2013). Piñon-juniper woodlands provide ecosystem services to humans and critical habitat for a variety of wildlife species (Brown *et al.*, 2001), and these recent changes in climate and disturbances have raised concern that these woodlands may become increasingly juniper dominated. Interestingly, piñon-juniper ecosystems have also been a major focus for land-management activities (i.e. tree-reduction treatments) over the past half-century to restore herbaceous cover and reduce the risk of wildland fires and these activities have the potential to strongly affect vegetation dynamics over both short and long time-scales.

Research Outline

The first part of my dissertation research (chapters 2-3) aims to understand how changing climate and recent drought-induced tree mortality may affect tree regeneration dynamics in piñon–juniper woodlands. The first research chapter of my dissertation is focused on the effects of climate on piñon pine cone production (chapter 2; Redmond et al., 2012). For the second research chapter of my dissertation, I examined tree regeneration following drought-induced piñon mortality across a vegetation structure and soil gradient in southwestern Colorado (chapter 3; Redmond and Barger, 2013).

The second part of my dissertation research (chapters 4-6) is focused on documenting the spatial extent and cost of past management treatments done within piñon-juniper woodlands of the Colorado Plateau (chapter 4; Redmond et al. 2014a). My research has also focused on the legacy effects of these past treatments on understory vegetation and woodland structure (chapter 5; Redmond et al. 2013) as well as the efficacy of current management practices at accomplishing management goals (chapter 6; Redmond et al. 2014b).

CHAPTER 2

DECLINES IN PIÑON PINE CONE PRODUCTION ASSOCIATED WITH REGIONAL WARMING

Adapted from: Redmond MD, Forcella F, and NN Barger. 2012. Declines in pinyon pine cone production associated with regional warming. Ecosphere 3: 120

Abstract

Global climate change is expected to produce large shifts in vegetation distribution and has already increased tree mortality, altering forest structure. However, long-term shifts will be partly dependent on the ability of species to reproduce under a novel climate. Few studies have examined the impact of climate change on the reproductive output of long-lived ‘masting’ species, or species characterized by episodic reproductive events. Here, I show that seed cone production among piñon pine (*Pinus edulis*), a masting species, declined by 40% from the 1974 decade (1969-1978) to the 2008 decade (2003-2012) in revisited stands throughout New Mexico and northwestern Oklahoma. Seed cone production was highly correlated with late summer temperatures at the time of cone initiation. Further, declines in seed cone production were greatest among populations that experienced the greatest increases in growing season temperatures, which were the populations located at the cooler, upper elevations. As growing season temperatures are predicted to increase across this region over the next century, these findings suggest seed cone production may be an increasingly important bottleneck for future piñon pine regeneration, especially in areas with greater increases in temperature. Declines in seed cone production may not only affect piñon pine population dynamics but also the various wildlife species that rely on piñon pine seeds. Since piñon pine has similar reproductive strategies as other semi-arid pine species, increasing temperature may negatively influence

reproductive output of other conifers. Further investigation into the full geographic and taxonomic extent of these seed declines are warranted**.**

Introduction

Altered precipitation regimes and increasing land surface temperatures associated with global climate change have resulted in significant shifts in vegetation distribution over the past several decades (Parmesan and Yohe 2003, Kelly and Goulden 2008, Chen et al. 2011), and these patterns are predicted to continue over the next century (Pearson et al. 2002). Regional warming has resulted in recent increases in tree mortality by increasing water deficits (van Mantgem and Stephenson 2007, van Mantgem et al. 2009, Allen et al. 2010), insect outbreaks (Raffa et al. 2008, Mitton and Ferrenberg 2012), and wildfires (Westerling et al. 2006), which have dramatically changed forest and woodland structure. Many trees that died in these regional mortality events established under climatic conditions that may be rare or may no longer exist. Thus, a clear need exists to better understand the key bottlenecks to forest and woodland regeneration given recent large-scale mortality events and predicted changes in climate.

Research examining forest and woodland regeneration in response to recent changes in climate has focused mainly on germination, growth and survival (Kitzberger et al. 2000, Castro et al. 2004). Few studies, however, have examined the impacts of climate change on reproductive outputs, especially in mast seeding species (species with highly synchronous intermittent production of large seed crops) (but see Mutke et al. 2005 and Peréz-Ramos et al. 2010). This is likely due to the fact that annual reproductive outputs are highly variable across time and space, requiring sources of long-term data.

Numerous studies have shown that climatic fluctuations influence mast seeding (Norton and Kelly 1988, Sork 1993, Houle 1999, Piovesan and Adams 2001, Kelly and Sork 2002, Peréz-

Ramos et al. 2010). Thus, it logically follows that reproductive outputs of mast seeding tree species may be affected strongly by changing climate. Indeed, in a long-term rainfall exclusion experiment, Peréz-Ramos and colleagues (2010) observed negative impacts of increased drought on acorn production in *Quercus ilex.* Although the mechanisms by which climate regulated masting events are not well understood, the leading hypotheses are that masting occurs during favorable climatic conditions due to higher available resources (e.g., resource-matching hypothesis) or that climate serves as an adaptive synchronizing cue (Sork 1993, Kelly 1994, Kelly and Sork 2002). Certain mast-seeding low elevation conifers, including piñon pine (*Pinus edulis*), ponderosa pine (*Pinus ponderosa*), and stone pine (*Pinus pinea*), grow in water-limited environments and have higher reproductive output during cool and/or wet summers (Forcella 1981*b*, Mutke et al. 2005, Mooney et al. 2011). Thus, recent changes in precipitation and temperature patterns associated with global climate change may be adversely affecting reproductive output of these species.

In this study, I compare changes in piñon pine reproductive output from the 1974 decade (1969-1978) to the 2008 decade (2003-2012)— a time period in which mean growing season (March – October) temperatures increased by c. 1.3 °C while annual precipitation stayed relatively constant (increased by c. 3 cm) (Fig. 2-1 and Table 2-1). Piñon pine is a widely distributed and dominant tree of the southwestern U.S. and provides a range of ecosystem services to humans and critical habitat for a variety of wildlife species (Brown et al. 2002). Additionally, piñon pine experienced large-scale mortality in vast areas across its range during the most recent multi-year (2002-03) drought (Breshears et al. 2005, Mueller et al. 2005). Following this widespread mortality event, there is a keen interest in examining potential bottlenecks to piñon pine regeneration. I compared data of piñon pine seed cone production, one component of reproductive output, from the 1974 decade to the 2008 decade at 9 sites across New Mexico and northwestern Oklahoma. I addressed the following questions:

1. Has piñon pine seed cone production changed from the 1974 decade to the 2008 decade across New Mexico and northwestern Oklahoma?
2. Have recent changes in climate, including changes in late summer temperatures and changes in growing season temperatures, influenced piñon pine seed cone production?

I predicted that increasing temperatures across the region led to declines in seed cone production from the 1974 decade to the 2008 decade. Given the negative exponential relationship between seed cone production and late summer temperatures found by Forcella (1981*b*), I hypothesized that if late summer temperatures increased in the 2008 decade then seed cone production would decline. Additionally, since increasing growing season temperatures can negatively affect piñon pine by directly increasing respiratory costs and indirectly by increasing water stress (Adams et al. 2009), I predicted that areas with greater increases in growing season temperatures from the 1974 decade to the 2008 decade would be more vulnerable to declines in seed cone production.

Table 2-1. Temperature and precipitation across all sites in the 1974 decade and the 2008 decade.

		Growing Season Temp. (°C)		Annual Precip. (cm)		Proportion of Cool Late Summers	
Site	Elev. (m)	1974 decade	2008 decade	1974 decade	2008 decade	1974 decade	2008 decade
K2	1295	17.2	18.0	39.5	40.0	0.5	0.5
K1	1426	17.2	18.0	39.5	40.0	0.5	0.5
FB	1950	15.4	16.6	43.1	44.8	0.6	0.5
LV	2054	12.8	14.0	40.7	40.1	0.6	0.5
SF	2072	14.3	15.2	28.8	32.1	0.6	0.3
SP	2160	13.1	14.3	47.5	48.0	0.7	0.6
P	2170	11.9	13.8	34.9	41.2	0.6	0.3
MP	2179	12.1	13.8	47.6	60.1	0.5	0.4
R	2213	12.4	13.6	39.4	41.3	0.8	0.4
Overall		**14.0**	**15.3**	**40.1**	**43.1**	**0.6 ± 0.0**^{A}	**0.4 ± 0.0**^{B}

Notes: Growing season temperature (March – October) and annual precipitation were calculated as mean monthly temperature or precipitation during the year of cone initiation (2 years prior to mature cone formation) in both decades. The proportion of years with below average (1950-2010) late summer temperatures was calculated using the mean daily maximum summer temperatures during the two week time period most highly correlated with seed cone production at each site (see Fig. 2-3). Fort Bayard is missing two years of weekly climate data in the 2008 decade and therefore the proportion was calculated using only 8 years. Values in the lower row are means ± 1 SE across all sites, with different letters denoting significant differences between the two decades, with $\alpha = 0.05$.

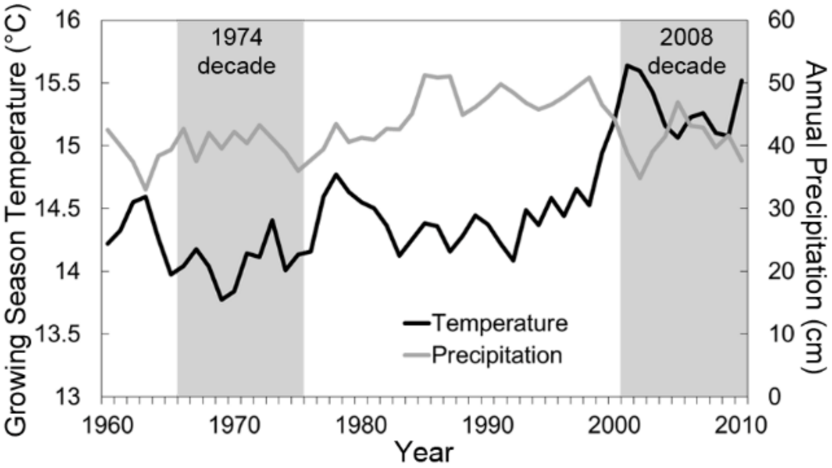


Figure 2-1. Three-year moving averages of mean growing season (March – October) temperature (°C) (black line) and annual precipitation (cm.) (grey line) from 1960 to 2010. Climate data are from the PRISM Climate Group and were averaged across all 9 sites.

Methods

Sampled Sites

Nine sites in New Mexico and northwestern Oklahoma previously sampled in 1978 to estimate seed cone production for the previous 10 years were revisited in 2011/2012 for this comparative study. Revisited sites were located within 1 km of the original sites and were similar in elevation (± 100 m), aspect (± 5 degrees), and slope (± 3 degrees) as those sampled in 1978. The 9 sites span four different ecoregions (EPA Terrestrial Ecosystems Level III Ecoregion Classification) with; 2 sites, Kenton 1 (K1) and Kenton 2 (K2), in the Southwestern Tablelands; 3 sites, Raton (R), Las Vegas (LV) and Pecos (P), in the Southern Rockies; 3 sites, Sandia Park (SP), Mountain Park (MP), and Fort Bayard (FB), in the Arizona/New Mexico Mountains; and 1 site, Santa Fe (SF) in the Arizona/New Mexico Plateau (Fig. 2-2). During the 2011/2012 sampling, there were no signs of fire, cutting, or any large mortality events in any of the sites, except for the Santa Fe site, which experienced greater than 80 percent mortality of adult piñon pines during the 2002-03 drought.

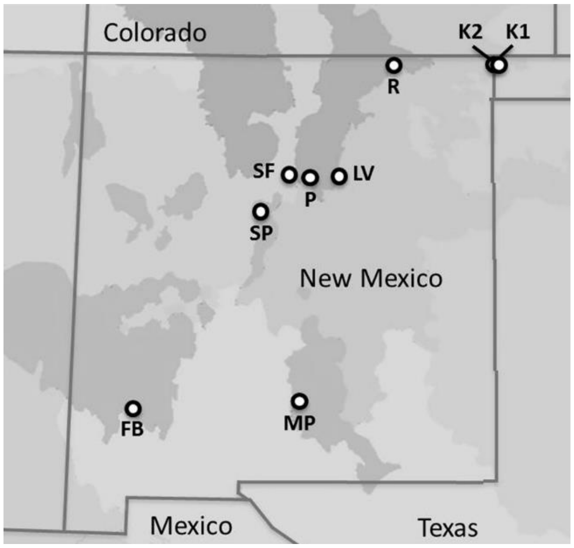


Figure 2-2. A map of the 9 sampled sites (white circles). Grey shading indicates different ecoregions (EPA Terrestrial Ecosystems Level III Ecoregion Classification).

Piñon Pine Seed Cone Production & Cone Abscission Scar Methodology

Piñon pine seed cones take 3 growing seasons (26 mo) to mature from the time of cone initiation (Little 1939, Mirov 1967). At cone initiation, microscopic buds develop during August or September. From the time of cone initiation to early summer when fertilization occurs, the microscopic buds develop into visible seed cones or conelets, which then overwinter. By the following fall, 26 mo after cone initiation, mature seed cones have formed (Little 1938, Mirov 1967). Similar to other pines (Weaver and Forcella 1986, Kajimoto et al. 1998, Crone et al. 2011), piñon pine seed cones leave visible abscission scars on tree branches. These abscission scars allow temporal variations in piñon pine seed cone production to be observed by counting cone scars (as well as any remaining cones or conelets) at each annual whorl on the branches (Forcella 1981*a*). Here, I used the cone abscission scar methodology to estimate annual seed cone production from 1969 – 1978 (data from the 1978 sampling) and from 2003 – 2012 (data from the 2011/2012 sampling). This methodology has been widely used across a range of pine species (Forcella 1981a,b, Weaver and Forcella 1986, Kajimoto et al. 1998, Crone et al. 2011). However, it is important to note that seed cone production estimates include both mature seed cones and aborted first year seed cones. Additionally, there is no data on whether detection of cone scars declines through time, however, this data showed no trend of a decline in cone scars through time in either the 1978 or 2011/2012 sampling (data not shown).

Field Methods

Sites were sampled in January of 1978 and between November 2011 and January 2012 following the methodology outlined by Forcella (1981*a*,*b*). At each site I examined 4 - 10 reproductive piñon pine trees in order to estimate seed cone production in the 1974 decade (1969-1978) and the 2008 decade (2003-2012). In 2011/2012 sampling, I selected cone-bearing trees that appeared healthy and had a similar basal diameter to those sampled in 1978. At 7 of the 9 sites, the average basal diameter of trees sampled in 2011/2012 was within 2 cm to trees sampled in 1978. At the 2 other sites, Santa Fe and Raton, average basal diameter was 8 - 10 cm larger in the 2011/2012 sampling.

During both the 1978 and the 2011/2012 sampling, I used the cone abscission scar methodology and counted young seed cones, mature seed cones, and seed cone abscission scars at the 10 most recent annual nodes on 5 - 10 cone bearing branches on each tree. However, 20 cone-bearing branches were examined on each tree at Kenton 1 in the 1978 sampling. Previous research on piñon pine from this region found that sampling 4-5 branches on 4-5 trees is a statistically sufficient sample size to estimate annual seed cone production at each site (for details see Forcella 1981*a*).

Annual Seed Cone Production Estimation

I estimated annual seed cone production at each site by calculating the mean seed cones produced per seed cone bearing branch (cones/branch) for each year from 1969 – 1978 (1974 decade) and from 2003 – 2012 (2008 decade). Previous research has shown that the number of seed cone bearing branches per tree increases as tree size increases (Forcella 1981*a*). However, there was no relationship between seed cones per branch and the number of seed cone bearing branches on a tree (Adjusted R^2 = -0.02, P = 0.99). There was also no relationship between the number of cones per branch and canopy area in a site (Adjusted R^2 = -0.10, P = 0.76). As a result, my estimation of annual seed cone production (mean cones per branch) was an appropriate estimation of changes in seed cone production from the 1974 decade to the 2008 decade at the tree-level, regardless of changes in tree density at the site-level.

Mast Years

To define mast years, for each site and each time period (1974 decade and 2008 decade), I first expressed yearly seed cone production as a standardized deviate of the annual mean seed cone production to the long-term mean calculated over all 10 years (i.e. (mean $\text{cones}_{\text{yearX}}$ – mean $\text{cones}_{\text{all years}}$)/$\text{SD}_{\text{all years}}$). I defined mast years as years in which the standardized deviate was greater than the absolute magnitude of the lowest standardized deviate (LaMontagne and Boutin 2007, 2009). Therefore, average seed cone years will have standardized deviates close to 0, low seed cone years will have negative standardized deviates, and high seed cone years will have positive standardized deviates that are beyond the range of the negative standardized deviates (LaMontagne and Boutin 2007). At all sites and in both decades, at least 80% of the trees produced cones during the defined mast years, highlighting the synchronicity in seed cone production of these populations.

Statistical Analysis

To examine changes in seed cone production across the study sites, I performed two separate two-tailed paired Student's t-tests to understand how total seed cone production (calculated as mean seed cone production across all 10 years in each decade) as well as how the strength of masting events (calculated as mean seed cone production during mast years in each decade) changed from the 1974 decade to the 2008 decade.

I examined the relationship between annual seed cone production and climate (precipitation and temperature) during the time frame when seed cone initiation occurs in piñon pine (Aug. 7- Sept. 24, 2 y prior to mature cone formation) (Little 1938, Mirov 1967). Climate data for 1967-1976 and 2001-2010 were obtained from the closest weather stations to each site (all < 40 kilometers) that had available climate data between Aug. 7 and Sept. 24. One site (Fort Bayard) had missing climate data in 2004 and 2010. Thus, these two years were not included in the analysis. Since the timing of cone initiation may vary between populations at different elevations and latitudes, I used 2-week running averages of daily maximum temperature and precipitation from Aug. 7- Sept. 24 (Little 1938, Mirov 1967). I chose this time frame a priori, since previous studies on pine species have found climate during seed cone initiation to be highly correlated with seed cone production (Lester 1967, Forcella 1981*a*, Mutke et al. 2005). I performed Spearman's rank correlation analyses at each site to evaluate the relationship between late summer temperature and precipitation during the year of seed cone initiation and annual seed cone production (i.e., 12 correlations per site since I used 2-week running averages). As temperatures have increased across this region over the past several decades, I hypothesized that there would be a decline in the frequency of years with cool late summer temperatures, which could lead to a decline in the frequency of masting events. Therefore, I performed a two-tailed paired Student's t-test to examine differences in the number of years with below average (1950-2010) late summer temperatures between the 1974 decade and the 2008 decade.

I examined the relationship between changes in seed cone production and changes in growing season temperatures from the 1974 decade to the 2008 decade. I used seed cone production data from mast years only, because the number of masting events may have differed in each decade due to the relatively short timespan sampled. Thus, at each site, I calculated the percent change in seed cone production from the 1974 decade to the 2008 decade, using data only from mast years. At each site, I also calculated the percent change in mean growing season temperatures (March – October) from the 1974 decade to the 2008 decade using climate data from the 3 years prior to seed conelet formation during mast years. I used climate data during the 3 years prior to seed conelet formation (i.e. the year of seed cone initiation and the 2 years prior), because climate of the previous 2-3 years influences growth of piñon pine (N.N. Barger, unpublished data), suggesting that cumulative warm temperatures may reduce non-structural carbohydrate reserves, which can influence seed cone production. I performed a simple linear regression of percent change in seed cone production as a function of percent change in growing season temperatures across the9 sites.

To better understand regional patterns of seed cone production and how they may vary with growing season temperatures, I performed a simple linear regression of mean seed cone production during mast years as a function of mean growing season temperatures during the 3 years prior to seed conelet formation during mast years. I performed this separately for the 1974 decade and the 2008 decade. Lastly, to better understand how patterns of regional variation in growing season temperatures may have changed from the 1974 decade to the 2008 decade, I performed a simple linear regression of percent change in mean growing season temperatures from the 1974 decade to the 2008 decade as a function of mean growing season temperature in the 1974 decade. For this analysis, I used growing season temperature data during the year of cone initiation in each decade (i.e. 1967 – 1976 and 2001 – 2010). For all analyses using growing season temperatures, mean monthly temperature data were from the PRISM Climate Group (PRISM Climate Group 2012) rather than local weather stations, since the PRISM Climate Group had a complete climate record (months of climate data were missing at certain weather stations). All analyses were performed using the statistical software R (R Development Core Team 2011), with $\alpha = 0.05$.

Results

Average seed cone production within mast years and total seed cone production declined by 43% and 40%, respectively, from the 1974 decade to the 2008 decade ($P < 0.001$; table 2-2). These declines were driven primarily by 7 of the 9 sites, which had > 40% declines in seed cone production within mast years, whereas the other two sites, Kenton 1 and Kenton 2, showed little change (table 2-2).

In 8 of the 9 study sites, seed cone production was negatively correlated with late summer temperature during the year of seed cone initiation (all Spearman's $\rho < -0.55$, all $P < 0.03$; Fig. 2-3). During the same 2 week period that was most highly correlated with temperature (see Fig. 2-3 caption), I also observed a positive relationship between late summer precipitation and seed cone production at 4 of the 9 study sites (Raton, Las Vegas, Sandia Park, and Mountain Park) (all Spearman's $\rho > 0.45$, all $P < 0.05$). Additionally, late summer precipitation and temperature during Sept. 3 – Sept. 17 and Aug. 21 – Sept. 3 was strongly correlated with seed cone production for Fort Bayard and Santa Fe, respectively (precipitation: all Spearman's $\rho > 0.51$, all $P < 0.03$; temperature: all Spearman's $\rho < -0.51$, all $P < 0.03$). Late summer precipitation and temperature were inversely related at 5 of those 6 sites that showed a strong correlation with precipitation and seed cone production (Santa Fe was the exception) (all Spearman's $\rho < -0.45$, all $P < 0.05$), which is consistent with previously observed temperature/precipitation relationships across this region. While seed cone production was correlated with both late summer temperature and precipitation at 6 of the 9 sites, I focus on the temperature relationship, as late summer temperatures increased in the 2008 decade relative to the 1974 decade whereas precipitation remained relatively constant (Fig 1 and table 2-1).

Table 2-2. Seed cone production across all sites in the 1974 decade and the 2008 decade.

	Mast Years Only (mean cones/branch)		All Years (mean cones/branch)		Frequency of Masting Events	
Site	1974 decade	2008 decade	1974 decade	2008 decade	1974 decade	2008 decade
K2	2.5	2.8	0.8	1.0	2	2
K1	2.7	2.2	1.2	0.9	2	3
FB	2.5	1.3	0.8	0.4	2	2
LV	2.3	1.3	1.0	0.4	2	2
SF	3.5	1.8	0.9	0.3	2	1
SP	3.5	2.1	1.1	0.7	2	3
P	3.5	1.0	1.0	0.4	2	2
MP	3.7	1.1	0.9	0.3	2	2
R	4.9	1.9	0.8	0.5	1	2
Overall	**3.2 ± 0.3**^{A}	**1.8 ± 0.2**^{B}	**0.9 ± 0.1**^{A}	**0.5 ± 0.1**^{B}	**1.9 ± 0.1**	**2.1 ± 0.2**

Notes: Values in the lower row are means ± 1 SE across all sites, with different letters denoting significant differences between the two decades, with $\alpha = 0.05$. In both decades, I calculated mean seed cone production (mean cones/branch) using data from mast years only as well as all years.

As temperatures have increased in the 2008 decade relative to the 1974 decade I expected there to be fewer years in the 2008 decade with cool late summer temperatures, and thus, potentially fewer opportunities for masting. Indeed, I observed a 26% decline in the frequency of years in the 2008 decade with below average late summer temperatures (mean decline ± 1 SE = 26 ± 7%; $P = 0.01$; table 2-1). Further, I hypothesized that the decline in seed cone production during mast years may be due to warmer late summer temperatures. However, at 6 of the 9 sites there was no increase in late summer temperatures during mast years from the 1974 decade to the 2008 decade. Las Vegas, Santa Fe, and Pecos, the other 3 sites, had a 0.5 °C, 2.4 °C, and 0.7 °C increase in late summer temperatures during mast years, respectively. These results suggest that late summer temperatures do not solely explain the declines in seed cone production during mast years.

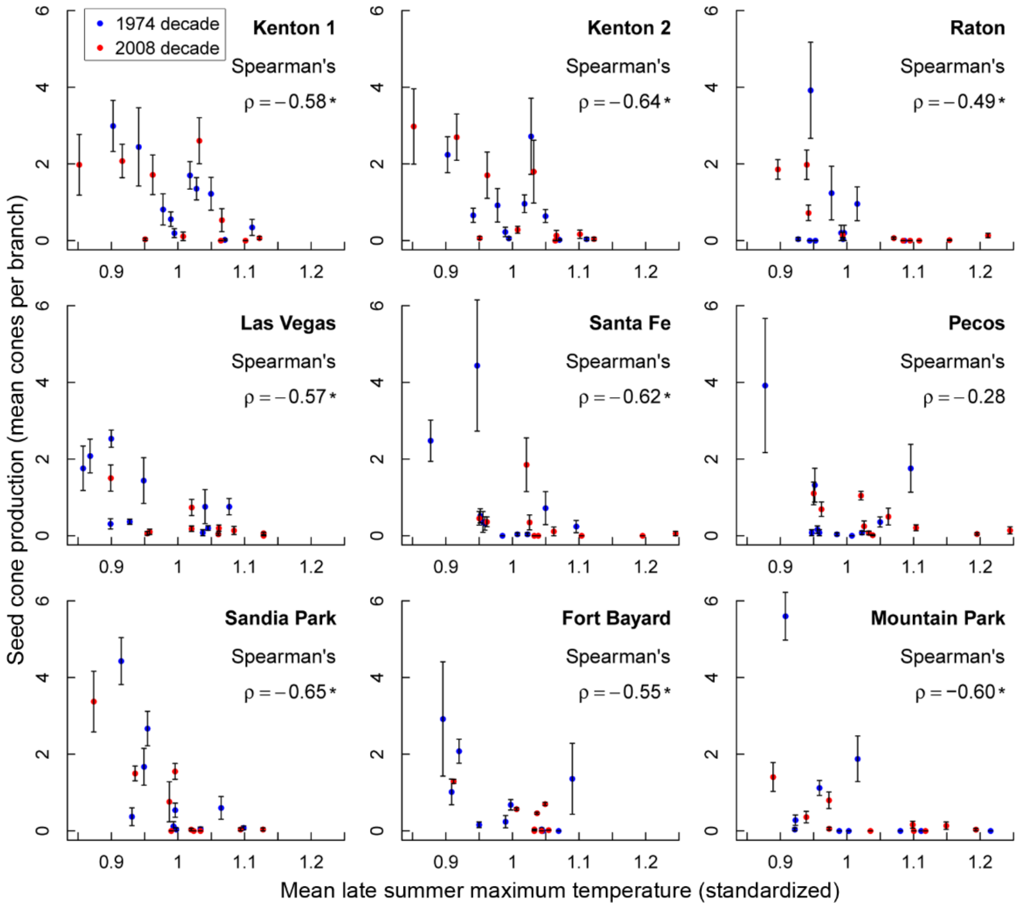


Figure 2-3. Seed cone production (mean cones per branch) and standardized late summer temperature (Temp (year of cone initiation)/Temp(1950-2010 Avg)) during cone initiation in the

1974 decade (blue circles) and the 2008 decade (red circles). The 2 week time period of late summer temperature that was most strongly correlated with seed cone production is Aug. 14 – Aug. 27 for all sites except Las Vegas (Aug. 21 – Sept. 3) and Fort Bayard (Aug. 28 – Sept. 10). Fort Bayard is missing two years of data in the 2008 decade due to missing climate data. Seed cone production for those years was 1.3 and 0.2. Significance levels at $P < 0.05$ are denoted with an asterisk and error bars are ± 1 SE.

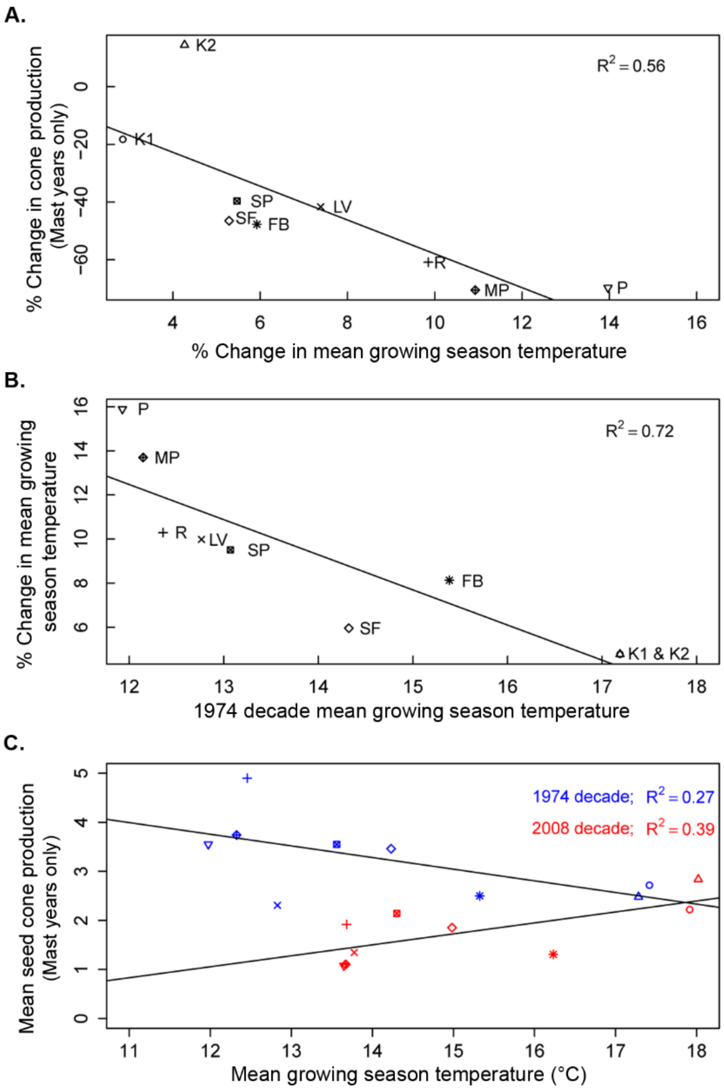


Figure 2-4. Changes in climate and cone production. (**A**) Percent change in mean seed cone production during mast years from the 1974 decade to the 2008 decade in relation to the percent change in mean monthly growing season (March – October) temperatures during the 3 years prior to seed conelet formation during mast years (slope = -5.86, Adjusted $R^2 = 0.56$, $P = 0.01$). Letters at the right of each symbol indicate the corresponding site. (**B**) Percent change in mean growing season temperatures from the 1974 decade to the 2008 decade during the years of cone initiation (2 years prior to cone maturation) in relation to mean growing season temperatures (°C) in the 1974 decade during the years of cone initiation (slope = -1.59, Adjusted $R^2 = 0.72$, P =

0.002). (**C**) Regional variations in seed cone production (mean cones per cone bearing branch during mast years) in relation to mean monthly growing season (March – October) temperatures (°C) during the 3 years prior to seed conelet formation during mast years in the 1974 decade (blue symbols) and the 2008 decade (red symbols). There was a marginally significant negative linear relationship in the 1974 decade (slope = -0.24, P = 0.09) and a significant positive relationship in the 2008 decade (slope = 0.23, P = 0.04). Each symbol corresponds to the site with the same symbol in Fig. 4a and b.

Growing season temperatures increased across all sites from the 1974 decade to the 2008 decade (table 2-1), but sites were highly variable in the percent increase in growing season temperatures (5 to 16%) (table 2-1). Interestingly, study sites with a greater increase in growing season temperature during the 3 years prior to seed conelet formation during mast years typically had a greater decline in seed cone production during mast years (Adjusted R^2 = 0.56, P = 0.01; Fig. 2-4a).

When I compared how regional patterns of seed cone production during mast years varied with growing season temperatures in the 1974 decade, I found a marginally significant, weak negative association between growing season temperatures during the 3 years prior to seed conelet formation during mast years and seed cone production during mast years (Adjusted R^2 = 0.27, P = 0.09; Fig. 2-4c), suggesting populations located in cooler areas had higher seed cone production in the 1974 decade. Contrary to the 1974 decade, in the 2008 decade there was a positive association between mean growing season temperature during the 3 years prior to seed conelet formation during mast years and seed cone production during mast years (Adjusted R^2 = 0.38, P = 0.04; Fig. 2-4c). Areas with cooler growing season temperatures in the 1974 decade had much greater increases in growing season temperatures from the 1974 decade to the 2008 decade (Adjusted R^2 = 0.72, P = 0.002; Fig. 2-4b). Therefore, this shift from a weak negative relationship to a positive relationship between seed cone production and growing season temperatures from the 1974 decade to the 2008 decade may be due to the greater declines in seed cone production that occurred at the cool, upper elevation sites (table 2-1 and Fig. 2-4a), as those sites had greater increases in growing season temperatures (table 2-1 and Fig. 2-4b).

Discussion

Growing attention has focused on the impacts of climate change, namely increasing temperatures and altered precipitation, on vegetation distribution and function (Walther et al. 2002, Parmesan and Yohe 2003, Kelly and Goulden 2008, Adams et al. 2009, Chen et al. 2011). However, little is known about the impacts of climate change on reproductive output of conifers. Results of my comparative study revealed clear declines (>40% at the majority of sites) in piñon pine seed cone production from the 1974 decade (1969-1978) to the 2008 decade (2003-2012). Mutke and colleagues reported similar patterns of declines in seed cone production from 1960 to 2000 in stone pine in Spain at the stand level (Mutke et al. 2005), which highlights that declines in seed cone production may be occurring across a wide range of pine species. Further, this study shows that declines in seed cone production were greatest in areas with greater increases in growing season temperatures, which suggests seed cone production may be an important bottleneck to piñon pine regeneration with climate change.

Similar to results of Forcella (1981*b*), I found late summer temperatures during the year of seed cone initiation to be strongly related to seed cone production across 8 of the 9 study sites (Fig. 2-3). These results are consistent with other studies that have found climate during seed cone initiation to be strongly correlated with seed cone production (Lester 1967, Houle 1999, Mutke et al. 2005) and suggest cool late summer temperatures are an adaptive synchronizing cue to initiate masting and/or strongly influence available resources (see Kelly and Sork 2002 for an overview of hypothesized reasons for mast seeding). In support of the adaptive synchronizing cue hypothesis, Forcella (1981*b*) observed high annual variability in biweekly temperatures during late summer (as opposed to mid-summer), which would provide the temperature extremes that are important for a synchronizing cue. Alternatively, in these semi-arid ecosystems, cool late summer temperatures may be important for reducing stress during the hottest time of the year and thus may influence available resources.

While I am unclear of the mechanism(s) underlying the negative relationship between seed cone production and late summer temperatures, there was a decrease in the frequency of cool late summers from the 1974 decade to the 2008 decade (table 2-1), indicating there were fewer years in the 2008 decade with suitable masting conditions. Fewer years with cool late summer temperatures will likely continue with climate change and may lead to a decline in the frequency of masting events. However, longer-term data are needed to examine changes in the frequency of masting events that occur on time scales of every 3-5 years.

My results suggest that increases in growing season temperatures are an important predictor of declines in seed cone production. From the 1974 decade to the 2008 decade, mean growing season temperature increased on average by c. 1.3 °C across the study sites (Fig. 2-1 and table 2-1), while annual precipitation remained relatively constant (increased by c. 3 cm) (Fig. 2-1 and table 2-1). Further, while I found an overall decline in seed cone production from the 1974 decade to the 2008 decade, sites were highly variable in the percent change in seed cone production (12 to -70%) and also in the percent increase in growing season temperatures (5 to 16%) (table 2-1 and Fig. 2-4b). Notably, sites with greater increases in growing season temperatures had significantly greater declines in seed cone production (Fig. 2-4a). Additionally, while cool late summer temperatures were highly correlated with seed cone production and may be a cue to initiate masting or are favorable climatic conditions, these results indicate that late summer temperatures did not, or at least not solely, affect changes in seed cone production within mast years from the 1974 decade to the 2008 decade. Although temperatures have increased over the past several decades, mean late summer temperatures during mast years did not increase from the 1974 decade to the 2008 decade at the majority (6 out of 9) of sites. Thus, late summer temperatures alone do not fully explain the decline in the strength of masting events at most of the sites.

The relationship between declines in seed cone production with increasing growing season temperatures in years leading up to masting events suggests that longer term temperature related stress may be an important factor in seed cone production. Higher temperatures can have both direct (respiratory costs) and indirect effects (water stress) on internal carbohydrate reserves in piñon pine (Adams et al. 2009), which are necessary for mast seeding species to reproduce (Isagi et al. 1997, Satake and Iwasa 2000, Miyasaki et al. 2002). Thus, increases in temperature may strongly influence internal carbohydrate reserves, effecting reproductive ability (Isagi et al. 1997, Satake and Iwasa 2000, Miyazaki et al. 2002). These results support the resource-matching hypothesis of mast seeding by highlighting how climate, which in this case are increases in growing season temperatures, can constrain resources and influence reproductive output in mast seeding species.

The results presented here suggest that areas with greater increases in temperature may be more vulnerable to declines in seed cone production. Climate models predict greater temperature increases at higher elevations (Giorgi et al. 1997), which is consistent with changes in growing season temperature across the research sites (table 2-1 and Fig. 2-4b). Thus, while populations at the upper elevation of species limits typically experience cooler climates and are predicted to be a refugia with increased warming (Pearson et al. 2002), these populations may be more vulnerable to declines in reproductive output due to greater increases in temperature. Indeed, in the 1974 decade, sites with cool growing season temperatures tended to have higher seed cone production (Fig. 2-4c). Contrary, in the 2008 decade, sites with warmer growing season temperatures tended to have higher seed cone production (Fig. 2-4c). This may be explained by the greater declines in seed cone production that occurred at the cool, upper elevation sites (Fig. 2-4a and table 2-1), which had the greatest increases in growing season temperatures (Fig. 2-4b). These results highlight how the cool, upper elevation populations may be more vulnerable to climate change than previously predicted.

The shift from a negative relationship between seed cone production and growing season temperatures in the 1974 decade to a positive relationship in the 2008 decade suggests populations are locally adapted to climate. If populations were not locally adapted to climate, I would expect the relationship between seed cone production and growing season temperatures to remain negative in the 2008 decade. However, this was not the case. Rather, populations located in warmer climates had higher cone production in the 2008 decade as compared to the populations located in cooler climates, which experienced greater increases in growing season temperatures and greater declines in cone production. Thus, the declines in cone production that occurred at the cool, upper elevation sites and led to the positive relationship between cone production and growing season temperature in the 2008 decade (Fig. 2-4c) suggest that local adaptation may play an important role in future species distributions. Most empirical climate change studies and species distribution modeling studies use space-for-time substitutions (Pickett 1989, Araújo and Rahbec 2006), which assume that species distributions and assemblages are in a constant steady-state with climate and do not incorporate local adaption (Araújo and Rahbec 2006, Pearson and Dawson 2003). However, my results suggest local adaptation may be important for understanding how populations may respond to climate change. For example, if I was to use a space-for-time substitution approach in the 1974 decade to understand how piñon pine seed cone production may be influenced by climate change, I would predict that seed cone production would be negatively affected by increasing temperatures (i.e. Fig. 2-4c, 1974 decade pattern). However, if I instead did the study in the 2008 decade, I would predict that seed cone production may increase with increasing temperatures (i.e. Fig. 2-4c, 2008 decade). Thus, the instability in the relationships between climate and seed cone production between the 1974 decade and the 2008 decade (Fig. 2-4c), likely due to population level adaptation and differential warming, highlights the potential inaccuracies of the space-for-time substitution approach in predicting how ecosystems may respond to climate change.

The declines in seed cone production (>40% at the majority of sites) that have occurred could have significant impacts on piñon pine population dynamics, especially given recent widespread mortality. Recruitment events among semi-arid pines are known to be highly episodic and dependent upon cool, wet climate periods (Brown and Wu 2005, League and Veblen 2006, Romme et al. 2009, Barger et al. 2009), highlighting how conditions for successful recruitment are limited. With declines in seed cone production, successful recruitment may become even more infrequent and seed production may become an important bottleneck to piñon pine regeneration.

Not only may declines in seed cone production influence future regeneration of these populations, but declines may negatively affect the variety of wildlife species that consume piñon pine seeds (Brown et al. 2001), such as pinyon jays *(Gymnorhinus cyanocephalus*) and Clark’s nutcrackers (*Nucifraga columbiana*). While my research was on piñon pine, similar declines may be occurring in other tree species, especially other semi-arid pines. I recommend further investigation of tree species reproduction to better understand the full geographic and taxonomic extent of these declines.

CHAPTER 3

TREE REGENERATION FOLLOWING DROUGHT AND INSECT-INDUCED MORTALITY IN PIÑON-JUNIPER WOODLANDS

Adapted from: Redmond MD and NN Barger. 2013. Tree regeneration following drought and insect-induced mortality in piñon-juniper woodlands. New Phytologist 200: 402-412.

Abstract

Widespread piñon (*Pinus edulis*) mortality occurred across the southwestern USA during 2002-2003 in response to drought and bark beetle infestations. Given recent mortality and changes in regional climate over the past several decades there is a keen interest in post-mortality regeneration dynamics in piñon-juniper woodlands. I examined piñon and Utah juniper (*Juniperus osteosperma*) recruitment at 30 sites across southwestern Colorado, USA that spanned a gradient of adult piñon mortality levels (10-100%) to understand current regeneration dynamics. Piñon and juniper recruitment was greater at sites with more tree and shrub cover. Piñon recruitment was more strongly facilitated by trees and shrubs than juniper recruitment. New (post-mortality) piñon recruitment was negatively affected by recent mortality. However, mortality had no effect on piñon advanced regeneration (juveniles established pre-mortality) and did not shift juvenile piñon dominance. My results highlight the importance of shrubs and juniper trees for facilitating piñon establishment and survival. Regardless of adult piñon mortality levels, areas with low tree and shrub cover may become increasingly juniper dominated due to few suitable microsites for piñon establishment and survival. In areas with high piñon mortality and high tree and shrub cover, my results suggest piñon is regenerating via advanced regeneration.

Introduction

Global climate change is predicted to increase the frequency and severity of drought events occurring under warmer temperatures (Meehl & Tebaldi, 2004; Seager *et al.*, 2007), which may lead to substantial shifts in vegetation distribution (Choat *et al.*, 2012). Extensive tree mortality has already occurred across the western USA (Breshears *et al.*, 2005; van Mantgem & Stephenson, 2007; van Mantgem *et al.*, 2009; Worrall *et al.*, 2010) and globally (Allen *et al.*, 2010; Carnicer *et al.*, 2011) over the past decade due to a combination of drought, insect-outbreaks, and warmer temperatures. These regional mortality events have altered water and energy fluxes (Adams *et al.*, 2012; Royer *et al.*, 2011; Guardiola-Claramonte *et al.*, 2011), carbon cycling (Kurz *et al.*, 2008; Brown *et al.*, 2010; Pfeifer *et al.*, 2011; Hicke *et al.*, 2012), and ecosystem services (Walton, 2012; Anderegg *et al.,* 2013). Yet at present we lack a clear understanding of how these regional mortality events may affect future forest and woodland composition, which is critical in understanding the long-term effects of recent tree mortality on these ecosystem processes and functions (Kurz *et al.*, 2008; Anderegg *et al.*, 2013). Thus, research examining tree regeneration patterns following recent mortality under a warmer, drier climate will help elucidate long-term changes in water and energy fluxes and carbon stocks.

Several abiotic and biotic factors are important drivers of successful tree regeneration under warmer, drier conditions. With increasing aridity, tree regeneration may become increasingly dependent upon the availability of cooler, wetter microsites to facilitate seedling establishment and survival (Kitzberger *et al.*, 2000; Sthultz *et al.*, 2007). In arid and semi-arid ecosystems, tree seedling establishment and survival is greater beneath tree and shrub canopies than in the adjacent canopy interspaces (Chambers *et al.,* 2001; Mueller *et al.,* 2005). Tree recruitment beneath canopies is likely due to reduced solar radiation resulting in less plant transpiration loss, cooler soil temperatures, and less soil water loss through evaporation as well as increased soil organic matter and nutrient availability (Callaway *et al.*, 1996; Kitzberger *et al.*, 2000; Chambers, 2001). Thus, facilitation, or the positive interaction among plants, by trees and shrubs may become increasingly important for tree regeneration by reducing water stress. However, trees and shrubs may also compete for resources, such as sunlight and water, and may negatively affect seedling growth and survival (Callaway *et al.*, 1996; Breshears *et al.*, 1997), particularly among later life stages (Callaway & Walker, 1997). Soil physical and chemical properties, such as texture and organic matter, influence soil water availability and may also be important in promoting seedling establishment and survival under a warmer, drier climate.

In this study I examine how vegetation structure and soil properties influence piñon pine (*Pinus edulis* Engelm., hereafter referred to as piñon) and Utah juniper (*Juniperus osteosperma* (Torr.) Little, hereafter referred to as juniper) regeneration dynamics following drought and insect-induced adult piñon mortality. I focus my research on woodlands co-dominated by piñon and juniper because they are widely distributed across the southwestern USA and provide a range of ecosystem services to humans and critical habitat for a variety of wildlife species (Brown *et al.*, 2001). Importantly, during the most recent multi-year drought (2002-2003) piñon experienced extensive mortality across populations, with mortality reaching upwards of 90% in some stands (Breshears *et al.*, 2005; Mueller *et al.*, 2005). This widespread piñon mortality event was caused by a combination of high temperatures, low precipitation, and high bark beetle (*Ips confusus)* infestation (Breshears *et al.*, 2005; McDowell *et al.*, 2008; Adams *et al.*, 2009). Mortality was highest among reproductively mature piñon trees (Mueller *et al.*, 2005; Floyd *et al.*, 2009), which resulted in large increases in relative dominance by adult juniper (Mueller *et* *al.*, 2005; Koepke *et al.*, 2010). While recent piñon mortality increased adult juniper dominance, future woodland composition will be largely determined by regeneration dynamics.

With increasingly arid conditions, several authors have hypothesized that juvenile juniper dominance may increase relative to piñon, because juniper is more drought tolerant and is also more abundant in warmer, drier sites (Linton *et al.*, 1998; West *et al.*, 2007; Breshears *et al.*, 2008; McDowell *et al.*, 2008). Additionally, while both piñon and juniper have greater rates of seedling establishment and survival beneath the canopy of trees and shrubs (Miller & Rose, 1995; Mueller *et al.*, 2005), juniper is better able to establish in open environments and is also better able to compete with herbaceous vegetation than piñon (Chambers *et al.*, 1999). Consequently, juniper establishment is commonly greater than piñon establishment following overstory tree and shrub removal (Tausch & Tueller, 1977; Everett & Ward, 1984; Redmond *et al.*, 2015). Following this, I predict that the high mortality of overstory piñon may lead to reduced suitable microsites for piñon establishment and shift the juvenile tree community to become more juniper dominated.

In addition to changes in suitable microsite availability, seed availability may influence piñon and juniper recruitment. Piñon cone production declined by over 40% in areas of New Mexico over the last several decades (Redmond *et al.*, 2012). These declines were associated with recent increases in temperature (Redmond *et al.*, 2012) and may negatively impact recent recruitment. Piñon seed viability also declines rapidly after one year of storage (Meeuwig & Bassett, 1983), unlike juniper (Johnsen, 1959). Thus, piñon recruitment following high adult mortality may be dependent upon survival of juveniles that established prior to the mortality (i.e. advanced regeneration) due to limited seed availability.

Through an observational study that examined piñon and juniper recruitment across a gradient of adult piñon mortality levels in southwestern Colorado, I addressed the following hypotheses: (1) piñon and juniper recruitment is greater at sites with more tree and shrub cover and higher soil available water capacity; (2) piñon recruitment is more strongly facilitated by overstory trees and shrubs than juniper recruitment; (3) piñon recruitment following high adult mortality is dependent upon advanced regeneration; (4) juvenile piñon dominance decreases with increased adult piñon mortality.

Methods

Study area

From May through June 2012, I sampled 30 sites across southwestern Colorado that experienced varying levels (10-100%) of adult piñon mortality during the 2002-2003 drought (Fig. 1). Sites were similar in elevation (2080 m ± 70 m), climate (mean annual temperature: 9.4 °C ± 0.8 °C; mean annual precipitation: 398 mm ± 28 mm; data from the PRISM Climate Database, http://www.prism.oregonstate.edu) and juniper mortality (<12%). I selected sites that were in the mid- to upper- elevation limits of piñon-juniper woodlands, as those elevations had the greatest mortality (Breshears *et al.*, 2005). Sites were located on either Gladel-Pulpit complex soils (ecological site: Pinyon -Juniper [Gladel] or Loamy Foothill [Pulpit]) or Wetherill soils (Loamy Foothill) (Natural Resources Conservation Service, 2006), which are the two most spatially extensive soil complexes in the region dominated by piñon and juniper (Natural Resources Conservation Service, 2006). Both of these soil complexes are characterized as well-drained soils derived from sandstone with a depth ranging from 0.5 to > 1.5 m (Natural Resources Conservation Service, 2006). To select sites, I first used Geographic Information Systems to locate areas within southwestern Colorado that were of the two soil complexes, between 2000 m and 2200 m in elevation, had a slope of < 10 %, and were located on federally owned land. I then used

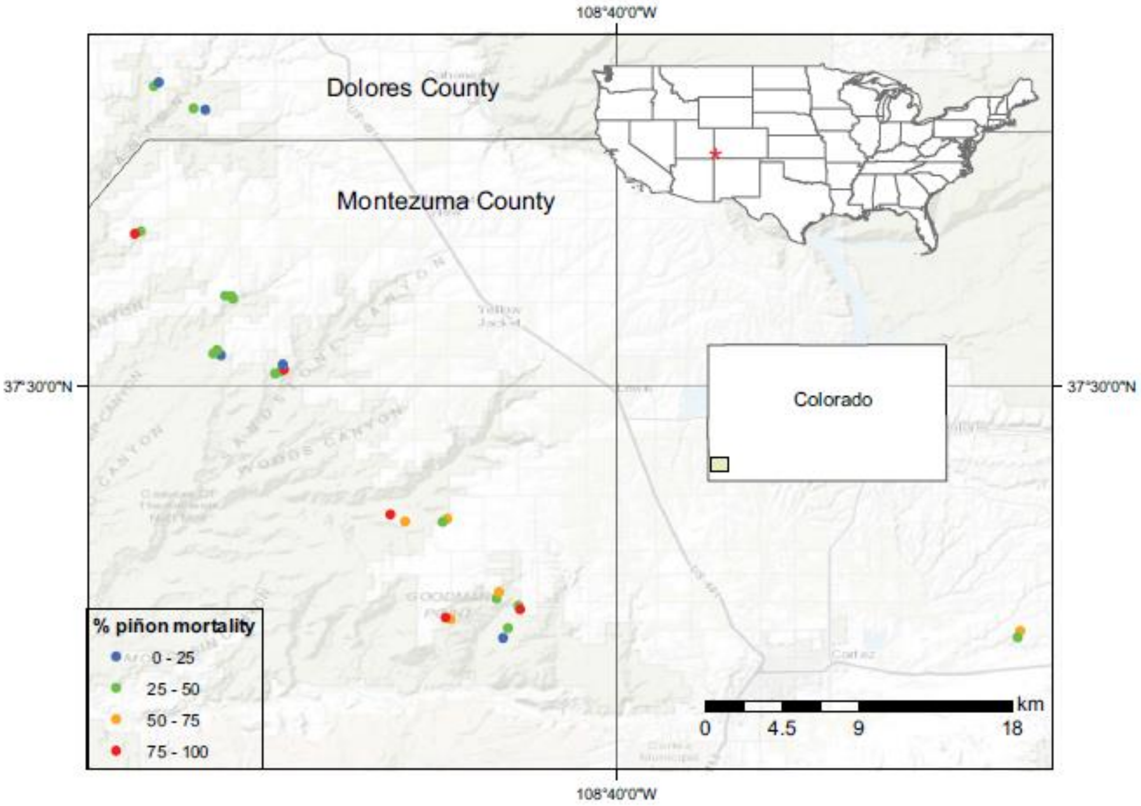


Figure 3-5. Map of the 30 sites sampled. Different colored circles illustrate the different levels of adult piñon mortality that occurred at each site based off adult stem density.

Google Earth (Version 7.0; Google Inc., Mountainview, CA, USA) imagery taken in 2011 to identify areas of high and low mortality that were within 1 km of a road. Following this, I selected 15 sites that were located on Wetherill soils and 15 sites that were located on Gladel-Pulpit soils, half of which were considered high-mortality (>60 % mortality) sites and half of which were considered low-mortality (< 40 % mortality) sites. All sites were generally at least 2 km apart (Figure 3-5). However, I included stands that were within 2 km of one another if they differed in percent mortality or differed by the NRCS soil map unit and vegetation characteristics. At my sites, the only two tree species were piñon and juniper. The common shrub species were antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus montanus*), and sagebrush (*Artemesia spp.*).

Data Collection

At each site I established three 50 m long transects spaced 25 m apart. I surveyed for all tree juveniles, which included seedlings (basal diameter < 2.5 cm) and saplings (basal diameter ≥ 2.5 cm and < 5 cm), along a 10 m belt at each transect (i.e. 1500 m^2 surveyed for tree juveniles per site). For all tree juveniles encountered, I recorded the species, status (dead or alive), basal diameter (diameter at the root collar), and microsite (beneath canopy vs. canopy interspace). Additionally, for each piñon seedling, I estimated whether the seedling established pre-mortality event (i.e. ≥ 10 years, which I refer to as an advanced seedling) or post-mortality event (i.e. ≤ 8 years, which I refer to as a new seedling) by counting the number of annual whorls along the main stem, a method that has been used to age piñon (Sthultz *et al.*, 2007) and other pine species (Collins *et al.*, 2011).

To quantify tree and shrub density, cover, basal area (BA) and mortality, at each site I established 5 circular plots that were 7 m in radius. One circular plot was located in the center of the middle transect and the other 4 circular plots were located at each end of the outer transects. I measured the height, 2 perpendicular canopy widths (live only), basal diameter (trees only), and status (live vs. dead) for each tree and shrub species located within each circular plot. For all dead trees, I also noted if the tree mortality was recent (≤ 10 years) by following the guidelines in Jacobi *et al.* (2005), which were based on piñon in southwestern Colorado. Trees were considered recently (≤ 10 years) dead if 33% or less of the branches were broken, most small limbs were present, and at least 50% of the bark was attached and not more than 2 mm from the tree.

To examine if piñon and juniper juveniles were randomly distributed within a site or were associated with specific microsites, I first determined the relative availability of microsites using the line point intercept method. Every 50 cm along each transect I recorded the microsite (tree and/or shrub presence vs. interspace), for a total of 100 points/transect and 300 points/site. I used the line point intercept method rather than data from the circular plots to determine the relative availability of microsites, because tree and shrub canopies often overlapped. Therefore, the circular plot data likely overestimated canopy cover.

At each site, soil cores were taken from 0-10 cm soil depth at each transect end (6 per site) to estimate soil available water capacity in surface soils. Soil cores were 2.5 cm in diameter and taken 1 m out from the canopy edge of juniper and/or piñon. Within a month of collection, soil samples were taken back to the University of Colorado where they were dried for 48 h at 60 °C, weighed, sieved through a 2 mm sieve and re-weighed. The 6 soil samples taken at each site were then combined, and organic matter content (%) was estimated using the loss on ignition method (Ball, 1964; Ben ‐ Dor & Banin, 1989) with a muffle furnace set at 580 °C. Percent sand, silt, and clay were estimated following Kettler *et al.* (2001). Using the estimates of percent sand, silt, clay, and organic matter content, I calculated soil available water capacity by subtracting the wilting point (θ_{1500}) from field capacity (θ_{33}), which I calculated using the equations in Table 1 of Saxton and Rawles (2006).

Data Analyses

I divided tree seedlings into two size classes based on their basal diameter (new seedlings: basal diameter ≤ 0.5 cm; advanced seedlings: basal diameter > 0.5 cm and < 2.5 cm), because I were unable to age all of the tree seedlings. These size classes were chosen using piñon seedling size-age data across the 30 sites, which indicate that 78% of the seedlings ≤ 0.5 cm were less than 9 years old (i.e. established post mortality), while 98% of the seedlings > 0.5 cm were greater than 10 years old (i.e. established prior to the mortality). I were unable to date juniper seedlings using the annual whorl method. However, piñon and juniper trees in southern Utah have a similar relationship between basal diameter and tree age among juveniles with a basal diameter ≥ 2.0 cm (Redmond *et al.*, 2013). This suggests that the size-age relationship among piñon and juniper seedlings may also be similar. Because I divided seedlings into age classes (new seedlings and advanced seedlings) based on their size for the analyses, it is important to note that some seedlings may be incorrectly classified, which may reduce my ability to detect differences in vegetation associations between new seedlings and advanced seedlings.

I evaluated the vegetation and soil characteristics associated with piñon and juniper recruitment by performing stepwise multiple linear regression analyses for each juvenile size class (new seedlings, advanced seedlings, and saplings). For these analyses, I used each site as a replicate by pooling and then averaging transect and circular plot data. In each linear regression model, juvenile density was used as a response variable and various vegetation and soil characteristics that were identified apriori were used as predictor variables (see Table 3-3 for a list of all predictor variables used and their hypothesized function). Please note that I used piñon basal area rather than canopy cover as a predictor variable for all regression analyses, because I did not collect canopy cover data of dead piñon trees. Further, live piñon basal area is a strong predictor of live piñon canopy cover (simple linear regression, $R^2 = 0.91$, $P < 0.0001$). I also used juniper basal area rather than canopy cover as a predictor variable for the regression analyses with juniper juveniles (Table 3-3), because juniper often did not grow vertically, so canopy cover likely overestimated seed availability in those cases.

Table 3-3. The predictor variables and their ecological function used in each stepwise multiple linear regression for each size class.

Predictor variables	Ecological Function
live piñon basal area	piñon seed availability and microsites post mortality
live + dead piñon basal area	piñon seed availability and microsites prior to mortality
percent piñon mortality	microsite changes (dead piñon microsites)
live shrub cover	microsite
live juniper cover (P only)	microsite
soil available water capacity	water availability
live juniper basal area (J & % P only)	juniper seed availability and microsite

Note - Predictor variables used to only predict piñon juvenile density, juniper juvenile density, or piñon juvenile dominance are denoted by "P", "J" and "% P", respectively. Piñon mortality was calculated based on basal area rather than stem density. All of the vegetation predictor variables were calculated using the pooled circular plot data.

Each complete model was simplified using the stepAIC procedure as part of the package MASS (Venables & Ripley, 2002) in R (R Development Core Team, 2011) following the procedure outlined in Zuur *et al.*, (2007). The stepAIC procedure examines all predictor variables using backward selection to produce a final model based on minimizing the Akaike's Information Criterion (AIC; Akaike, 1973). Piñon new seedlings and juniper saplings were log transformed to meet assumptions of these tests.

Following the same procedure as above, I examined the vegetation and soil characteristics associated with piñon dominance for each juvenile size class to determine potential changes in future stand composition across my study sites (see Table 3-3 for the list of predictor variables). Piñon dominance was calculated as:

$$\text{Piñon dominance}_{\text{size class X}} = \frac{(\text{Piñon Density}_{\text{size class X}})}{(\text{Piñon Density}_{\text{size class X}} + \text{Juniper Density}_{\text{size class X}})}$$

To understand if recent increases in aridity and recent mortality have shifted piñon dominance, I first examined if juvenile piñon dominance had shifted relative to adult piñon dominance, regardless of piñon mortality levels. To do this, I performed paired Student T-tests to compare juvenile piñon dominance at each size class (new seedling, advanced seedling, and sapling) with adult piñon dominance prior to recent mortality (calculated using live and dead tree density). To understand if recent mortality shifted juvenile piñon dominance relative to adult piñon dominance, I performed regression analyses to examine if difference in dominance between juveniles and adults (response variable) was affected by piñon mortality (predictor variable). I calculated the difference in dominance between juveniles at each size class and adults by dividing juvenile piñon dominance$_{\text{size class X}}$ by adult piñon dominance prior to recent mortality.

To understand if overstory trees and shrubs have a facilitative or competitive effect on piñon and juniper recruitment, and how this effect may differ between the two species and between the three juvenile size classes, I used the relative interaction index proposed by Armas *et al.*, (2004). The interaction index reveals whether competition or facilitation is occurring within each microsite by representing the relative difference in seedling density occurring beneath tree and shrub canopies and in the interspace and is calculated as:

$$I = \frac{(\text{Density}_{\text{Beneath Canopy}} - \text{Density}_{\text{Interspace}})}{(\text{Density}_{\text{Beneath Canopy}} + \text{Density}_{\text{Interspace}})}$$

Thus, the interaction index ranges from -1 to 1, with a positive interaction index representing a facilitative effect of canopy microsites on recruitment and a negative interaction index representing a competitive effect of canopy microsites. For each species and each juvenile size class, I estimated juvenile density at each microsite by dividing the total number of juveniles found underneath the canopy (or interspace) microsite by the total cover of live and dead shrubs and trees (or the total cover of area with no trees and shrubs), which was calculated using the line point intercept data. Because I wanted to compare how the interaction index varies between the two species and the three juvenile size classes, I only used sites that had a sufficient number of juveniles sampled in each size class and each species. To do this, I only used sites that given a uniform distribution of juveniles I would expect at least one individual of each size class and each species to be located beneath the canopy (i.e. total # of individuals$_{\text{species X, size class Y}}$ × proportion canopy cover ≥ 1). I omitted 14 sites from the analysis since those sites did not meet the criteria. Using the 16 sites that met this criteria, I calculated the interaction index at each site for each species and each juvenile size class. I then performed a series of non-parametric paired Wilcoxon signed rank tests (9 paired tests total) to understand if the interaction index differed between piñon and juniper within each juvenile size class (3 paired tests) and if the interaction index differed between each juvenile size class within each species (6 paired tests). I used non-parametric paired Wilcoxon signed rank tests rather than a paired two-way ANOVA due to the non-normality of the data, even after transformations.

I also examined the effect of canopy presence on piñon sapling survival by comparing interaction indices of live piñon saplings and dead piñon saplings beneath the canopy of trees and shrubs. Similar to above, I only used sites that had a sufficient number of live and dead piñon saplings such that given a uniform distribution I would expect to find at least one live and dead sapling underneath the canopy. Using the 18 sites that met this criteria, I performed a paired Wilcoxon Signed Rank test to understand if the interaction index differs between live and dead piñon saplings.

Since multiple comparisons (10) were conducted using interaction indices, I applied the False Discover Rate (FDR) correction using a standard step-up procedure to control the inflation of type I error derived from repeated testing (Benjamini & Hochberg, 1995; García, 2004). All analyses were performed in R (R Development Core Team, 2011), with $\alpha = 0.05$.

Results

As intended, the study sites spanned a gradient of adult piñon mortality levels, with mortality ranging from 16 – 100% based on basal area (9 – 100% based on stem density). Additionally, there was high variability in shrub cover (0-14%), tree density (169-1105 stems ha^{-1}), and tree basal area (12-52 m^2 ha^{-1}) across the study sites (Table 3-4), as well as some variability in soil available water capacity (11-16%). Piñon and juniper juvenile (i.e., seedlings and saplings) densities were also highly variable across the study sites, with juvenile densities ranging from 27 to 948 stems ha^{-1} for piñon and 40 to 827 stems ha^{-1} for juniper (Table 3-4). Among both piñon and juniper, density of advanced seedlings (i.e. seedlings that likely established prior to adult mortality) was over 2.5 times higher than density of new seedlings (i.e. seedlings that likely established following adult mortality) on average (Table 3-4). However, the difference in density between new seedlings and advanced seedlings was highly variable across the 30 study sites, such that at some sites new seedlings were over 1.4 times more abundant than advanced seedlings while at other sites advanced seedlings were over 25 times more abundant than new seedlings.

Vegetation and soil characteristics associated with tree recruitment

Density of piñon new seedlings was positively associated with live shrub cover, live piñon basal area, and live juniper cover ($R^2 = 0.63$, $P < 0.0001$; Table 3-5; Figure 3-6). Notably, there was no relationship between percent piñon mortality and piñon new seedling density. Given that live piñon basal area was strongly associated with piñon new seedling density, these results suggest that only current live piñon abundance influences new seedling establishment.

Table 3-4. Stem density (stems ha-1) and piñon dominance (%) across the 30 sites.

Size Class	Piñon Density	Juniper Density	Piñon Dominance
new seedlings	67 ± 16 (0 - 300)	34 ± 5 (0 - 107)	54 ± 5 (0 - 100)
advanced seedlings	194 ± 20 (13 - 480)	193 ± 19 (6 - 333)	51 ± 3 (22 - 93)
sapling	137 ± 16 (0 - 327)	90 ± 16 (0 - 480)	58 ± 5 (0 - 100)
adult (pre-mortality)	488 ± 54 (78 - 1039)	447 ± 25 (169 - 753)	49 ± 3 (13 - 77)
adult (post-mortality)	268 ± 34 (0 - 623)	421 ± 24 (155 - 727)	35 ± 4 (0 - 70)

Data are means ± 1 SE. The range is included in parentheses.

Density of piñon advanced seedlings was also positively associated with live shrub and juniper cover (Table 3-5; Figure 3-6). However, unlike piñon new seedlings, density of piñon advanced seedlings was positively associated with piñon basal area prior to adult mortality and soil available water capacity (final model $R^2 = 0.64$, $P < 0.0001$; Table 3-5; Figure 3-6). Given that piñon basal area prior to adult mortality was a strong predictor of piñon advance seedling density, these results suggest that recent mortality did not affect the abundance of advanced seedlings.Wheras there was a strong association between the density of piñon seedlings and vegetation structure (Table 3), piñon sapling density was only positively associated with live shrub cover ($R^2 = 0.31$, $P = 0.001$; Table 3-5).

Juniper juveniles were more weakly associated with vegetation and soil characteristics than piñon juveniles. Juniper new seedling density was positively associated with live piñon basal area and live juniper basal area, whereby 26% of the variability of juniper new seedlings was explained by these two variables (Table 3-5). Unlike juniper new seedlings, there was no relationship between juniper advanced seedling density and the predictor variables ($R^2 = 0.09$, $P = 0.11$; Table 3-5). There was weak evidence that the presence of adult junipers may inhibit advancement of juniper to the sapling size class: juniper sapling density was weakly and negatively related to juniper basal area ($R^2 = 0.21$, $P = 0.01$; Table 3-5).

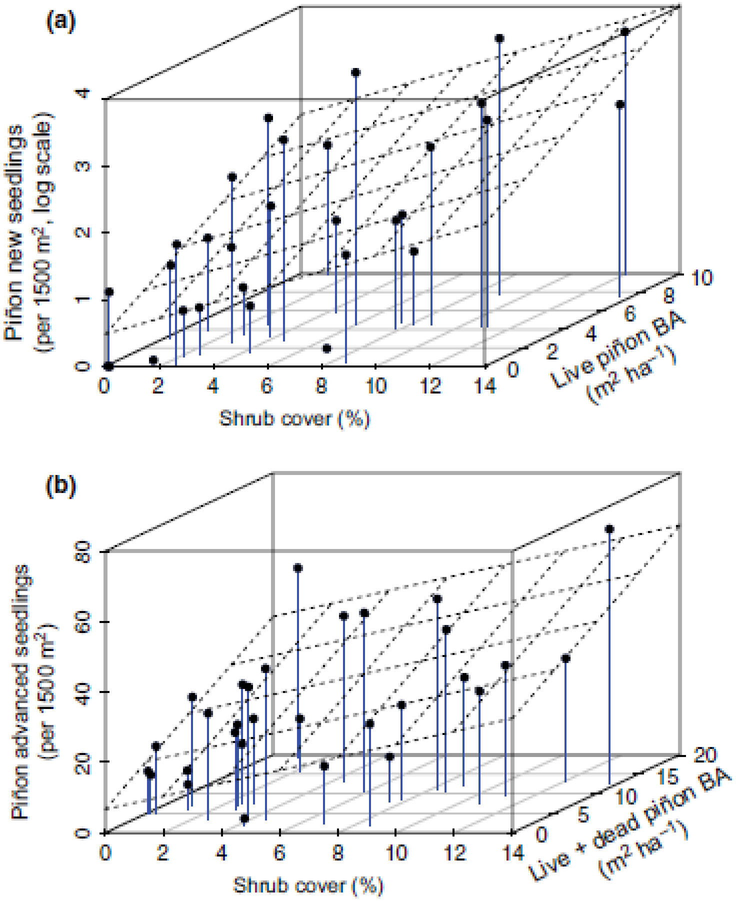


Figure 3-6. (A.) Plot of the logarithms of the density of piñon new seedlings against % shrub cover and live adult piñon basal area (BA). (B.) Plot of the density of piñon advanced seedlings against % shrub cover and live and dead adult piñon basal area.

Vegetation and soil characteristics associated with juvenile piñon dominance

Juvenile piñon dominance across the study sites was highly variable, ranging from 19-86% (Table 3-4). Piñon dominance among new seedlings was positively influenced by live shrub cover ($R^2 = 0.32$, $P = 0.002$; Table 3-5). Dominance of both piñon advanced seedlings and piñon saplings was positively associated with live shrub cover, live juniper basal area, and live + dead piñon basal area (R^2 = 0.35 and 0.59 for advanced seedlings and saplings, respectively; Table 3-5). These results highlight how tree and shrub microsites are important for juvenile piñon dominance and suggest that percent piñon mortality did not influence juvenile piñon dominance.

Table 3-5. Results of the best linear models based on stepAIC used to predict piñon and juniper densities and piñon dominance in each juvenile size class.

Size Class	R^2	*P*-value	Predictor variables	β_s	*P*-value
Piñon					
new seedling	0.63	<0.0001	live shrub cover	0.50	**0.001**
			live piñon basal area	0.47	**0.002**
			live juniper cover	0.36	**0.01**
adv. seedling	0.64	<0.0001	live shrub cover	0.70	**< 0.001**
			live + dead piñon basal area	0.55	**0.004**
			live juniper cover	0.38	**0.01**
			soil available water capacity	0.31	**0.03**
sapling	0.31	0.001	live shrub cover	0.56	**0.001**
Juniper					
new seedling	0.26	0.02	live piñon basal area	0.40	**0.02**
			live juniper basal area	0.34	0.05
adv. seedling	0.09	0.11	soil available water capacity	0.30	0.11
sapling	0.21	0.01	live juniper basal area	-0.46	**0.01**
Piñon Dominance					

new seedling	0.32	0.002	live shrub cover	0.56	**0.002**
adv. seedling	0.35	0.01	live shrub cover	0.39	**0.02**
			live juniper basal area	0.33	0.06
			live + dead piñon basal area	0.30	0.08
sapling	0.59	<0.0001	live juniper basal area	0.56	**0.0002**
			live shrub cover	0.46	**0.001**
			live + dead piñon basal area	0.30	**0.03**

The standardized regression coefficient (β_s) and *P*-value is given for each predictor variable used in the final model based on stepAIC. $n = 30$ (except $n=28$ for piñon dominance of new seedlings due to a lack of new seedlings at two sites).

There were no significant differences between adult piñon dominance prior to recent mortality and juvenile piñon dominance among all size classes (paired Student T-tests; $P > 0.09$; Figure 3-7; Table 3-4), suggesting that there was no directional shift in juvenile piñon dominance relative to adult piñon dominance across the 30 sites. There was also no relationship between piñon mortality and the difference in piñon dominance among juveniles and adults ($R^2 < 0.1$; $P > 0.1$; Figure 3-7). While there was some variability in the relationship between juvenile piñon dominance and adult piñon dominance (Figure 3-7), these results suggest that overall the juvenile tree community is similar to that of the adult tree community prior to the recent mortality (Figure 3-7).

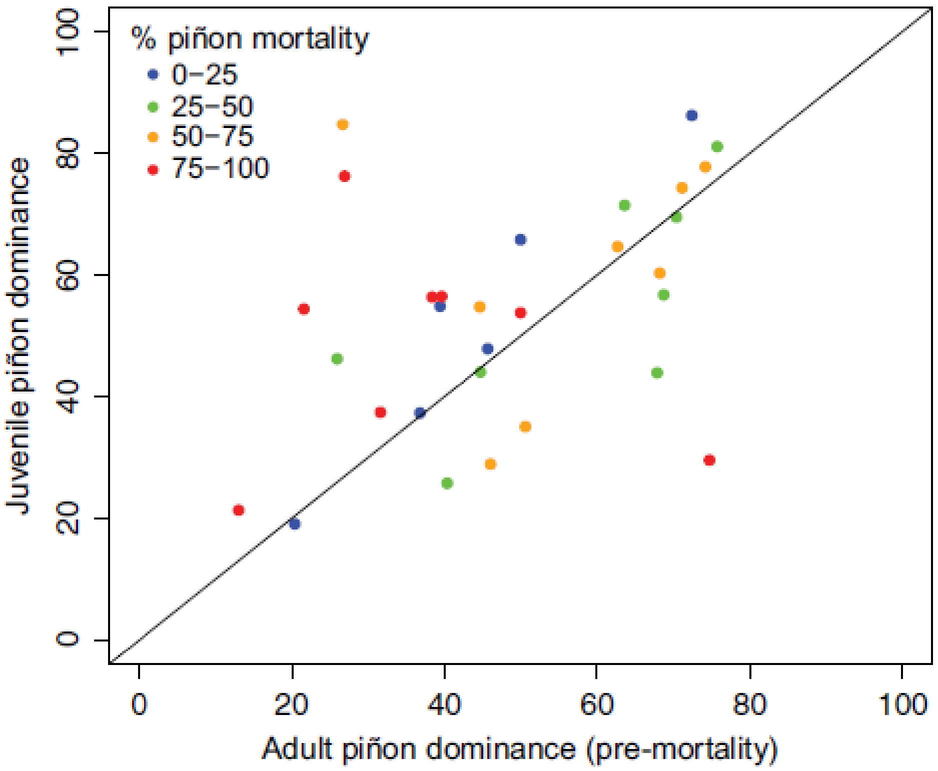


Figure 3-7. The relationship between juvenile piñon dominance and adult piñon dominance across the 30 sampled sites. Different colored circles illustrate the different levels of adult piñon mortality that occurred at each site based off adult basal area. The line illustrates where juvenile piñon dominance is equal to adult piñon dominance.

Net effects of facilitation and competition by trees and shrubs

Consistent across all juvenile size classes, both piñon and juniper were more likely to be found beneath tree and shrub canopies than in the interspace, as evidenced by the high, positive interaction indices (indicating facilitation) between shrub and tree cover and juvenile piñon and juniper trees (Figure 3-8). Additionally, while piñon and juniper new seedlings had high interaction indices (> 0.90) with over 90% of new seedlings occurring beneath trees and shrubs, piñon and juniper saplings had significantly lower interaction indices (0.76 and 0.40, respectively; Figure 3-8) Unlike new seedlings, piñon advanced seedlings and saplings had significantly higher interaction indices than juniper (Figure 3-8), suggesting that at these larger juvenile size classes, juniper is less able to survive beneath tree and shrub canopies than piñon.

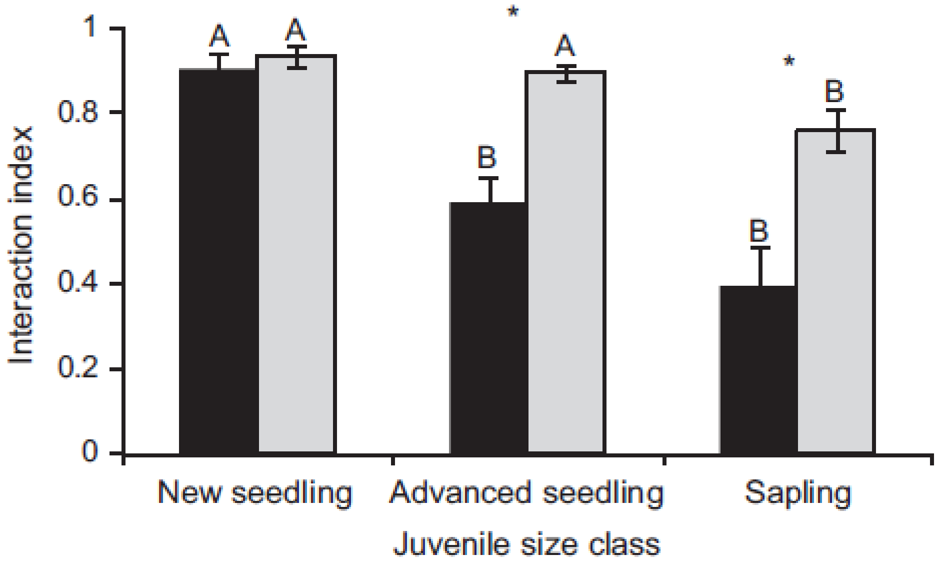


Figure 3-8. The interaction index values between shrub and tree cover and live juvenile piñon and juniper trees. Interaction index values between 0 and 1 represent a facilitative effect of shrub and tree cover on piñon and juniper recruitment, with increasingly positive values representing an increasingly facilitative effect. Asterisks denote significant differences between piñon and juniper juveniles within each size class, while different letters denote significant differences between juvenile size classes within each species. Error bars are ± 1 SE.

Both live and dead piñon saplings were more likely to be found beneath the canopy of a tree or shrub than in the interspace as evidenced by the high positive interaction indices between shrub and tree cover and piñon sapling densities (mean interaction index ± 1 SE = 0.76 ± 0.06 and 0.83 ± 0.07 for live and dead piñon saplings, respectively). However, interaction indices did not differ between live and dead piñon saplings (paired Wilcox Signed Rank test, P = 0.3), indicating that piñon sapling survival was the same in both canopy and interspace microsites.

Discussion

Vegetation and soil characteristics associated with tree recruitment

These results suggest recovery following recent piñon mortality will be dependent upon advanced regeneration, findings which are consistent with other studies examining tree regeneration following drought and insect-induced tree mortality (Veblen *et al.,* 1991; Axelson *et al.,* 2009; Diskin *et al.*, 2011; Collins *et al.*, 2011; Kayes & Tinker, 2012). New (post-mortality) piñon recruitment was strongly positively associated with live adult piñon densities, and was thus negatively affected by recent piñon mortality. The low levels of new piñon recruitment following high mortality is likely due to seed limitations as piñon seed viability declines rapidly after the first year (Meeuwig & Bassett, 1983), and may also be due to declines in canopy microsites. Notably, piñon advanced (pre-mortality) seedlings and saplings were not affected by overstory piñon mortality, and instead were positively associated with piñon densities at the time of establishment (i.e. live + dead piñon basal area). These results highlight the importance of advanced regeneration for piñon recovery and support previous findings of low juvenile piñon mortality in areas with high adult piñon mortality (Negrón & Wilson, 2003; Mueller *et al.,* 2005). The relatively high levels of advanced regeneration following drought and beetle-induced mortality in this study and others (Veblen *et al.,* 1991; Axelson *et al.*, 2009; Diskin *et al.*, 2011; Collins *et al.*, 2011; Kayes & Tinker, 2012), suggest there is a greater bottleneck in obtaining new recruitment, which is dependent upon seed production, dispersal, germination and seedling establishment, as compared to advanced regeneration, which is only dependent upon juvenile survival following recent mortality.

Shrub and juniper cover was strongly positively associated with piñon juvenile densities (Table 3), which supports my hypothesis that trees and shrubs facilitate piñon establishment and is consistent with other field observations and experimental studies (Floyd, 1982; Chambers, 2001; Mueller *et al.*, 2005; Sthultz *et al.,* 2007). The shading provided by trees and shrubs reduces solar radiation leading to lower soil temperatures and less evapotranspiration (Breshears *et al.*, 1997; Chambers, 2001; Royer *et al.*, 2010, 2012) and may result in higher soil water contents (Chambers, 2001). Higher nutrient availability and higher organic matter content have also been reported underneath trees and shrubs in piñon-juniper woodlands (Padien & Lajtha, 1992; Chambers, 2001), which may also positively influence piñon recruitment.

In addition to vegetation structure, these results suggest high soil available water capacity may be important for promoting piñon juvenile survival. Regionally, there was greater adult piñon mortality in areas with lower soil available water capacity (Peterman *et al.*, 2012). While the range of soil available water capacity across the sites was relatively narrow compared to other studies (Peterman *et al.*, 2012), there was a positive association between soil available water capacity and piñon advanced seedling densities. This positive association may be due to greater piñon seedling survival during the 2002-2003 drought in areas with higher soil available water capacity. Because piñon recovery following high adult mortality will likely be dependent upon advanced regeneration, these results suggest that areas with lower soil available water capacity may have less piñon regeneration following high adult mortality.

Juniper juveniles were not as strongly associated with vegetation structure as piñon and were also more commonly found in the canopy interspaces than piñon. These results support my hypothesis that piñon is more dependent upon overstory trees and shrubs to facilitate seedling establishment and survival and are consistent with previous field studies (Chambers *et al.*, 1999). However, juniper new seedlings were still strongly facilitated by overstory trees and shrubs, unlike juniper advanced seedlings and saplings. This suggests that competition for light, and potentially water, may be more important than the facilitative effects of overstory trees and shrubs once juniper seedlings become established.

Shifts in the juvenile tree community

Counter to my predictions, piñon mortality resulted in no shift in the juvenile tree community, suggesting that future woodland composition may be similar to the woodland composition in the past. The lack of a shift in the juvenile tree community is in contrast to other studies that examined tree regeneration patterns following drought and/or beetle-induced mortality (Veblen *et al.,* 1991; Suarez & Kitzberger, 2008; Collins *et al.*, 2011; Kayes & Tinker, 2012). However, all of these studies examined tree regeneration following mortality of relatively shade-intolerant species, such as lodgepole pine (*Pinus contorta*). Contrary, piñon is more shade tolerant than juniper (Barney & Frischknecht, 1974; Chambers *et al.*, 1999), which I hypothesize enabled piñon to have higher juvenile densities prior to the mortality, leading to sufficient advanced regeneration. Recovery following drought and insect-induced tree mortality will be largely dependent upon juveniles present in the community prior to the mortality event (Veblen *et al.,* 1991; Suarez & Kitzberger, 2008; Collins *et al.*, 2011). Thus, there may be greater shifts in the juvenile tree community following overstory mortality of shade-intolerant tree species due to little advanced regeneration.

Juvenile piñon dominance was still highly variable across the study sites, and was positively related to tree and shrub cover. This suggests that there may be a shift in the juvenile tree community in the future. Once more dead piñon snags fall, piñon dominance may become negatively impacted by the loss in canopy microsites. There has also been significant shrub mortality and juniper dieback in piñon-juniper woodlands in northern Arizona following recent droughts (Gitlin *et al.*, 2006; Koepke *et al.*, 2010), which could further reduce suitable microsites and affect future piñon dominance. In addition, drought and insect-induced mortality events are predicted to increase in the southwestern USA (Williams *et al.,* 2013). These predicted future mortality events may result in a shift in juvenile piñon dominance. In particular, as these older juveniles grow they will likely become more susceptible to bark beetle attack and less likely to survive future droughts (Floyd *et al.*, 2009), which may result in less advanced regeneration.

Net effects of facilitation and competition by trees and shrubs

Juveniles of both piñon and juniper across all size classes were more likely to be found underneath the canopy of trees and shrubs than in the adjacent interspace, which supports the hypothesis that trees and shrubs facilitate piñon and juniper establishment (Miller & Rose, 1995; Chambers, 2001; Mueller *et al.*, 2005; Sthultz *et al.*, 2007). The high percentage of piñon and juniper seedlings underneath tree and shrub canopies may also be partly due to caching of seeds underneath trees and shrubs by birds and small mammals (Vander Wall & Balda, 1977; Vander Wall, 1997).

New seedlings of piñon and juniper were more likely to be found underneath the canopy of trees and shrubs than saplings. There are two, non-mutually exclusive, hypotheses for why there is a decline in the positive association between shrub and tree canopies and tree juveniles with juvenile age. One hypothesis is that as juveniles become older, increased competition with overstory trees and shrubs may outweigh the facilitative effects. In support of this hypothesis, both juniper and various shrub species have been reported to negatively impact adult piñon growth through below-ground competition (Haskins & Gehring, 2004; McHugh & Gehring, 2006), and shifts from facilitation to competition is known to occur among a variety of plant species with changes in life stages (Callaway & Walker, 1997). Another hypothesis is that these older juveniles established during cooler, wetter climate conditions, and thus, were not as dependent upon tree and shrub microsites at the time of establishment. In support of this hypothesis, previous research on piñon (Sthultz *et al.*, 2007) and other tree species (Greenlee &

Callaway, 1996; Kitzberger *et al.*, 2000) have found the net effects of competition and facilitation to vary across spatial and temporal gradients of abiotic stress.

Interestingly, there was no difference in survival between piñon saplings located beneath the canopy of a tree or shrub and those located in the canopy interspace. This suggests that at this life history stage facilitation and competition were equal between canopy microsites and piñon saplings in the study area. However, piñon sapling density was positively associated with shrub cover. This may be due to the facilitative effects of shrubs on piñon seedling establishment and the aboveground competitive release that occurs once the sapling grows taller than the shrub.

Conclusion

Drought and insect-induced piñon mortality events have dramatically altered woodland structure across the southwestern USA (Breshears *et al.*, 2005; Mueller *et al.*, 2005), affecting water and energy fluxes and carbon stocks (Royer *et al.*, 2011; Adams *et al.*, 2012; Hicke *et al.*, 2012). These results indicate that piñon mortality did not strongly affect successional trajectories in piñon-juniper woodlands due to advanced regeneration. Accordingly, this landscape appears resilient to recent drought and beetle-induced mortality due to the high densities of juveniles that survived the drought. However, piñon and juniper have slow growth rates in these semi-arid ecosystems (Despain, 1989*;* Barger *et al.,* 2009), which suggests that ecosystem processes and function may be altered in high mortality stands for 50 years or more. As hypothesized, trees and shrubs appear to facilitate both piñon and juniper seedling establishment, and piñon juveniles were more dependent upon tree and shrub microsites than juniper. Piñon advanced seedlings were also positively associated with soil available water capacity, unlike juniper. These results highlight the greater drought tolerance of juniper relative to piñon (Linton *et al.*, 1998; West *et al.*, 2007; Breshears *et al.*, 2008; McDowell *et al.*, 2008) and suggest tree and shrub microsites may become increasingly important for future piñon recruitment given predicted increases in aridity across the southwestern USA (Seager *et al.*, 2007; Williams *et al.*, 2013).

CHAPTER 4

VEGETATION MANAGEMENT ACROSS COLORADO PLATEAU BLM LANDS: 1950-2003

Adapted from: Redmond MD, Golden ES, Cobb NS, and NN Barger. 2014. Vegetation Management across Colorado Plateau BLM lands: 1950-2003. Rangeland Ecology and Management 67: 636-640.

Abstract

Large tracts of land across the western U.S. have been managed over the last century in an effort to increase forage production, reduce the risk of wildland fires, and/or restore ecosystem structure and function. Yet documentation of this land treatment history is lacking. Using data collected from Bureau of Land Management (BLM) field offices across the Colorado Plateau, I quantified the number, spatial extent, and implementation cost of tree-reduction and seeding treatments done in piñon (*Pinus edulis*)-juniper (*Juniperus osteosperma, J. monophylla, J. scopulorum*) woodlands between 1950 and 2003. Over 247,000 hectares of land were treated, corresponding to 6.6% of the piñon-juniper vegetation type within BLM-owned lands. Tree-reduction treatments involving chaining, bulldozing, or cabling were most prevalent between the 1950s and 1970s, with over 163,000 ha of land treated with these methods. Prescribed burning became increasingly prevalent in the 1980s, with over 43,000 ha burned. In more recent years, hydroaxe treatments have become common (4,400 ha treated), but to a much lesser extent than prescribed burns. Over 60% of these tree-reduction treatments were done in conjunction with revegetation or seeding treatments. Implementation costs of these tree-reduction treatments were over 26.7 million USD, with the hydroaxe treatment having nearly three times the cost of implementation than all other tree-reduction treatments. The spatial extent of these tree-reduction

treatments and associated implementation costs highlight the importance of research examining the efficacy of these treatments and the potential legacy effects. The land use history reported in this study and the accompanying freely accessible online database is a useful tool to guide research and management objectives and methodology.

Introduction

Over the past century, large tracts of land across the western U.S. have been managed in an effort to increase forage production, reduce the risk of wildland fires, and/or restore ecosystem structure and function. Yet clear documentation of the spatial extent, implementation cost, and types of management actions is lacking. Here, I focus on the management history of woodlands dominated by piñon (*Pinus edulis)* and juniper (*Juniperus monosperma*, *J. osteosperma*, *J. scopulorum*) (hereafter piñon-juniper), a spatially extensive vegetation type in the western U.S. and one of the predominant vegetation types administered by land management agencies in the continental U.S. (Romme et al. 2009).

Beginning in the late 19th century, piñon-juniper woodlands increased in tree density and expanded into adjacent grasslands and shrublands in certain areas (Tausch et al. 1981; Weisberg et al. 2007; Miller et al. 2008; Jacobs et al. 2008). This expansion was coupled with a decline in understory plant cover (Miller et al. 2000; Reiner 2004; Van Auken 2009) that reduced forage production and habitat quality for some wildlife species (Miller et al. 2000; Noson et al. 2006). Historical (1950s-1970s) treatment objectives were to restore understory plant cover and increase forage production. In addition to increasing forage production for livestock, more recent (1990s-current) treatment objectives aim to reduce the risk of catastrophic fire and to restore ecosystem structure and function (NFP 2000; BLM 2008). This shift in objectives, combined with new technology, has likely shifted the predominant treatment methods being applied (BLM 2008).

While it is clear that large tracts of piñon-juniper woodlands have been managed over the past 70 years, treatment data relevant to resource planning and ecosystem studies have not been widely available for use. In this study, my objectives were to quantify the number, spatial extent, and implementation cost of all tree-reduction and seeding treatments done in piñon-juniper woodlands on BLM-owned land on the Colorado Plateau from 1950 to 2003.

Methods

Data Collection

I focused this study on treatment history of piñon-juniper woodlands on BLM-owned land of the Colorado Plateau (for environmental characteristics associated with the treatment locations see

Table ***4-6***). Treatment history data were retrieved from each BLM field office within the Colorado Plateau and digitally archived. This required visiting each field office, scanning paper records, and entering these records into a database. Data collected about each treatment application included: treatment methods, location, implementation cost, purpose, and spatial extent. All of the information collected can be found in the accompanying online database through the Merriam Powel Center for Environmental Research at Northern Arizona University (http://perceval.bio.nau.edu/MPCER_OLD/pj/pjwood). Only management actions involving piñon and juniper tree-reduction treatments were included in this study.

Table 4-6. Elevation (m), mean annual temperature (MAT, ºC), and mean annual precipitation (MAP, mm) of the locations where vegetation management actions occurred within each BLM field office. Data are means with the range in parentheses. Climate data were obtained from the PRISM Climate Database (http://prism.oregonstate.edu).

State	Field Office	Elevation (m)	MAT (ºC)	MAP (mm)
AZ	Arizona Strip	1756 (1271 - 2243)	12 (10 - 13)	357 (299 - 450)
CO	Glenwood Springs	2313 (1759 - 2764)	6 (6 - 6)	342 (342 - 342)
CO	Grand Junction	2193 (1749 - 2475)	8 (8 - 9)	361 (323 - 439)
CO	Little Snake	2101 (2031 - 2175)	7 (7 - 8)	340 (330 - 363)
CO	San Juan	2009 (1658 - 2415)	10 (9 - 10)	368 (348 - 390)
CO	Uncompahgre Basin	2227 (1760 - 3220)	8 (4 - 9)	444 (345 - 662)
CO	White River	2048 (1732 - 2400)	8 (7 - 8)	405 (308 - 504)
NM	Albuquerque	2196 (2031 - 2532)	8 (8 - 9)	332 (304 - 369)
NM	Farmington	1967 (1739 - 2289)	10 (9 - 10)	384 (346 - 421)
UT	Cedar City	1849 (1398 - 2401)	10 (9 - 13)	350 (316 - 377)
UT	Kanab	1955 (1561 - 2507)	9 (6 - 12)	320 (245 - 399)
UT	Moab	2003 (1709 - 2331)	9 (8 - 10)	390 (342 - 489)
UT	Monticello	2032 (1672 - 2516)	10 (8 - 11)	370 (316 - 494)
UT	Price	1994 (1762 - 2431)	8 (8 - 8)	333 (284 - 378)
UT	Richfield	2115 (1865 - 2598)	8 (6 - 10)	391 (243 - 667)
UT	St. George	1616 (1305 - 1798)	14 (13 - 15)	358 (345 - 384)
UT	Vernal	2098 (1686 - 2610)	7 (6 - 9)	316 (257 - 349)

Data Analyses

Tree-reduction methods included bull dozing, cabling, railing, chaining, prescribed burning, hydroaxing and wood-cutting (Table 4-7). For analyses, I grouped the bull dozing, cabling, railing, and chaining treatments (hereafter collectively referred to as chaining), because these four treatments result in similar soil and vegetation disturbances. When prescribed burning was applied in conjunction with other tree-reduction methods, such as chaining, I classified these treatments as prescribed burning. All tree-reduction treatments that involved seeding were also classified as revegetation treatments.

Table 4-7. Description of the various vegetation management actions conducted in piñon-juniper woodlands.

Method	Description
Bull Doze	Vegetation is pushed over and uprooted by a tractor with a heavy blade, and then left in windrows or piles.
Cable	Heavy steel cables are dragged behind a tractor in a "U", "J", or half circle pattern, also used to scarify soil surface in preparation for seeding.
Chain	Heavy chains are pulled in a "U" or "J" shaped pattern behind two crawler-type tractors, also used to scarify soil surface in preparation for seeding.
Rail	A modified version of chaining in which railroad rails are attached to chain links in order to increase soil disturbance and uproot shrubs. This technique is also referred to as "Ely chaining".
Woodcut	Includes all firewood cuts, hand thin, prunes, and harvests.
Prescribed Burn	The controlled application of fire to the land to achieve site-specific fire and resource management objectives.
Hydroaxe	A bull hog shredder, also referred to as a hydromower or rotary axe, chips trees in place, creating a mulch bed on the treatment area

I quantified total implementation cost of each tree-reduction method (hydroaxe, prescribed fire, chaining, and woodcut) within each decade and adjusted for inflation. I used the inflation calculator provided by the U.S. Department of Labor, which is based on the average Consumer Price Index for a given calendar year (http://www.bls.gov/data/inflation_calculator.htm), to quantify implementation cost of each treatment as if it were in the year 2010. Cost values were missing for 21% of the treatments, and thus, total cost is the minimum total cost of all tree-reduction treatments. To compare the implementation costs associated with the different tree-reduction methods and how this cost varied with time, I excluded all treatments that had also been seeded or had multiple tree-reduction methods applied. Using these criteria, I calculated implementation cost per hectare of each treatment after accounting for inflation (using the same methodology described above). To understand how treatment implementation cost varied with time, I performed a linear regression for each tree-reduction method with implementation cost per hectare (after accounting for inflation) as the response variable and year as the predictor variable. To compare the implementation costs associated with the different tree-reduction methods, I performed a one-way ANOVA with tree-reduction treatment as the fixed effect and implementation cost per hectare as the response variable. When significant, post hoc analyses were performed using Tukey's HSD. Because the implementation cost of chaining increased with time (Figure 4-9), and because this treatment method was common in the 1950s and 1960s, I performed a similar ANOVA as above but excluded all treatments that were done prior to 1970. All analyses were performed in R (R Development Core Team 2011), with α = 0.05.

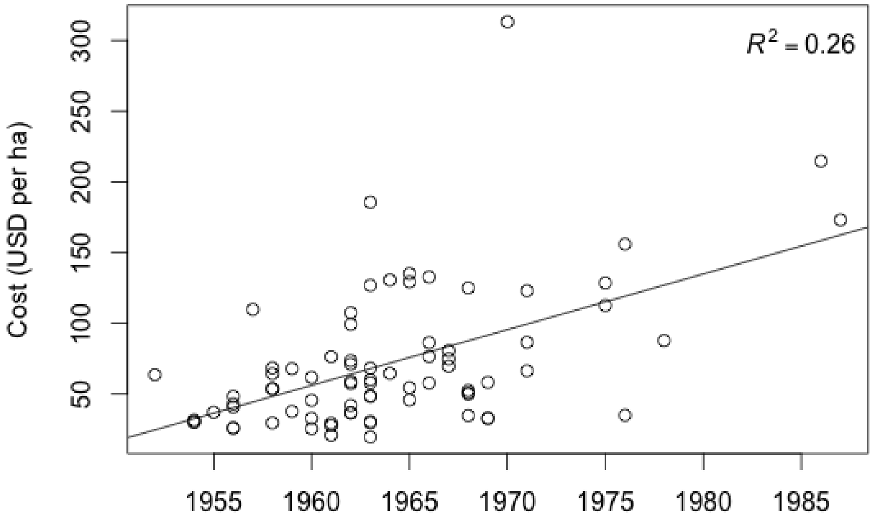


Figure 4-9. The cost of chaining piñon-juniper woodlands from 1950-1990. In this study, chaining includes bulldozing, cabling, and chaining. There was a significant increase (P <0.0001) in the cost of chaining from 1950 to 1990.

Results

From 1950 to 2003, over 240,000 hectares of piñon-juniper woodlands were treated by the BLM across the Colorado Plateau (Table 4-8 and Figure 4-10). Tree-reduction treatment methods varied throughout this time, with chaining common earlier in the 20th century and prescribed burning and hydroaxing common later in the 20th century (Table 4-8). In addition, treatment methods varied by field office—certain field offices used prescribed burning as a predominant treatment method while others predominantly used chaining (Figure 4-10).

Table 4-8. The number (trt. count), spatial extent (trt. area), and minimum total implementation cost (min. cost) for each type of tree-reduction treatment done between 1950 and 2003 by the Bureau of Land Management in the Colorado Plateau. Revegetation is the percentage of treatments that included a seeding treatment, based on treatment area.

Time Period	**Trt. Type**	**Trt. Count** (no. year[1])	**Trt. Area** (ha year^{-1})	**Min. Cost**[1] (USD year^{-1})	**Revegetation**[2] (%)
1950s	burn	0.2	52	$2,932	100
	chain	4.4	2,939	$226,068	58
1960s	burn	1.4	381	$54,202	99
	chain	27.7	13,413	$1,520,681	80
	woodcut	0.1	20	$2,013	0
1970s	burn	1.0	271	$22,048	57
	chain	4.0	2,156	$230,447	64
	woodcut	0.1	42	$15,861	100
1980s	burn	6.7	1,301	$95,532	51
	chain	3.9	803	$154,739	87
	hydroaxe	0.1	1	----[3]	100
	woodcut	2.2	66	$1,585	42
1990s	burn	3.6	958	$57,373	23
	chain	0.7	63	$15,742	67
	hydroaxe	0.2	23	$5,838	70
	woodcut	1.7	183	$21,371	28
2000-03	burn	5.7	3,550	$218,942	26
	chain	0.3	37	$8,040	100
	hydroaxe	4.3	1,058	$331,218	15
	woodcut	1.3	63	$36,415	61
unknown	unknown	0.2	30	$419	60
Total[4]		636	247,153	$26,665,415	67

[1] This is the minimum total implementation cost per year (after accounting for inflation; see methods) because treatment cost data was missing from 21% of the treatments.
[2] This is the minimum percentage of revegetation treatments, because some revegetation treatments may have not been documented.
[3] Data unavailable.
[4] The total row shows the total number, extent and cost of all tree-reduction treatments done between 1950 and 2003 (rather than per year).

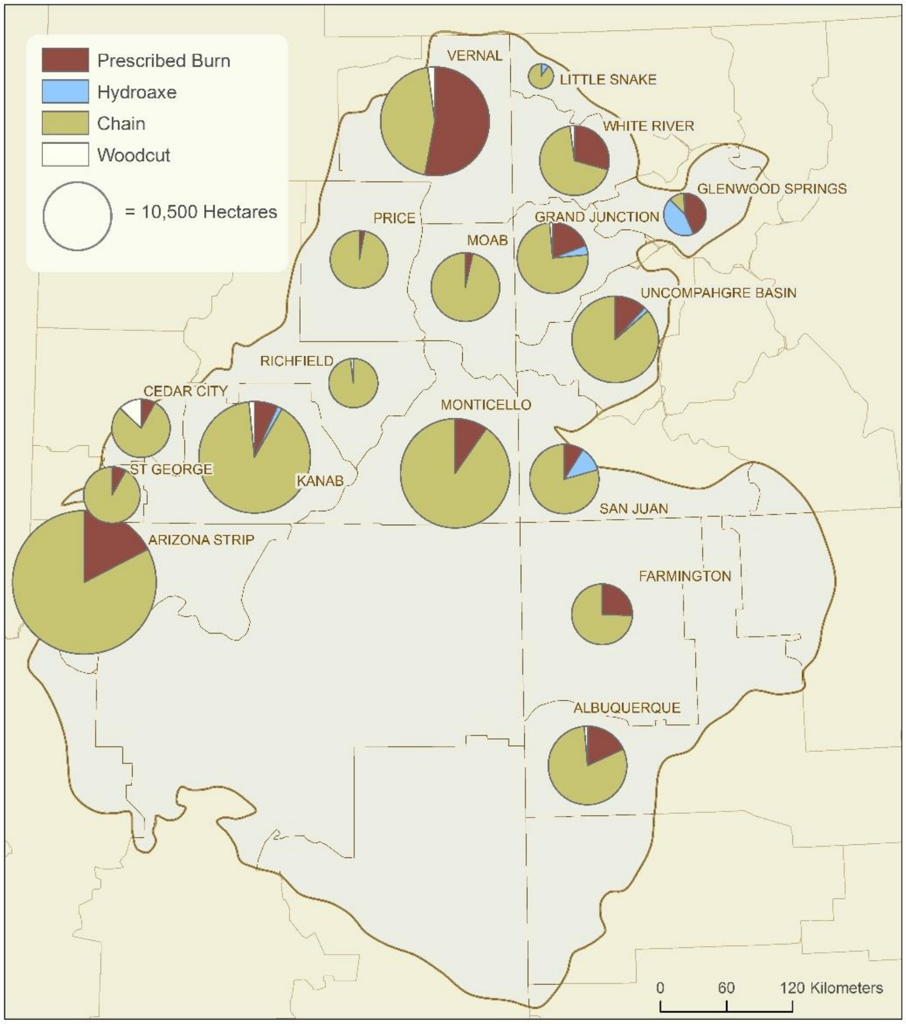


Figure 4-10. Map of the different tree-reduction treatments implemented within each BLM field office in the Colorado Plateau between 1950 and 2003. The size of each pie chart indicates the spatial extent of the total area treated within each BLM field office.

Seed applications were applied to at least 61% of tree-reduction treatments. These seed applications predominantly consisted of perennial grasses, such as *Agropryron cristatum* (L.) Gaertn. (crested wheatgrass) and *Pascopyrum smithii* (Rydb.) A. Love (western wheatgrass), but some also contained perennial forbs and shrubs such as *Melilotus officinalis* (L.) Lam. (sweetclover) and *Atriplex canescens* (Pursh) Nutt. (fourwing saltbrush). Seed applications included aerial broadcasting, hand seeding, seed drilling, or a using a dribbler (Table 4-9). Prior to seeding, a rollerchopper, plow, or harrow was often used to prepare the seed bed (Table 4-9).

Table 4-9. Description of the types of revegetation treatments conducted in piñon-juniper woodlands.

Method	Description
Seeding	
Hand broadcast	Method of seeding that involves uniformly scattering seeds using handheld seeders.
Aerial broadcast	Method of seeding that involves scattering seeds from a small airplane or helicopter. This method is particularly useful when seeding large areas.
Seed driller	Method of seeding that uses a machine (or seed drill) that precisely positions seeds in the soil and then covers the seeds.
Dribbler	Method of seeding that uses a machine (or dribbler) that drops seeds onto the soil and presses the seed into a firmed seedbed. Tractor-pulled seed dribbler
Seed Bed Preparation	
Harrow	A method of seedbed preparation in which the soil is disturbed through the use of a harrow, which is pulled behind a large tractor. Seed is broadcast in front of the harrow and turned under the soil as the harrow passes.
Plow	Pointed metal-toothed implements are pulled behind a tractor to uproot and chop roots and vegetation, which are left near the soil surface to encourage seed growth.
Rollerchop	A large, heavy drum that is equipped with several full-length blades is pulled behind a tractor to cut and crush vegetation. The drum can be filled with water to increase its weight. The rollerchopper can be used to both prepare seedbeds and cover seeds after seeding.
Aerator	A large, heavy drum with tines that is pulled behind a tractor or dozer to break up the soil and improve water infiltration, and to crush older shrub overstory while leaving some vegetation to re-colonize treated area.

Note - See Stevens and Monsen (2004) for a more thorough description of many of these methods.

A total of 26.7 million USD was spent on the 500 tree-reduction treatments on the Colorado Plateau (out of 636 total treatments) for which the implementation cost was recorded (Table 4-8). There was no strong relationship between treatment implementation cost and year of treatment among the hydroaxe, woodcut, and prescribed burn tree-reduction treatments, after accounting for inflation and excluding all tree-reduction treatments that had also been seeded ($P > 0.10$). However, there was a significant positive relationship between treatment implementation cost and year of treatment among the chaining treatments ($R^2 = 0.26$; $P < 0.0001$; Figure 4-9). There was also a significant effect of treatment method on implementation cost ($F = 21$, $P < 0.0001$), with hydroaxing having three fold higher implementation costs than all other treatments ($P < 0.0001$; Figure 4-11). Wood-cutting had higher implementation costs than prescribed burning ($P = 0.02$; Figure 4-11). When examining only tree-reduction methods that occurred since 1970, hydroaxing was still significantly higher in cost than all other treatments ($P < 0.02$). Chaining also had significantly higher implementation costs than prescribed burning ($P = 0.009$), while there was no difference between wood-cutting and prescribed burning ($P = 0.09$).

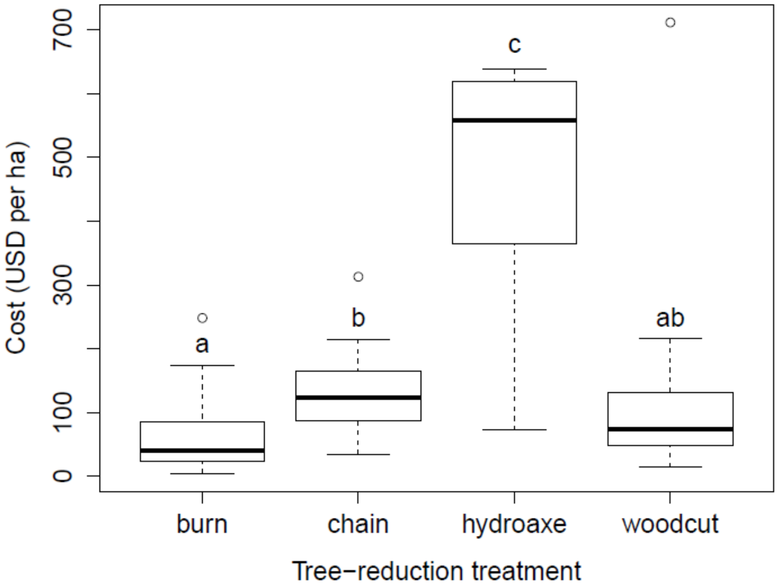


Figure 4-11. The implementation cost associated with each tree-reduction treatment in piñon-juniper woodlands across the Colorado Plateau. Treatments that occurred prior to 1970 were not included. Different letters denote significant differences among treatments, with $\alpha = 0.05$. The box indicates the 25th and 75th percentile (inter-quartile range) of the data, the bolded line inside the box indicates the median, the whiskers indicate the range, and the points outside of the whiskers indicate potential outliers.

Discussion

On the Colorado Plateau, over 247,000 hectares of piñon-juniper woodlands were treated with tree-reduction treatments between 1950 and 2003, representing 6.6% of woodlands managed by the BLM. These tree-reduction treatments may alter herbaceous communities (Owen et al. 2009; Huffman et al. 2013; Redmond et al. 2013), tree composition (Redmond et al. 2013), and soil erosional processes (Gifford 1973; Farmer et al. 1999; Pierson et al. 2007; Cline et al. 2010). Further, the array of treatment methods may differentially affect vegetation cover and soil erosion (Owen et al. 2009; Huffman et al. 2013; Redmond et al. 2014b).

Chaining was the predominant treatment method between 1950 and 1979 (Table 4-8). Beginning in the 1980s, prescribed burning became a more prevalent management technique. This shift in methodology may be partially explained by the increased recognition that chaining may adversely affect archeological sites or cultural resources (Debloois et al. 1974; Haase 1983) and may result in faster woodland recovery following treatment (Tausch and Tueller 1977; Skousen et al. 1989; Bristow 2010). By the early 2000s, the predominant tree-reduction treatments were hydroaxing and prescribed burning, while chaining was rare. At this time, treatment objectives were aimed to reduce the risk of catastrophic fire and to restore ecosystem structure and function (NFP 2000; BLM 2008).

Over 60% of tree-reduction treatments also involved seeding treatments (Table 4-8). Seeding treatments have the potential to increase herbaceous cover following tree-reduction treatments (Redmond et al., 2014a), particularly because the seed bank may have become depleted (Koniak and Everett 1982; Poulsen et al. 1999). Seeding treatments may also reduce the abundance of invasive species (Thompson et al. 2006, Sheley and Bates 2008), especially following fire. Many of the seeding treatments involved reseeding with drought tolerant, highly productive, non-native perennial grasses, such as crested wheatgrass. These non-native perennial grasses are still abundant 40 y later on some treated areas (Redmond et al. 2013).

A minimum of 26.7 million USD were spent implementing these tree-reduction treatments, with the hydroaxe treatment having the highest implementation cost per hectare treated (Figure 4-11). While implementation costs are one consideration when developing management plans, it is highly important to also consider the effectiveness of different treatments at accomplishing restoration and/or fuel-reduction goals, over both the short- and long-term timescales.

Implications

The spatial extent and cost of past tree-reduction treatments is rarely readily available for science and management purposes. Yet digitally archived information on treatment history is an important tool for researchers and land managers. For example, the information reported in this study and accompanying freely accessible online database (http://perceval.bio.nau.edu/MPCER_OLD/pj/pjwood/) can help guide research objectives and methodology to understand the legacy effects of past treatments. I found that over 65% of past tree-reduction treatments involved chaining, highlighting the need for studies to document the long-term effects of chaining on ecosystem structure and function. The online database contains information for each individual tree-reduction treatment, such as location, treatment type, and revegetation methods if applicable (*note*– this resource does not contain data on vegetation or soil responses to treatments). The online database can therefore be used to locate areas that have had past treatments. This unique dataset is useful for tree-reduction studies and future management, as well as a range of other studies that require land use history.

CHAPTER 5

LONG-TERM EFFECTS OF CHAINING TREATMENTS ON VEGETATION STRUCTURE IN PIÑON-JUNIPER WOODLANDS OF THE COLORADO PLATEAU

Adapted from: Redmond MD, Cobb NS, Miller ME and NN Barger. 2013. Long term effects of chaining treatments on vegetation structure in piñon-juniper woodlands of the Colorado Plateau. Forest Ecology & Management 305: 120-128.

Abstract

Over the last half-century a range of methods have been utilized to reduce trees and shrubs in order to reduce wildfire risk and promote herbaceous vegetation to support livestock and wildlife. I examined the long-term (20 to 40 year) effects of past tree-reduction treatments on vegetation and ground cover in piñon-juniper woodlands, which is the third most extensive vegetation type in the continental United States. Tree-reduction treatments were conducted between 1963 and 1988 in Grand Staircase Escalante National Monument, Utah by the U.S. Bureau of Land Management and involved chaining followed by seeding to remove trees and often shrubs. Treatments were effective at increasing perennial grass cover and reducing tree cover over multiple decades. The increase in perennial grass cover was predominantly due to a nonnative species that was seeded, *Agropyron cristatum* (crested wheatgrass). Surface fuel loads were nearly twice as high in treated areas, likely changing fire behavior and increasing habitat complexity. Treated areas had higher bare mineral soil cover and lower biocrust cover, which may influence soil erosional processes. Interestingly, treated areas had significantly less *Pinus edulis* (piñon pine) recruitment compared to untreated areas, while there was no change in *Juniperus osteosperma* (Utah juniper) recruitment. These results indicate that treated areas may become more *J. osteosperma* dominated in the future due to increased establishment of *J. osteosperma* compared to *P. edulis*. These results show that while treatments were effective at reducing tree cover and increasing herbaceous cover, there were long-term (40 year) treatment

effects on vegetation composition and ground cover that need to be taken under consideration when developing future management strategies.

Introduction

Across the western U.S., there is an increasing need to effectively manage ecosystems to both mitigate hazardous wildfires and maintain, and in some cases restore, the structure, function, diversity and dynamics of forest and rangeland ecosystems. Of particular importance to the management of public lands in the western U.S. are ecosystems dominated by various species of piñon (e.g., *Pinus edulis and P. monophylla*) and juniper (e.g., *Juniperus monosperma, J. osteosperma*, and *J. occidentalis*), which collectively represent the third most extensive vegetation type in the continental U.S. and are one of the predominant vegetation types administered by federal land-management agencies in the U.S. (Romme et al., 2009).

During the past half-century, piñon-juniper (P-J) ecosystems have been a major focus for land-management activities due to their great spatial extent, the multiple ecosystem services they provide, and historic changes in the structure and extent of P-J populations. Across the western U.S., P-J populations have established in adjacent grassland and shrubsteppe vegetation, and existing woodlands have experienced increased tree recruitment and stand densities over the last century (Barger et al., 2009; Miller and Rose, 1999; Miller et al., 2008; Tausch et al., 1981). In thickening woodlands and where trees have established in adjacent grasslands and shrubsteppe, competition from trees has contributed to declines in forage production for livestock and diminished habitat quality for some wildlife species (Bates et al., 2005; Clary and Jameson, 1981; Noson et al., 2006). In some settings, increasing tree dominance and decreasing herbaceous cover have contributed to increases in runoff and soil erosion (Wilcox, 1994), with implications for long-term ecosystem sustainability.

Thus, since the 1950s a variety of tree-reduction methods have been used across large tracts of public lands in the western U.S. in attempts to restore herbaceous cover and production. These early treatment methods, which predominantly involved green chaining and seeding, were effective at increasing herbaceous cover (Aro, 1971; Tausch and Tueller, 1977) and, in certain cases, reducing runoff and soil erosion in the short-term (Farmer et al. 1999; Gifford, 1973). However, the effectiveness of these treatments at maintaining low tree densities, high herbaceous cover, and reducing soil erosion in the long-term are largely unknown (but see Pierson et al., 2007 and Skousen et al., 1981).

Despite this lack of knowledge, concern over threats posed by wildland fire over the last decade has led to sharp increases in the number and extent of new tree-reduction projects, some of which use the same chaining techniques common in the 1960s. Many of these projects have been conducted in conjunction with the U.S. National Fire Plan, which aims to reduce the risk of catastrophic wildland fire while restoring ecological functions to forests and woodlands across the U.S. Whereas past management treatments primarily focused on forage production for livestock, managers are now tasked with treating for multiple objectives, including fire prevention and maintenance of ecosystem attributes such as soil stability and fertility, hydrologic processes, and ecosystem resistance to invasion by exotic plants. Thus, there is a clear need for understanding the longer-term effects of tree-reduction on vegetation structure and soil properties in these ecosystems.

In this study, I examined how past chaining treatments influenced plant communities and soil surface characteristics at 17 paired (treated vs. untreated) sites that were chained and seeded between 1963 and 1988. I also examined whether vegetation and soil surface responses changed as time since chaining treatment increased (from 18 to 43 years). I predicted that these past chaining treatments would lead to increased herbaceous cover and decreased tree cover. Additionally, I hypothesized that as time since chaining treatment increased there would be an increase in tree cover leading to a decline in herbaceous cover. I focused this study in Grand Staircase-Escalante National Monument located in southern Utah on the Colorado Plateau, where numerous chaining treatments have occurred (Chapter 4; Redmond et al., 2014a).

Methods

Study Area and Treatment Methods

From May thru August 2006, I sampled 17 paired (treated vs. untreated) sites located within P-J woodlands in Grand Staircase-Escalante National Monument, Utah that had been treated between 1963 and 1988 by the Bureau of Land Management (BLM) (see Table 5-10). For the treated sites, I focused on tree-reduction treatments involving chaining and seeding (Table 5-10), as those were the most common treatment methods used by the BLM and were applied to over 169,000 hectares of land across the Colorado Plateau since the 1940s (Chapter 4; Redmond et al., 2014a). The chaining treatment method involves two tractors pulling heavy chains (18 to 40 kg/link) in a “U” or “J” shaped pattern to pull over and uproot trees and often shrubs (BLM, 2008). Smooth chains were used at all sites except for site 126 where Ely chaining was used. An Ely chain had short pieces of hardened railroad rails welded perpendicular to each link to increase soil disturbance and uproot more trees and shrubs. Both smooth and Ely chaining disturb soils, and in all of the treatments examined in this study, plant debris was left in the treatment to reduce erosion (BLM, 2008). All treatments involved seeding, however, the seeding methods and species mixes seeded into the area varied (see Table 5-10 for details). Seeding was done using aerial or hand broadcasting, where seeds are left on the soil surface, or by drilling or using a dribbler, where equipment is used to bury seeds (BLM, 2008).

Table 5-10. Treatment year, treatment method, species seeded, amount seeded (in parenthesis next to species seeded in kg ha-1), method of seeding for all treated sites, and mean slope, aspect, and elevation for each paired site. The order in which treatment combinations were applied is denoted by slashes with methods in chronological order (i.e. Chain/Plow/Seed indicates the site was chained, then plowed, then seeded).

Paired Site	**Slope**	**Aspect**	**Elev. (m)**	**Year Treated**	**Treatment Method**	**Species Seeded**	**Seeding Method**
137	2°	S	1960	1963	Chain/Seed	*A. cristatum (7.8)*	Drill
139	2°	E	2027	1964	Chain/Windrow/Seed	*A. cristatum (6.7)*	Drill
127	1°	W	1840	1965	Plow/Chain/Seed	*A. cristatum (6.7)*	Aerial Broadcast
129	1°	E	1960	1965	Chain/Chain/Seed	*A. cristatum (6.7)*	Aerial Broadcast
130	4°	S	1973	1965	Chain/Chain/Seed	*A. cristatum (6.7)*	Aerial Broadcast
133	3°	SE	1604	1965	Chain/Chain/Seed	*A. cristatum (6.7)*	Aerial Broadcast & Drill
135	5°	SE	2148	1965	Chain/Seed	*A. cristatum (6.7)*	Aerial Broadcast
110	2°	SE	1886	1966	Chain/Seed/Chain	*A. cristatum (6.7)*	Aerial Broadcast
131	4°	S	2002	1966	Chain/Chain/Seed	*A. cristatum (6.7)*	Aerial Broadcast
132	5°	E	2042	1968	Chain/Plow/Seed	*Elymus junceus (5.6)*	Aerial Broadcast
134	3°	SE	1762	1969	Chain/Chain/Seed	*A. cristatum (5.6), Atriplex cansecens (0.3), Medicago sp. (5.6), Purshia tridentata (0.3)*	Aerial Broadcast
113	5°	SE	1950	1971	Chain/Seed/Seed	*A. intermedium (5.8)*	Aerial Broadcast
150	5°	SW	1892	1981	Chain/Chain/Seed	*A. cristatum (4.5), A. trichophorum (2.2), E. junceus (3.4), Meliotus officinalis (1.1), P. tridentata (0.3)*	Aerial Broadcast
126	1°	S	2028	1982	Chain/Plow/Seed	*Other Herbs (7.1)*	Aerial or Hand Broadcast
128	6°	SW	2192	1982	Chain/Seed	*A. cristatum (9.0), E. junceus (6.7), A. intermedium (2.2), M. officinalis (2.2), A. cansecens (0.3)*	Aerial Broadcast & Dribbler
107	2°	E	2036	1983	Chain/Seed	*A. cristatum (4.5), A.trichophorum (3.4), M. offiinalis (0.9), Onobrychis sp. (0.9)*	Aerial Broadcast
123	1°	E	1859	1988	Chain/Seed	*A. cristatum, E. junceus*	Drill

Wheras all treatments involved chaining and seeding, the combination of treatment methods varied (Table 5-10). For example, some sites were double chained and then seeded (denoted as chain/chain/seed in Table 5-10) while other sites were chained once and then plowed and seeded (denoted as chain/plow/seed in Table 5-10). All paired untreated sites were adjacent to the treatment area and of similar slope (± 9°), aspect (± 75°), elevation (± 75 m) and of the same soil map unit (Natural Resource Conservation Service, 2006).

Sites were located in either persistent P-J woodlands or wooded shrublands (Romme et al., 2009), with vegetation consisting of overstory *Pinus edulis* Engel. (twoneedle piñon) and *J. osteosperma* (Torr.) Little (Utah juniper). All paired sites had at least one tree with a basal trunk diameter greater than 22 cm, suggesting that trees had established prior to the 20th century at the study sites (Despain 1989; Barger et al., 2009). The dominant shrub in the area is big sagebrush (*Artemesia tridentata* Nutt. and *Artemesia tridentata* Nutt. ssp. *tridentata*), which ranged from 0 to 35% cover in the untreated areas. Other shrub species common at many of the sites included, broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt. and Rusby), Mormon tea (*Ephedra viridis* Coville), and antelope bitterbrush (*Purshia tridentata* (Pursh) DC.).

Mean annual temperature and precipitation from 1960 to 2010 in the study area was 11.8 °C and 251 mm, respectively (http://prism.oregonstate.edu). Annual precipitation in 2006 was slightly below average (240 mm), but within one standard deviation of the 50 year mean (http://prism.oregonstate.edu). Mean annual temperature in 2006 was similar to the 50 year mean (11.7 °C) (http://prism.oregonstate.edu).

Field Methods

For all paired sites, I used GIS to randomly locate three points within each treated and untreated area. At each point I established three 10 X 10 m subplots, each located 75 m apart, for a total of 9 subplots per site.

To quantify tree density and cover, I recorded the species status (live or dead), height (live trees only), two perpendicular canopy widths (live trees only), and the basal trunk diameter (BTD) for all trees (adults, ≥ 5 cm BTD; saplings, ≥ 2.5 cm and < 5 cm BTD; and seedlings, BTD < 2.5 cm) rooted within each subplot. To quantify shrub density, I counted the number of each shrub species located within each subplot. Following, two observers did an ocular estimate of percent cover for each shrub species within each 10 X 10 m subplot, which were then averaged. To quantify herbaceous and soil cover, I randomly placed one 1 m^2 quadrat within each quadrant of the 10 X 10 m subplot and estimated percent cover bare ground, rock, litter, and biocrusts located within each 1 m^2 quadrat as well as percent cover for each plant species.

To quantify surface fuel loads, I randomly established one 10 m transect going through the center of each subplot and recorded the small and large diameter of each downed, dead woody material (twigs, stems, branches, bolewood) from trees and shrubs that intersected the transect (see methods in Brown, 1974). For fuels greater than 7.6 cm I classified wood as sound (≤ 50% decay) or rotten (>50% decay).

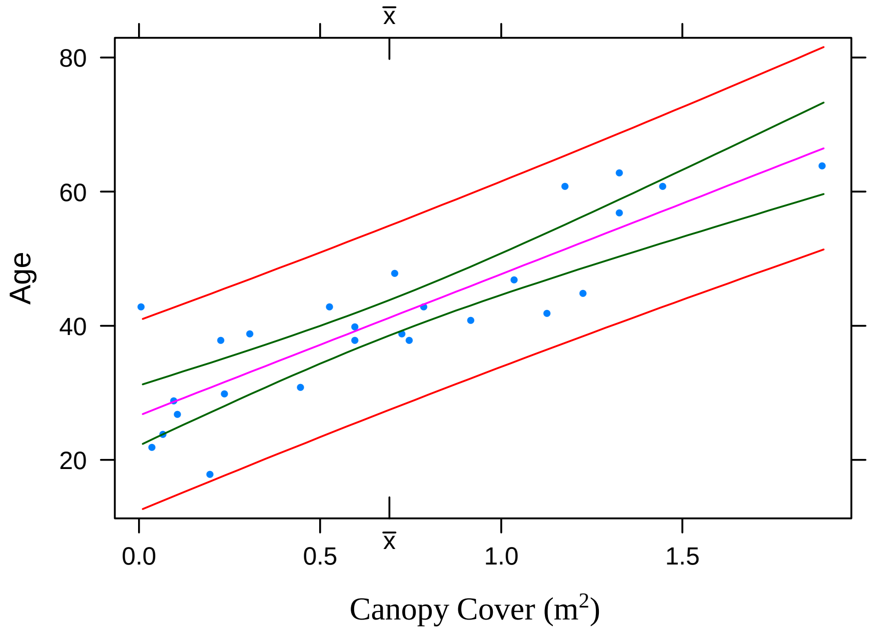
Data Analysis

To understand the effects of chaining and seeding on vegetation, biocrusts, and surface fuel load I performed a paired (treated vs. untreated) Student's t-test across the 17 sites. In cases where the response variable was not normally distributed, even after multiple transformations were attempted, I performed a paired Wilcoxon Signed Rank test. I omitted sites 110, 113, and 123 from all surface fuel load analyses due to missing data.

I evaluated understory diversity, which included all shrubs, graminoids, and forbs, using two indices: species richness (N_0), calculated as the mean number of species per 10 X 10 m subplot and species heterogeneity (N_2), calculated as the reciprocal of Simpson's Index (Hill, 1973). Species heterogeneity shares the same units as species richness and incorporates both species richness and species evenness (Peet, 1974).

To understand the long-term effects of chaining on tree recruitment dynamics, I examined the number of *P. edulis* and *J. osteosperma* trees that likely recruited after each treatment among the sites that were treated between 1963 and 1971. Based on the size-age relationship for *P. edulis* ($\text{age}_{\text{tree x}} = 2.45 * \text{BTD}_{\text{tree x}} + 26.8$; Figure 5-12) and *J. osteosperma* ($\text{age}_{\text{tree X}} = 21.1 * \text{canopy}_{\text{tree X}} + 26.6$; Figure 5-12), I considered trees with a BTD ≤ 5 cm for *P. edulis* and trees with a canopy $\leq 0.64\ \text{m}^2$ for *J. osteosperma* to have recruited after treatment (i.e. ≤ 40 years old). Using this size cut-off, I examined the differences in the numbers of trees that recruited in the last 40 years (i.e. recruited post-treatment) in the treated and untreated sites by conducting paired (treated vs. untreated) Student's t-test using data across the 12 sites that were treated between 1963 and 1971. Additionally, I did paired (treated vs. untreated) Student's t-tests to examine if *P. edulis* dominance (calculated as: $\text{density}_{P.\ edulis}/(\text{density}_{P.\ edulis} + \text{density}_{J.\ osteosperma})$) differed between the treated and untreated sites among the trees that recruited post-treatment as well as among the trees that recruited prior to treatment. Lastly, to examine changes in recruitment patterns across all of the 17 paired sites, I examined differences in seedling (BTD < 2.5 cm) and sapling (BTD <5 cm and ≥ 2.5 cm) densities among the treated and untreated sites by doing paired (treated vs. untreated) Student's t-tests. In cases where the

A. *Juniperus ostosperma*



B. *Pinus edulis*

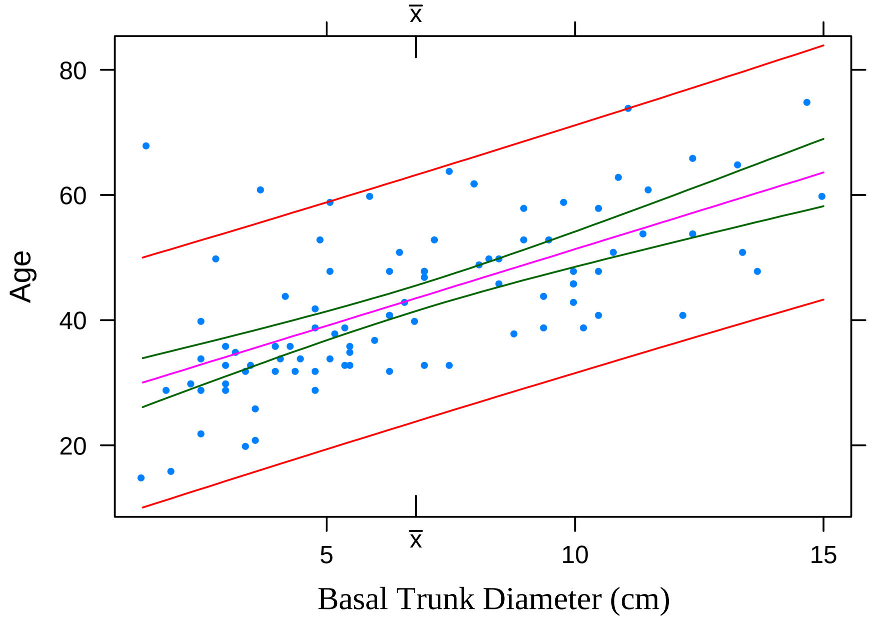


Figure 5-12. The relationship between tree canopy cover (m2) and tree age for J. osteosperma (A.) and tree basal trunk diameter (BTD) and tree age for P. edulis (B.), with the data pooled across the four sites.Canopy cover is shown for J. osteosperma while BTD is shown for P. edulis, because canopy cover was the best predictor for J. osteosperma age while BTD was the best predictor for P. edulis age. The regression line (pink) and the 95% confidence (green) and prediction (red) intervals are shown for J. osteosperma (A.) and P. edulis (B.).

response variable was not normally distributed, even after multiple transformations were attempted, I performed a paired Wilcoxon Signed Rank test.

I also performed linear regressions to examine how year since treatment influenced the percent difference in herbaceous cover, shrub cover, tree density and basal area, ground cover, and fuel load (1 – 1000 h fuels). All analyses were performed using the statistical software R (R Development Core Team, 2011), with $\alpha = 0.05$.

Results and Discussion

Changes in herbaceous cover

Past chaining treatment methods were effective at increasing understory cover, even 40 years post-treatment. Total herbaceous cover was over four times as high (8.1% as opposed to 1.7%) in sites that had been treated as compared to untreated sites (paired t-test, $P = 0.001$; Figure 5-13). Interestingly, while there was a trend of higher herbaceous cover among sites that had been treated more recently (i.e. 1980s), there was no strong relationship between year of treatment and difference in herbaceous cover among paired treated and untreated sites ($R^2 = 0.16$, $P = 0.07$; Table 5-11). This lack of a strong relationship may be due to the paired sampling design (i.e. rather than comparing pre-treatment and post-treatment data at each treated site, I compared post-treatment data with data from an adjacent untreated site). Additionally, there was high variability in vegetation cover among the untreated sites (Table 5-11), which may also reduce my ability to detect how vegetation may change over time following treatment.

When comparing differences in cover among herbaceous functional groups, there was no significant difference between treated and untreated sites in percent cover of annual forbs, annual graminoids, or perennial forbs (all paired Wilcoxon tests, all $P > 0.12$; Figure 5-13). However, perennial graminoids had significantly higher cover in treated sites (6.4% cover) than untreated sites (0.3% cover) (paired Wilcoxon test, *P* = 0.006; Figure 5-13). Previous research examining the impacts of chaining immediately (1 – 2 years) following chaining found increases in annual and perennial forbs (Skousen et al., 1989; Tausch and Tueller, 1977). However, 8 – 10 years following chaining these studies report increases in perennial graminoids and shrubs while forbs return to pre-treatment levels (Skousen et al., 1989; Tausch and Tueller, 1977), results which concur with my findings.

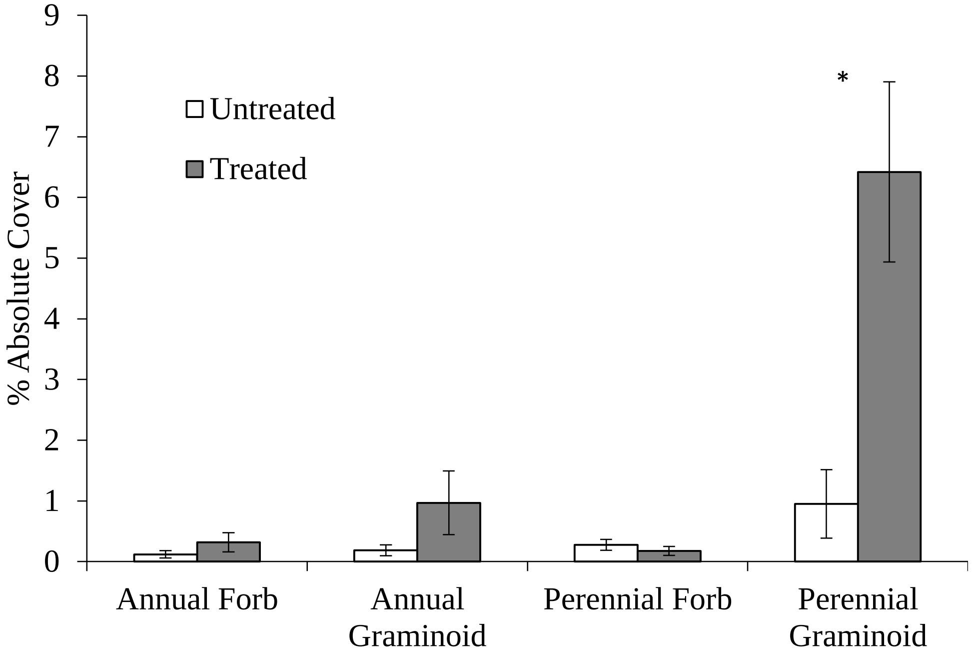


Figure 5-13. Percent absolute cover of annual forbs, annual graminoids, perennial forbs, and perennial graminoids in treated (chained and seeded) and untreated sites at Grand Staircase-Escalante National Monument, Utah. Data are means ± 1 SE and an asterisk denotes significant differences between treated and untreated sites, with $\alpha = 0.05$.

Table 5-11. Herbaceous cover (%), *Artemesia tridentata* cover (%), other shrub sp. cover (%), tree cover (%), tree density (trees per ha), tree basal area (m2 per ha), and 1-1000 h surface fuel loads (metric t ha-1) in each untreated (U) and treated (T) paired site. Bottom row includes mean ± 1 SE. Different letters denote significant differences between treated and untreated sites, with α = 0.05.

Paired Site	**Year**	**Herbaceous Cover**		***A. tridentata* Cover**		**Other Shrub sp. Cover**		**Tree Cover**		**Tree Density**		**Tree Basal Area**		**Surface Fuel Loads**	
		U	**T**	**U**	**T**	**U**	**T**	**U**	**T**	**U**	**T**	**U**	**T**	**U**	**T**
137	1963	0	1	0	17	7	18	18	3	522	178	31	2	11	35
139	1964	2	2	1	25	9	5	14	5	389	244	16	3	9	5
127	1965	10	7	10	27	23	14	11	7	189	211	11	10	1	14
129	1965	5	1	36	10	3	10	14	12	367	356	11	7	14	18
130	1965	0	6	6	36	6	7	20	0	411	33	19	0	16	12
133	1965	1	1	2	8	15	14	4	0	78	22	12	1	9	41
135	1965	1	9	0	13	8	13	21	4	478	144	27	4	12	19
110	1966	1	12	20	19	0	3	14	11	178	256	11	9	-	-
131	1966	0	1	0	15	13	9	20	8	356	289	19	8	36	76
132	1968	1	12	0	5	14	17	13	4	300	178	27	4	16	13
134	1969	0	1	0	27	21	16	12	1	256	44	39	1	41	81
113	1971	1	23	8	26	16	0	30	0	311	0	27	0	-	-
150	1981	0	0	0	13	9	9	15	4	456	256	31	4	13	57
126	1982	1	17	4	37	7	8	24	0	500	22	18	0	16	2
128	1982	0	20	3	2	19	15	13	6	511	367	21	4	28	51
107	1983	1	15	11	21	5	9	20	2	444	89	14	1	1	46

123	1988	2	8	18	5	10	11	10	0	33	0	3	0	-	-
Mean (± 1 SE)		2 (1)[a]	8 (2)[b]	7 (2)[a]	18 (3)[b]	11 (2)[a]	10 (1)[a]	16 (1)[a]	4 (1)[b]	340 (36)[a]	158 (30)[b]	20 (2)[a]	4 (1)[b]	16 (3)[a]	33 (7)[b]

The high cover of perennial graminoids in the previously treated sites is predominately due to the increase in *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass), the most commonly seeded species (Table 5-10). This species also accounts for the large increase in nonnative species cover, which was over ten times higher in the treated sites (5.6% cover on average) as compared to the untreated sites (0.5% cover on average) (paired Student's T test, $P = 0.006$). Among native species cover, there was an insignificant trend of higher native species cover in the treated sites (2.0% cover on average) as compared to the untreated sites (0.9% cover on average) (paired Wilcoxon test, $P = 0.09$).

Seeded species

Agropyron cristatum was the most commonly seeded species and was seeded in at least 14 of the 17 treated sites (Table 5-10). This species had significantly higher cover in the treated sites (4.4% cover) as compared to the untreated sites (0.4% cover) (paired Wilcoxen test, $P = 0.006$) and was the dominant species at the majority of the treated sites (10 of 17 sites). The only other species seeded that was present at the sites was *Elymus junceus* Fisch. (Russian wildrye), which was present in 2 of the 3 seeded treatment sites. Sites 123 and 128, which were seeded with *E. junceus* and *A. cristatum* (Table 5-10), had low *E. junceus* cover (0% and 0.2% cover, respectively) in the treated sites, similar to the paired untreated sites (both 0% cover). In the other *E. junceus* seeded site (site 132), which was seeded with only *E. junceus*, there was high *E. junceus* cover in the treated site (10% cover) unlike the paired untreated site (0% cover). While both *A. cristatum and E. junceus* are adapted for heavy grazing, *E. junceus* is more drought tolerant than *A. cristatum* and is also able to tolerate more alkaline levels than *A. cristatum* (Monsen *et al.*, 2004). In the study area, however, it appears that *A. cristatum* may be more competitive than *E. junceus.* When seeded without *A. cristatum, E. junceus* was effective at becoming established and remained a dominant herbaceous species for 40 years post-treatment.

These results show that the commonly seeded *A. cristatum* is effective at becoming established following seeding, which is consistent with other tree-reduction studies (Ott et al., 2003; Skousen et al., 1989), and remains a dominant herbaceous species for 40 years post-treatment. *Agropyron cristatum* is one of the most frequently planted nonnative grasses in western North America due to its high productivity, ease of establishment, grazing resistance, and ability to survive droughts (Lesica and DeLuca, 1996; Smoliak and Dormaar, 1985). The dominance and persistence of *A. cristatum* following these chaining treatments suggest that *A. cristatum* may be outcompeting other native species that would otherwise become more dominant (Henderson and Naeth, 2005; Walker, 1999; Wilson and Gerry, 1995).

Bromus tectorum

Bromus tectorum L. (cheatgrass), a highly invasive annual grass, was detected in 8 of the 17 paired sites. Within those 8 paired sites, *B. tectorum* had low cover (≤ 3%), with no significant difference in cover between treated (mean ± SE: 0.2 ± 0.1%) and untreated (1.0 ± 0.5%) sites (paired Student's t-test, $P = 0.09$). These results suggest that the chain and seed method did not affect *B. tectorum* abundance 40 years post-treatment. Similarly, while Skousen et al. (1989) found large increases in *B. tectorum* cover immediately (2 years) following chaining and seeding in P-J woodlands in central Utah, there was little increase in *B. tectorum* in the long-term (10-20 years) (Skousen et al., 1989). The lack of a long-term increase in *B. tectorum* cover following chaining and seeding in this study and others may be due to the establishment and growth of perennial grasses, which may have resulted in competitive exclusion of *B. tectorum* (Chambers *et al.*, 2007; Ott et al., 2003; Thompson *et al*, 2006). Further, *A. cristatum* may be particularly effective at outcompeting *B. tectorum* compared to other native perennial grasses (Cox and Anderson, 2004; Leffler *et al.*, 2011). Taken together, these results suggest that seeding with perennial graminoids, especially *A. cristatum*, may reduce the risk of *B. tectorum* invasion. Another potential explanation for the low cover of *B. tectorum* in the treated sites may be that *B. tectorum* has low invasibility in P-J woodlands in this study area (Crall et al., 2006), which is supported by the low cover of *B. tectorum* in the untreated sites. Thus, areas with larger populations of *B. tectorum* may potentially see long-term increases in *B. tectorum* following chaining and seeding.

Changes in shrub cover

Treated sites had 60% higher shrub cover than untreated sites (paired Student's t-test, P = 0.009; Table 5-11), which was due to the large increase in *A. tridentata*. In particular, *A. tridentata,* the dominant shrub, was over twice as high in chained and seeded sites (Table 5-11; paired Student's t-test, P = 0.002). While there was an increase in shrub cover overall, when *A.tridentata* was excluded from the analysis, there was no difference in shrub cover between treated and untreated sites (Table 5-11; paired Student's t-test, P = 0.7). These results highlight how certain shrub species benefit from chaining treatments, while other shrub species are unaffected, which is consistent with observations from other tree-reduction studies in P-J woodlands (Rippel et al., 1983).

Changes in understory diversity

While previous research found a decline in understory diversity immediately following chaining (O'Meara et al., 1981), these results suggest there were no long-term effects of chaining treatments on understory plant diversity: both in terms of species richness (paired Student's t-test, *P* = 0.4) and species heterogeneity (paired Student's t-test, *P* = 0.7). Species richness was much higher in both treated (mean ± SE: 11.0 ± 1.0) and untreated sites (10.4 ± 0.8) than species heterogeneity (3.0 ± 0.3 in treated sites and 2.9 ± 0.3 in untreated sites), highlighting how a select number of species, primarily *A. cristatum* (treated sites only) and *A. tridentata* (both treated and untreated sites), dominated understory cover.

Changes in soil surface characteristics

The percent bare mineral soil cover was significantly higher in the treated sites as compared to the untreated sites (paired Student's t-test, $P = 0.01$; Figure 5-14), while litter, biocrust, and rock cover was significantly lower in treated sites as compared to untreated sites (all paired Student's t-tests, all $P < 0.02$; Figure 5-14). Higher bare mineral soil cover may increase wind and water erosion (Wilcox, 1994; Davenport et al., 1998). Additionally, biocrusts can be important sources for fixed nitrogen in these semi-arid ecosystems (Belnap, 1996), and also for preventing soil and nutrient loss through wind and water erosion (Barger et al., 2006; Belnap and Gillette, 1998). While both higher bare mineral soil cover and lower biocrust cover may increase erosion, the higher herbaceous cover in the treated areas (Table 5-11) has likely reduced soil and water loss, because vegetation patches can serve as a sink for both water and sediment (Wilcox et al., 2003; Ludwig et al., 2005). Therefore, the potential negative effects of increased bare mineral soil cover and decreased biocrust cover on soil erosion may be offset by the increase in herbaceous vegetation. Indeed, previous research found a decrease in soil erosion one to six years following chaining in a P-J woodland in northern Utah, which was associated with an increase in understory vegetation (Farmer et al., 1999). The change in vegetation cover may also offset the potential losses of fixed nitrogen due to reduced biocrust cover.

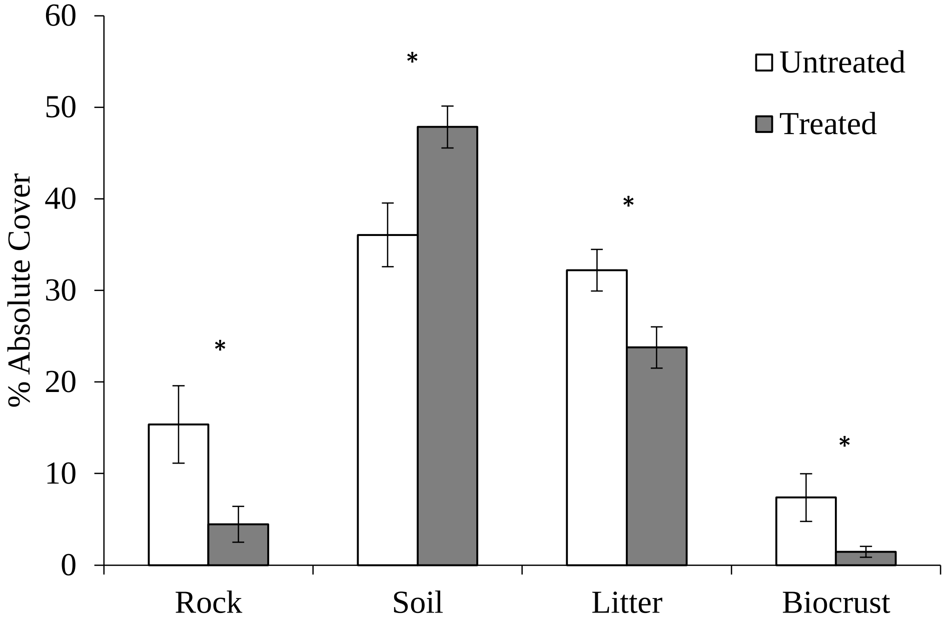


Figure 5-14. Percent absolute cover of rock, bare mineral soil, litter, and biocrust cover in treated (chained and seeded) and untreated sites at Grand Staircase-Escalante National Monument, Utah. Data are means ± 1 SE and an asterisk denotes significant differences, with α = 0.05.

The changes in ground cover in the treated areas may be due to the physical effects of chaining or the post-treatment effects of livestock grazing. Livestock grazing has been an important economic activity in this study area (Grand Staircase-Escalante National Monument) since the late 1800s and is still common today. Grazing is known to reduce biocrusts in piñon-juniper woodlands (Beymer and Klopatek, 1992). Additionally, in sagebrush-dominated ecosystems within Grand Staircase-Escalante National Monument, persistent heavy grazing has significantly impacted soil hydrologic conditions (Miller, 2008). The treated sites may have been grazed more often than the untreated sites due to their higher herbaceous cover (Figure 5-13). Thus, post-treatment management (i.e. grazing) may have played a role in the differences in bare mineral soil and biocrust cover between the treated and untreated sites.

There was no relationship between year of treatment and difference in soil, litter, rock, or biocrust cover among paired treated and untreated sites (linear regressions, all $R^2 < 0.0$ and $P > 0.35$). These results suggest that ground cover doesn't seem to vary among sites that were chained 20 and 40 years ago. However, the lack of a relationship may be partly due to a relatively small sample size (17) given the heterogeneity of the sampling area and the paired study design.

Changes in tree cover, density, and recruitment

Chaining was effective at reducing tree abundance for 40 years following treatment: tree basal area was five fold higher in the untreated sites as compared to the treated sites (paired Student's t-test, $P < 0.001$; Figure 5-15A) and tree density was twice as high in the untreated sites as compared to the treated sites (paired Student's t-test, $P < 0.004$; Figure 5-15B). These results suggest that chaining can be effective at decreasing tree density and basal area for 40 years, counter to what previous research has suggested (Skousen et al., 1989; Tausch and Tueller, 1977).

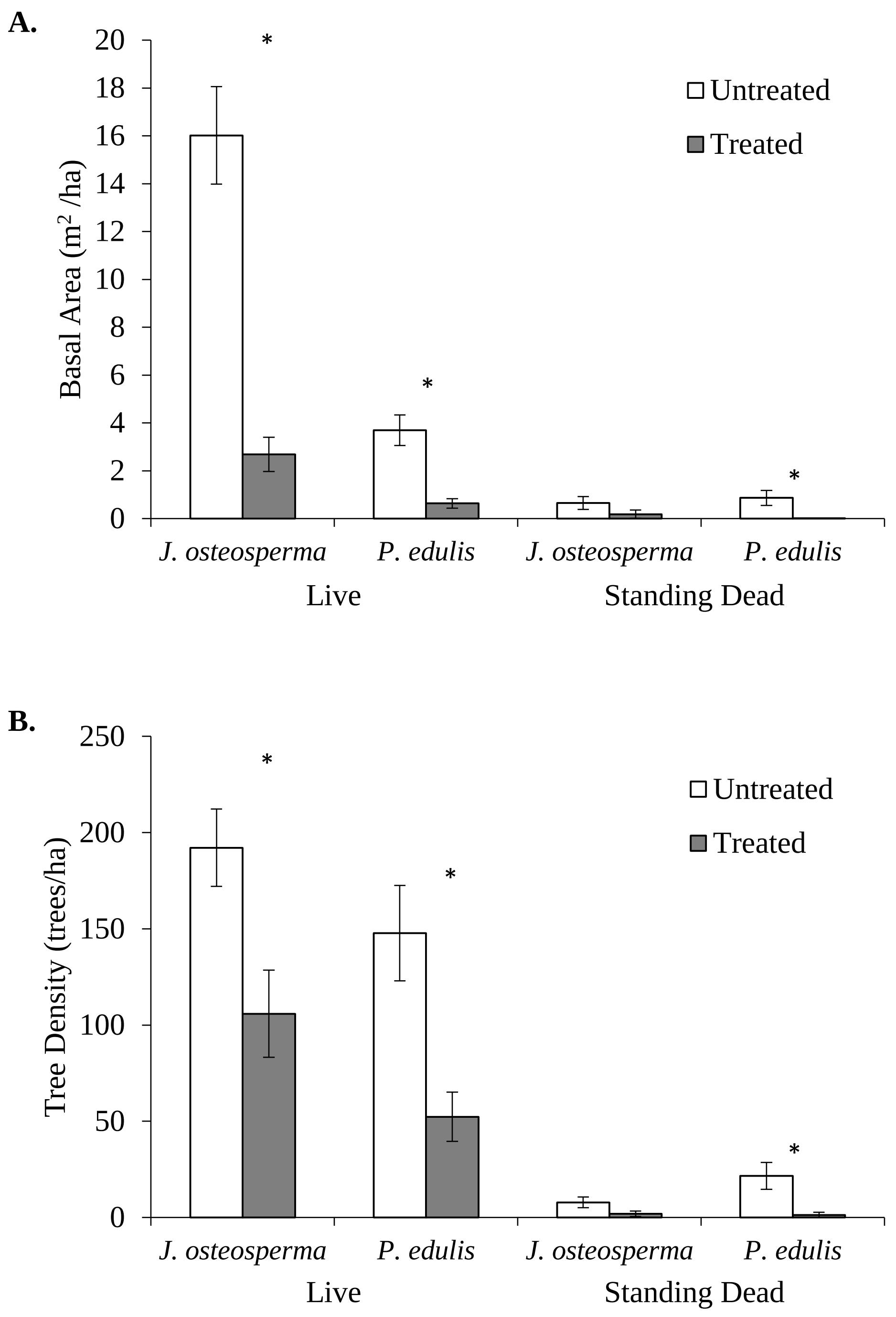


Figure 5-15. Differences between treated (chained and seeded) and untreated sites in J. osteosperma and P. edulis basal area (A.) and tree density (B.) among live (left side) and standing dead (right side) adult trees (BTD ≥ 5 cm). Data are means ± 1 SE and an asterisk denotes significant differences, with α = 0.05.

The low levels of adult tree basal area and density in the chained areas is likely due to the slow regeneration rate of *P. edulis* and *J. osteosperma.* Based on the linear regression of tree size and tree age from two of the paired-sites (Figure 5-12), 40 year old *P. edulis* trees were only 5 cm in basal trunk diameter (BTD) (Figure 5-12). Similarly, 40 year old *J. osteosperma* trees had a small canopy (0.64 m^2) and were only ~ 6 cm in BTD (Figure 5-12). Thus, the majority of adult trees in the treated area were trees that had established prior to treatment and were not killed during treatment. This is further highlighted by the low canopy cover (<0.5%) of trees that recruited after treatment as compared to trees that recruited prior to treatment (16%) in the treated areas (Figure 5-16a). These results illustrate the slow regeneration rate of these woodlands and how the number of trees surviving treatment strongly determines the rate of recovery. Thus, the long-term effectiveness of chaining may be largely due to the number of juvenile trees that survived the treatment (Skousen *et al.*, 1989; Figure 5-16a), which may explain the difference in rates of recovery between this study and others (Skousen et al., 1989; Tausch and Tueller, 1977). Given the low cover of newly recruited trees over the past 40 years in this study area (Figure 5-16a), these results suggest that if all trees were killed during treatment there may be little tree cover (<1%) 40 years after treatment.

While there was a trend of lower tree density and basal area among sites that had been chained more recently (i.e. 1980s) (Table 5-11), there was no strong relationship between year of treatment and difference in tree density or basal area among paired treated and untreated sites (linear regression, both $R^2 < 0.08$ and $P > 0.4$; Table 5-11). The lack of a relationship is likely due to the slow regeneration rate of *P. edulis* and *J. osteosperma* and may also be a function of the relatively low sample size given the paired sampling design and the high heterogeneity of P-J woodlands.

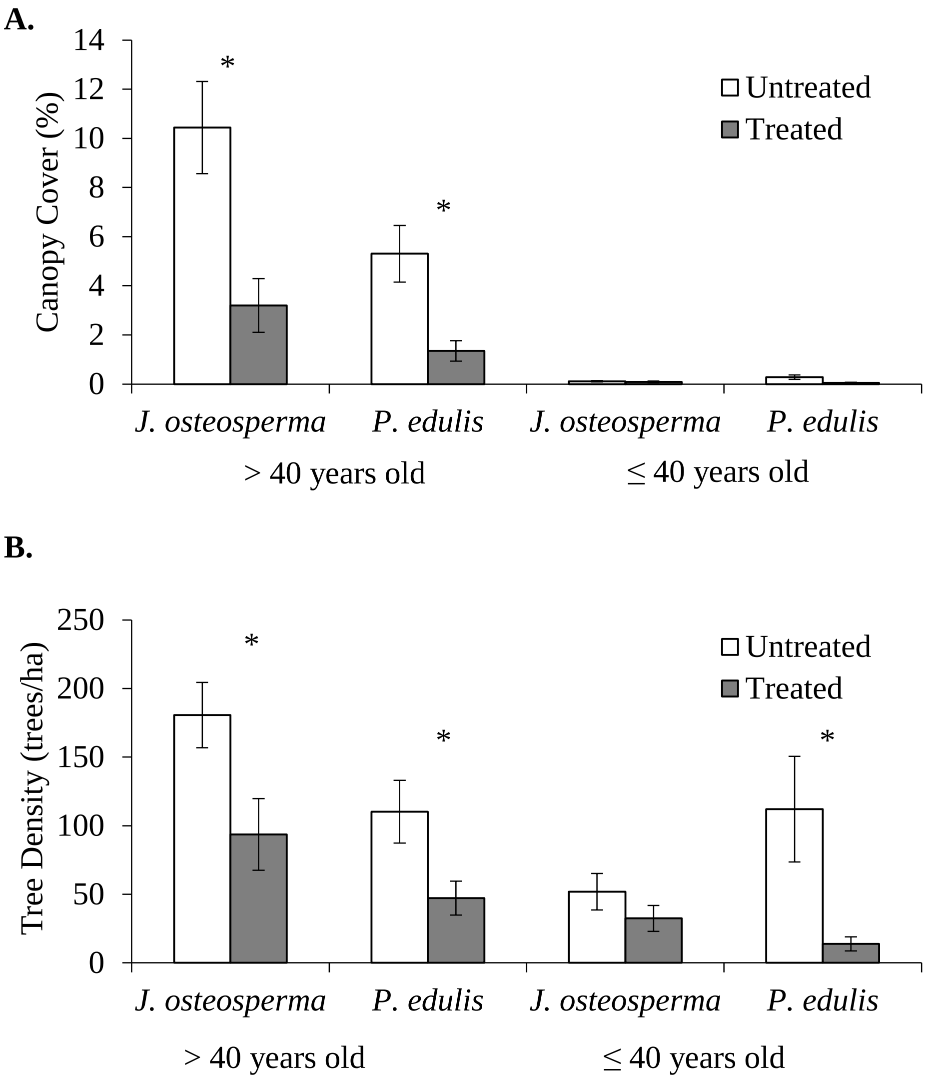


Figure 5-16. Differences between treated (chained and seeded) and untreated sites in J. osteosperma and P. edulis canopy cover (a.) and tree density (b.) among trees > 40 years old (i.e. trees that likely established prior to treatment) and trees ≤ 40 years old (i.e. trees that likely established prior to treatment) and trees ≤ 40 years old (i.e. trees that likely established post-treatment. Data are means ± 1 SE and only include the 12 sites that were treated between 1963 and 1971. An asterisk denotes significant differences between treated and untreated sites, with α = 0.05.

Unlike *J. osteosperma*, *P. edulis* regeneration may be negatively affected by chaining treatments, and consequently, treated woodlands may become increasingly *J. osteosperma* dominated. There was over 50% less recruitment of *P. edulis* during the last 40 years in treated sites compared to untreated sites among the sites treated between 1963 and 1971 (paired

Wilcoxon test, $P = 0.01$; Figure 5-16b), while there was no difference in *J. osteosperma* recruitment among treated and untreated sites (paired Student's t test, $P = 0.3$; Figure 5-16b). Additionally, while *P. edulis* dominance among trees that were greater than 40 years old (i.e., trees that established prior to treatment) was similar in treated (mean ± SE: 36% ± 7%) and untreated (mean ± SE: 35% ± 7%) sites (paired Student's t test, $P > 0.8$; Figure 5-16b), *P. edulis* dominance was significantly lower in treated sites (mean ± SE: 20% ± 7%) as compared to untreated sites (mean ± SE: 63% ± 9%) among trees that were less than 40 years old (i.e., trees that likely established after treatment) (paired Wilcoxon test, $P = 0.02$; Figure 5-16b). Further, across all sites, there were over 10 times fewer *P. edulis* seedlings and saplings (BTD < 5 cm) in the treated sites as compared to the untreated sites (Figure 5-17), whereas there was little difference in *J. osteosperma* seedling and sapling abundance (Figure 5-17). These results support the idea that *J. osteosperma* is an earlier successional species that has higher establishment following disturbances compared to species of piñon (*P. monophylla* and *P. edulis*) (Barney and Frischknecht, 1974; Chambers et al., 1999). The differential recruitment response of *P. edulis* and *J. osteosperma* to chaining and other disturbances may be due to their differential abilities to establish and survive outside of the canopy of trees and shrubs (Redmond et al., 2015). *J. osteosperma* is more drought tolerant than *P. edulis* (Linton et al., 1998; McDowell et al., 2008; Mueller et al., 2005), and while 90% of *P. edulis* juveniles are found underneath the canopy of trees and shrubs, significantly fewer (70%) *J. osteosperma* juveniles are found underneath the canopy of trees and shrubs (Chapter 3; Redmond and Barger, 2013). Therefore, the decline in tree and shrub cover associated with the chaining method may have negatively affected *P. edulis* establishment more than *J. osteosperma* establishment due to reduced tree and shrub canopy cover.

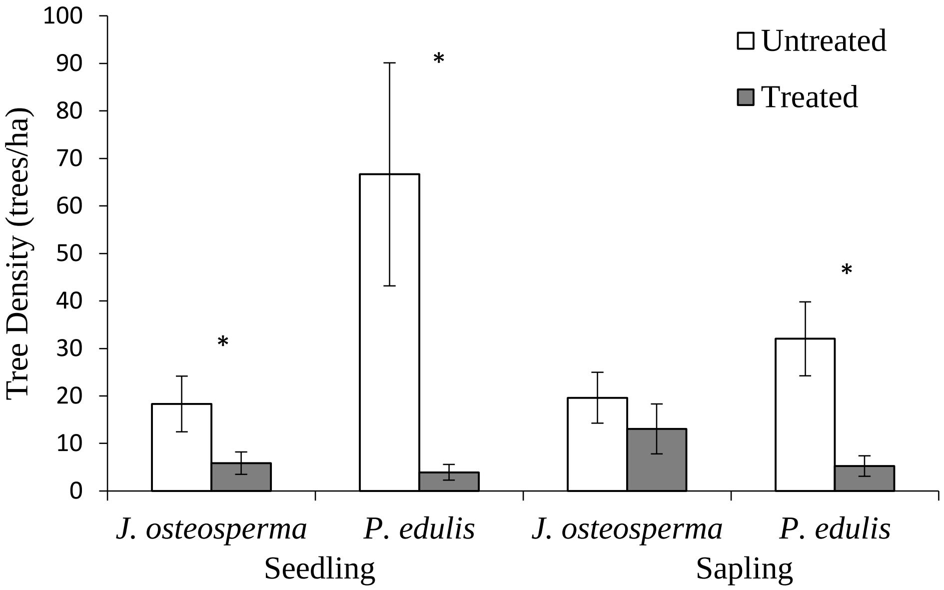


Figure 5-17. Differences between treated (chained and seeded) and untreated sites in J. osteosperma and P. edulis seedling (BTD < 2.5 cm) and sapling (BTD <5 cm and ≥ 2.5 cm) densities. Data are means ± 1 SE and an asterisk denotes significant differences between treated and untreated sites, with $\alpha = 0.05$.

These results suggest that the chaining and seeding treatment method may result in an increase in *J. osteosperma* dominance, which could negatively impact wildlife and communities that rely on *P. edulis* for forage, fuel wood, and habitat (Brown et al., 2001). Additionally, there has been high drought-related mortality of *P. edulis* in certain areas across its range since 2002 (Breshears et al., 2005; Clifford et al., 2011), especially among reproductively mature trees (Floyd et al., 2009). There have also been recent declines in *P. edulis* cone production associated with increasing temperatures (Redmond et al., 2012). Thus, both recent mortality and decreased reproduction could further reduce *P. edulis* as a co-dominant in P-J woodlands.

Changes in surface fuel loads

While there were no differences between the treated and untreated sites in smaller diameter (1 – 10 h) surface fuels or 1000 h rotten surface fuels (Table 5-12), there were nearly two times more 100 h fuels and over five times more 1000 h fuels in the treated sites (Table 5-12). These results are consistent with other studies that found an increase in surface fuel loads following mechanical treatments that did not involve fire (Stephens and Moghaddas, 2005; Stephens et al., 2009). The high amount of 100 h and 1000 h surface fuels present 40 years after treatment demonstrates one of the differences of not physically removing, burning, or grinding up (i.e. mastication) killed trees, as wood decays slowly in these semi-arid ecosystems (Jacobi et al., 2005). These larger diameter surface fuels may increase habitat complexity and benefit ground-dwelling arthropods (Clifford et al., 2008; Grove, 2002) and may also alter fire behavior by increasing the length of time fire heats the soil surface (Clifford et al, 2008). However, despite the increased surface fuel loads (Table 5-12), the probability of catastrophic wildfires may not be higher in treated areas given the significantly lower canopy cover (Table 5-11; Clifford et al., 2008). There was no relationship between year since treatment and surface fuel loads ($R^2 = 0.09$, $P = 0.15$; Table 5-11), which highlights the slow decay rate of wood in semi-arid ecosystems.

Table 5-12. Average (± 1 SE) fuel loads (metric t ha-1) in treated (chained and seeded) and untreated sites. Different letters denote significant differences between treated and untreated sites, with $\alpha = 0.05$.

Fuel Component	Untreated	Treated
1 h	0.01 (0.00)^a	0.01 (0.00)^a
10 h	0.30 (0.02)^a	0.39 (0.04)^a
100 h	1.6 (0.2)^a	3.0 (0.3)^b
1-100 h	1.9 (0.2)	3.3 (0.3)
1000 h sound	3.1 (1.5)^a	17.3 (5.9)^b
1000 h rotten	10.9 (2.8)^a	12.7 (3.2)^a

Conclusion

Tree-reduction treatments involving chaining and seeding have been applied to over 169,000 hectares of P-J woodlands across the Colorado Plateau over the past half-century (Redmond et al., 2014a) and are still used as a management technique. These treatments clearly have long-term (40 year) effects on ecosystem dynamics that need to be taken under consideration when developing future management strategies.

Management-Intended Long-term (40 year) Effects of Past Chaining Treatments

- Past chaining treatments effectively increased perennial grass cover, and thus, increased forage production. The increase in perennial grass cover was predominately due to the increase in *A. cristatum*, a nonnative bunchgrass that was seeded following treatment.
- Past chaining treatments effectively reduced tree cover. While trees were present in all treated sites, their populations had significantly lower densities in treated sites as compared to untreated sites. Additionally, I found slow tree regeneration in the treated sites (40 year old trees were less than 7 cm in basal trunk diameter), highlighting the slow growth of *P. edulis* and *J. osteosperma* in these semi-arid woodlands of the Colorado Plateau.
- While previous research found a decline in understory diversity immediately following chaining (O'Meara et al., 1981), my results suggest past chaining treatments did not affect species diversity in the long-term.
- No long-term treatment effects on the abundance of *B. tectorum*, a common invasive species, were detected. This may be partly due to the low invasibility of *B. tectorum* in the study area as well as competitive exclusion by *A. cristatum* and other perennial grasses (Chambers et al., 2007).

Unintended Long-term (40 year) Effects of Past Chaining Treatments

- Treated areas had higher bare mineral soil cover and reduced biocrust cover, which may be due to the direct effects of chaining and seeding or due to post-treatment grazing patterns.
- Past chaining treatments may result in more *J. osteosperma* dominated (as compared to *P. edulis* dominated) woodlands. Treated areas had over 10 times fewer *P. edulis* seedlings and saplings than untreated areas, whereas there was no difference in *J. osteosperma* seedling and sapling density. Further, within the 12 sites that were treated between 1963 and 1971, *P. edulis* dominance was 69% lower among trees that recruited in the last 40 years in the treated areas as compared to the untreated areas.
- Past chaining treatments increased nonnative species cover. This increase was predominately due to *A. cristatum,* a nonnative species that was seeded.

CHAPTER 6

LIMITS TO UNDERSTORY PLANT RESTORATION FOLLOWING FUEL-REDUCTION TREATMENTS IN A PIÑON-JUNIPER WOODLAND

Adapted from: Redmond MD, Zelikova TJ and NN Barger. 2014. Limits to understory plant restoration following fuel-reduction treatments in a piñon-juniper woodland. Environmental Management 54: 1139-1152.

Abstract

National fuel-reduction programs aim to reduce the risk of wildland fires to human communities and to restore forest and rangeland ecosystems to resemble their historical structure, function, and diversity. There are a number of factors, such as seed bank dynamics, post-treatment climate, and herbivory, that determine whether this latter goal may be achieved. Here, I examine the short-term (2 y) vegetation response to fuel-reduction treatments (mechanical mastication, broadcast burn, and pile burn) and seeding of native grasses on understory vegetation in an upland piñon-juniper woodland in southeast Utah. I also examine how wildlife herbivory affects the success of fuel-reduction treatments. Herbaceous cover increased in response to fuel-reduction treatments in all seeded treatments, with the broadcast burn and mastication having greater increases (234 and 160%, respectively) in herbaceous cover than the pile burn (32%). In the absence of seeding, herbaceous cover only increased in the broadcast burn (32%). Notably, fuel-reduction treatments, but not seeding, strongly affected herbaceous plant composition. All fuel-reduction treatments increased the relative density of invasive species, especially in the broadcast burn, which shifted the plant community composition from one dominated by perennial graminoids to one dominated by annual forbs. Herbivory by wildlife reduced understory plant cover by over 40% and altered plant community composition. If the primary management goal is to enhance understory cover while promoting

native species abundance, this study suggests that mastication may be the most effective treatment strategy in these upland piñon-juniper woodlands. Seed applications and wildlife exclosures further enhanced herbaceous cover following fuel-reduction treatments.

Introduction

A combination of fire suppression policies, timber harvest practices, historical livestock grazing, and changing climate has altered forest and woodland structure and species composition over the past century (Weaver 1943; Covington and Moore 1994; McIver et al. 2009; Schwilk et al. 2009; Barger et al. 2009; Redmond et al. 2013). In certain areas, these changes have increased fuel loads, altered understory plant communities, and decreased critical habitat for some wildlife species (Clary and Jameson 1981; Bates et al. 2005; Noson et al. 2006; McIver et al. 2009). In response to these historic changes, fuel management activities under the National Fire Plan over the past 15 years have focused on reducing the risk of catastrophic wildfire while restoring these ecosystems to reflect their historical structure, function, diversity, and dynamics (NFP, 2000).

Piñon-juniper (P-J) woodlands of the western US are a spatially extensive vegetation type that has been targeted for fuel reduction and restoration over the past decade. In some sites, evidence of P-J expansion into adjacent vegetation types and increases in density or ‘thickening’ are associated with declines in understory cover, resulting in diminished habitat quality for certain wildlife species, decreased forage production for livestock, and, potentially, increased soil erosion (Clary and Jameson 1981; Wilcox 1994; Bates et al. 2005; Noson et al. 2006; Pierson et al. 2007). The common practice of fuel-reduction treatments, which is often combined with seed applications, is generally successful in increasing understory cover and productivity (Gifford and Shaw 1973; Brockway et al. 2002; Bates et al. 2005; Owen et al. 2009; Ross et al. 2012; Huffman et al. 2013; Redmond et al. 2013).

While it is clear that fuel-reduction treatments generally increase resource availability (i.e. light, water, and nutrients) for understory plant communities (Roundy et al. in press), the magnitude of these increases may greatly differ by treatment type. For example, treatments that involve prescribed fire may increase short-term nutrient availability (Owen et al. 2009), but may reduce overall soil fertility over longer time scales due to erosional nutrient losses (Neary et al. 1999). However, both the short and long-term effects of fire may vary based on burning conditions and soil and vegetation properties at a specific site (Certini, 2005). Mechanical mastication, an alternative to the use of prescribed fire, provides a mulch layer to protect soils from erosion and often increases soil moisture retention (Gifford and Shaw 1973; Brockway et al. 2002; Owen et al. 2009; Young et al. 2013a). The thick layer of residual mulch, however, may also inhibit seed germination and establishment (Battaglia et al. 2010; Young et al. 2013b).

Although fuel-reduction treatments can increase resource availability for understory plants, the reduction of competitors and increase in soil resources may create a pathway for invasive plant establishment (Evangelista et al. 2004; Owen et al. 2009; Ross et al. 2012; Bates et al. 2013; O’Connor et al. 2013). Prescribed fire and mastication treatments have been shown to increase invasive species cover in the first three years after treatment (Potts and Stephens 2009; Owen et al. 2009; Ross et al. 2012; Bates et al. 2013). In an effort to increase native plant cover and reduce the abundance of invasive species following fuel-reduction treatments, seed applications are a common restoration strategy. These seed applications may be particularly important for understory regeneration in areas with already low understory plant cover due to a depleted seed bank (Koniak and Everett 1982; Poulsen et al. 1999). By increasing herbaceous plant establishment, these seed applications may also suppress invasive species through competition (Floyd et al. 2006; Thompson et al. 2006; Sheley and Bates 2008), particularly following fire.

Herbivore pressure following fuel-reduction treatments may also alter the recovery time and composition of understory plant communities. Although livestock grazing is generally not permitted by federal land management agencies during the first two growing seasons following fuel-reduction treatments, native herbivores may play a significant role in structuring post-treatment plant community responses. Large herbivores such as mule deer and elk are widely recognized for their capacity to alter plant community composition and structure (Manier and Hobbs 2007), but small mammals can also play a significant role (Gutiérrez et al. 1997; Manrique et al. 2007). Jackrabbits preferentially feed on new rangeland seedlings (McAdoo et al. 1987) and jackrabbit herbivory also limits grass establishment in desert shrublands (Bestelmeyer et al. 2007). In the Mojave Desert, burning dramatically altered small mammal communities and resulted in a mammal community that preferentially browsed grasses (Horn et al. 2013), highlighting the potential for interacting effects between wildlife, vegetation, and fuel-reduction treatments.

My overarching goal in this study was to evaluate short-term (i.e. 2 year) vegetation responses to common fuel-reduction treatments in an upland piñon-juniper woodland. I focused this study on three common fuel-reduction treatments used by federal land management agencies: mechanical mastication and two prescribed burning techniques (pile burn and broadcast burn). My objectives were to: 1) identify the fuel-reduction treatment(s) that promotes the highest native plant cover and diversity; 2) determine the need for post-treatment seed applications to promote native plant establishment; and 3) evaluate the role of post-treatment herbivore pressure in structuring the plant community. Fuel-reduction treatments and native seed applications require significant investments of time and financial resources (Redmond et al., In Review). Thus a better understanding of the understory plant community response to common fuel-reduction treatments and native seed applications is critical for planning future projects.

Methods

Study Area

This study was conducted on Wray Mesa located on Bureau of Land Management (BLM) land within the Upper Colorado Plateau region of southeastern Utah, USA (38°17’30.75”N, 109°4’20.87”W). Wray Mesa is located at 2250 m in elevation, near the upper-elevation limit of P-J woodlands. The mean growing season (Mar-Oct) temperature is 13 °C and the mean annual precipitation is 398 mm (years 1970 - 2012; http://www.prism.oregonstate.edu). Precipitation follows a bimodal distribution, with snow in the winter and monsoonal rains in July and August. The soils at the study site are classified as a fine sandy loam, Bond-Rizno series (http://websoilsurvey.nrcs.usda.gov; Table 6-13), which is an upland shallow loam piñon-juniper ecological site (NRCS, 2004). Dominant overstory tree species are *Pinus edulis* Engelm. (piñon pine) and *Juniperus osteosperma* (Torr.) Little (Utah juniper); common shrub species are species of *Artemesia* (*A. tridentata* Nutt. spp. vaseyana [mountain big sagebrush] and *A. nova* A. Nelson [black sagebrush]) and *Amelanchier utahensis* Koehne (Utah serviceberry); and common herbaceous species are *Elymus elymoides* (Raf.) Swezey (squirreltail), *Poa fendleriana* (Steud.) Vasey (muttongrass), and *Pedicularis centranthera* A. Gray (dwarf lousewort).

Experimental Design

I designed a 4 X 2 factorial experiment to examine the effects of different fuel-reduction treatment methods (4 levels: mastication [M]; pile burn [P]; broadcast burn [B]; and control [C]) and seeding (2 levels: seeded [S] and unseeded [U]) on understory vegetation. I focus on the understory vegetation response to fuel-reduction treatments and seeding during the first two growing seasons following treatment, as that is the amount of time the vegetation is given to recover before livestock grazing is permitted. I divided the study area (160 hectares total) into eight units of similar slope (4.4º ±1º) aspect (182º ± 20º), size (~ 12 HA), and of the same ecological site (NRCS, 2004). I randomly assigned each treatment combination to one of the eight units. Each unit had similar soil properties (Table 6-13) and the pre-treatment vegetation data suggests tree cover was similar among each unit. While each unit was similar in soil and vegetation characteristics, each treatment was only applied in one unit due to the constraints in implementing fire treatments across multiple small blocks.

Table 6-13. Soil texture, bulk density (g cm-3), total carbon (mg/g soil), and total nitrogen (mg/g soil) in each fuel-reduction and seeded (seeded = S, unseeded = U) treatment in 2010 (prior to treatment). Total carbon (C) and total nitrogen (N) are given for three different soil depths (0-2 cm, 2-5 cm, and 5- 10 cm). Data are means and 1 SE is included in parentheses.

	Control		**Mastication**		**Broadcast**		**Pile-burn**	
	U	**S**	**U**	**S**	**U**	**S**	**U**	**S**
Texture								
% Sand	59 (3)	50 (3)	52 (3)	58 (4)	54 (4)	59 (2)	45 (3)	53 (3)
% Silt	31 (2)	37 (2)	34 (2)	35 (3)	35 (4)	32 (2)	41 (3)	34 (2)
% Clay	10 (1)	13 (2)	14 (2)	8 (1)	11 (1)	10 (1)	15 (3)	12 (1)
Bulk Density	1.2 (0.1)	1.1 (0.1)	1.2 (0.1)	1.2 (0.1)	1.1 (0.1)	1.1 (0.1)	1.2 (0.1)	1.1 (0.1)
Total C								
0 -2	1.6 (0.4)	2.5 (0.2)	2.7 (0.5)	3.0 (0.8)	2.2 (0.1)	2.3 (0.4)	2.8 (0.8)	2.1 (0.5)
2 - 5	1.2 (0.2)	1.8 (0.3)	2.0 (0.3)	1.9 (0.3)	2.0 (0.2)	2.0 (0.3)	1.9 (0.4)	1.6 (0.3)
5 - 10	1.2 (0.2)	1.7 (0.2)	2.1 (0.5)	1.7 (0.2)	2.1 (0.2)	2.0 (0.3)	2.0 (0.3)	1.5 (0.0)
Total N								
0 -2	0.1 (0.0)	0.2 (0.0)	0.2 (0.0)	0.2 (0.0)	0.3 (0.1)	0.2 (0.0)	0.2 (0.0)	0.1 (0.0)
2 - 5	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.2 (0.1)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
5 - 10	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)

In the fall and winter of 2010, the BLM implemented the three fuel-reduction treatment methods (M, P, and B) in the designated sections. The mastication treatment, which was implemented between Nov. 2010 and Jan. 2011, used a wood mulcher, or “bullhog” to remove trees and scatter the mulch across the landscape. In the broadcast burn treatment, trees were hand cut and the resulting slash was scattered across the landscape, left to dry for 3 months, and then burned in October 2010. In the pile burn treatment, trees were hand cut and the resulting slash was piled into multiple 2 m diameter x 2 m height paraboloids. Piles were left to dry for 3 months and burned in October 2010. The BLM applied seed by hand broadcasting 374 kg (approximately 665 seeds per m^2) of a native seed mix into the four seeded treatments between October and November of 2010. In the mastication treatment, seeding was applied prior to treatment (Oct. 2010) whereas in the broadcast burn and pile burn treatment seed applications were applied post-treatment (Nov. 2010). The native seed mix was comprised of *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (blue grama), 9%; *E. elymoides*, 42%; *Koeleria macrantha* (Ledeb.) Schult. (prairie junegrass), 6%; *Pascopyrum smithii* (Rydb.) A. Love (western wheatgrass), 30%; *Poa secunda* J. Presl (Sandberg bluegrass), 9%; and *Sprobolus cryptandrus* (Torr.) A. Gray (sand dropseed), 3%. With the exception of *S. cryptandrus*, all of these seeded species were present in the study area in 2010 (prior to treatment) or present in the unseeded control plots in 2011 or 2012, confirming that these seeded species are native to the specific study area.

In March 2011, a total of 32 wildlife utilization cages were installed to evaluate the effects of wildlife on understory vegetation, with four utilization cages installed in each fuel-reduction and seeding treatment. Livestock grazing was not permitted in the study area during the two years following treatments, which allowed us to isolate the impacts of wildlife on understory vegetation. Cages were 0.56 m in radius and 0.91 m in height and were made using 5.08 cm X 10.16 cm wire mesh. Chicken wire (2.54 cm hex mesh, 30 cm in height) was added to the base of each cage to exclude small mammals. Paired controls were established approximately 2 meters adjacent to each cage. Both cages (four per fuel-reduction and seeding treatment, 32 total) and paired controls were located in areas with light litter or mulch cover and were not directly beneath the canopy of a tree. Thus, both cages and paired controls were located in microsites that tend to have higher understory plant cover.

Data Collection

In the spring of 2010, prior to treatment, I established ten 35-m transects within each of the eight treatment units. These transects were randomly located within each unit with the criteria that each transect had to be at least 25 m apart from another transect. In June of 2010 (pre-treatment), 2011 (1 growing season post-treatment), and 2012 (2 growing seasons post-treatment), I measured plant cover using the line-point intercept method by recording foliar cover every 50 cm along each transect, for a total of 70 points/transect (Herrick et al. 2006). Specifically, a pin flag was dropped from approximately 1 m in height and all plant species contacting the pin flag were recorded. The top canopy hit (i.e. trees or shrubs > 1 m tall) was also recorded at each point. In addition to plant cover I also quantified herbaceous density, which is better at detecting rare plant species and new recruitment. To quantify herbaceous density, I placed a 0.25 m^2 quadrat every 2 m along the transect line for a total of 17 placements (4.25 m^2) along each transect. Within each quadrat I recorded the number of herbaceous individuals for each species. For any potentially rhizomatous species, such as *Carex rosii* Boott (Ross' sedge), I counted the number of stems rather than the number of individuals.

In August of 2012, I measured the percent cover of understory vegetation in each cage (inside) and in each paired control (outside). To do this, I placed a 0.5 m X 0.5 m grid divided into 100 cells within each cage and in the adjacent control. I then dropped a pin flag at each cell and recorded all understory plant functional groups (shrubs, annual forbs, perennial forbs, annual graminoids and perennial graminoids) whose canopy intersected the pin flag.

Statistical Analyses

To examine the effects of fuel-reduction treatments and seeding on vegetation I performed fixed effect two-way ANOVAs, with each transect as a replicate. If there were pre-treatment differences in vegetation, I used the percent change [(post-treatment − pre-treatment)/(pre-treatment + 1)*100] in vegetation as the response variable in the ANOVA. In two of the analyses (percent change in herbaceous density one growing season post-treatment and percent change in herbaceous density two growing seasons post-treatment), I omitted one outlier from the pile burn treatment that was seeded. While all other transects in the pile burn seeded treatment had a percent change in herbaceous density between -50% and 45% both one growing season and two growing seasons after treatment, this outlier had a percent change in herbaceous density of 8,000 and 56,000 one growing season and two growing seasons post-treatment, respectively. This is because no individuals were found in 2010 at this transect, while 80 and 566 individuals were found in 2011 and 2012, respectively. When the ANOVA revealed significant treatment effects, post-hoc pairwise comparisons were performed using t-tests. To control for the inflation of type 1 error derived from repeated testing, I used the False Discovery Rate (FDR) approach (Benjamini and Hochberg 1995; García 2004; Verhoeven et al. 2005). These analyses were done in R (R Development Core Team 2011), with alpha = 0.05.

I evaluated herbaceous diversity, which included all graminoids and forbs, two years post-treatment using two indices: species richness (N_0) and species heterogeneity (N_2). Species richness was calculated as the mean number of species per transect, based on the herbaceous density data. Species heterogeneity was calculated as the reciprocal of Simpson's Index (Hill 1973), based off herbaceous density. Species heterogeneity shares the same units as species richness and incorporates both species richness and species evenness (Peet 1974). I followed the same procedure as above (fixed effect two-way ANOVA) to analyze the effects of fuel-reduction treatments and seeding on herbaceous diversity.

To assess the interactive effects of fuel-reduction and seeding treatments on the understory plant community composition, I complimented the above univariate analyses with a non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on a Bray-Curtis similarity index, calculated from square-root transformed relative plant cover data. Fuel-reduction treatments, seeding, and their interaction were included in the PERMANOVA model as fixed effects. I used a distance-based redundancy analysis (dbRDA), based on Principal Coordinates Analysis (PCO) output, to examine shifts in plant community composition and visualize the location of plots in multivariate space. The multivariate PERMANOVA, dbRDA and PCO analyses were performed in PRIMER (PRIMER-E, version 6; Clarke and Gorley 2006).

To understand the effects of wildlife herbivory on understory vegetation I performed a fixed-effect three-way ANOVA, with understory plant cover as the response variable and fuel-reduction treatment, seeding, and cage as the predictor variables. Because there were no significant interactions in the fixed-effect three-way ANOVA for total understory plant cover, I then performed paired (inside cage vs. outside) Student's t-tests to examine if there were differences in cover of annual forbs, perennial forbs, perennial graminoids, and shrubs inside the cages and outside the cages. In cases where the response variable was not normally distributed, even after multiple transformations, I performed a paired Wilcoxon Signed Rank test. I did not examine the effect of wildlife herbivory on annual graminoids, because no annual graminoids were present in the cage treatments or in the adjacent controls. These analyses were done in R (R Development Core Team 2011), with alpha = 0.05.

Results

Climate Variability

Climate during the three years (2010, 2011, and 2012) of the study was highly variable (Table 6-14). In particular, 2010 (pre-treatment) was an abnormally wet winter and spring, receiving 85 mm more total precipitation from Dec. 2009 - May 2010 than the 1970-2012 average (172 mm; Table 6-14). The following year (1 growing season post-treatment), winter and spring precipitation was equal to the 1970-2012 average, while winter and spring precipitation in 2012 (2 growing seasons post-treatment) was abnormally low, receiving 71 mm less than the 1970-2012 average (Table 6-14).

Table 6-14. Winter (Dec. - Feb.), spring (Mar. - May), summer (Jun. - Aug.), and fall (Sept. - Nov.) total precipitation (mm) and mean temperature (°C) between Dec. 2009 and Nov. 2012 compared to the long-term (1970-2012) average at Wray Mesa, UT (data from http://prism.oregonstate.edu).

	Precipitation				**Temperature**			
	2010	**2011**	**2012**	**Avg**	**2010**	**2011**	**2012**	**Avg**
Winter	160	83	85	86	-4.4	-2.3	-1.5	-2.0
Spring	96	88	15	86	6.3	6.4	9.4	7.4
Summer	110	108	66	104	19.9	20.2	21.2	19.6
Fall	99	94	41	123	9.4	9.2	10.7	8.8

This reduction in precipitation was associated with declines in understory plant cover: understory plant cover in the control plots declined by 61% during the three years of the study (12 ± 2% [mean ± 1 SE], 9 ± 2%, 5 ± 1% for 2010, 2011 and 2012, respectively; Figure 6-18).

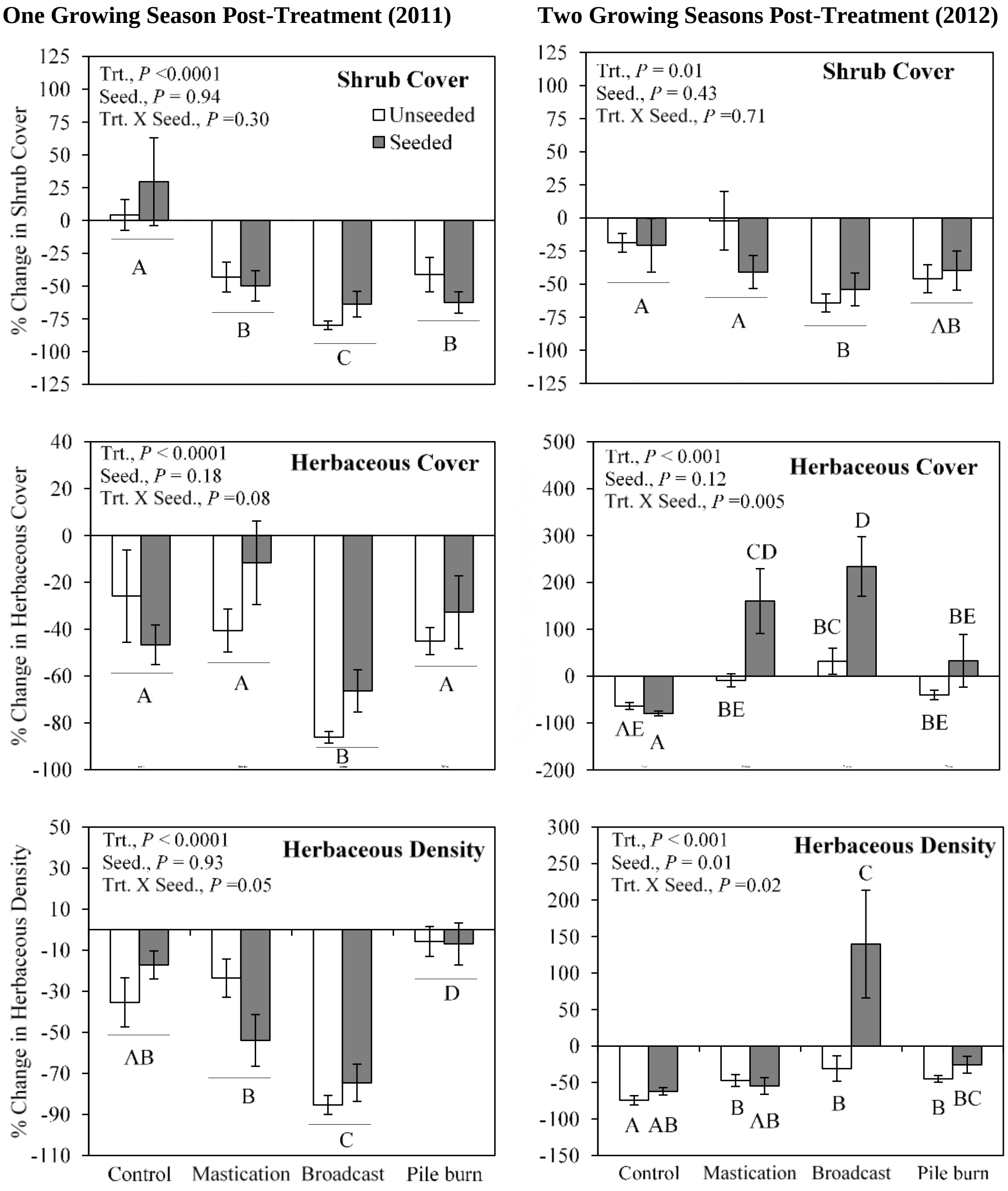


Figure 6-18. Percent change in shrub cover (top), herbaceous cover (middle), and herbaceous density (bottom) one (left) and two (right) growing seasons following each fuel-reduction treatment. Data are means ± 1 SE, and different letters denote significant differences (α= 0.05) between treatments.

Understory plant response to fuel-reduction treatments

All fuel-reduction treatments reduced tree cover (from 52% to < 8% cover; $P < 0.0001$), but the magnitude of reduction varied by treatment type. Tree cover was significantly lower in the broadcast burn and mastication (≤2%) than the pile burn (7%; $P < 0.04$), likely due to the greater number of ‘tree islands’, or small patches of untreated land, in the pile burn treatment.

Fuel-reduction treatments decreased total understory plant cover in the first growing season following treatment. Shrub cover declined in all fuel-reduction treatments as compared to the control ($P < 0.001$, Figure 6-18). Herbaceous density and cover responses to fuel-reduction treatments in the first growing season varied by treatment type. The broadcast burn reduced herbaceous cover ($P < 0.0001$; Figure 6-18), while the pile burn and mastication had no effect (Figure 6-18). Herbaceous plant density was also reduced by the broadcast burn ($P < 0.0001$; Figure 6-18). The pile burn resulted in marginally higher herbaceous plant density as compared to the control ($P = 0.05$; Figure 6-18).

There was a trend of reduced shrub cover two growing seasons post-treatment in all fuel-reduction treatments (Figure 6-18), but only the broadcast burn had significantly greater declines compared to the control ($P < 0.05$; Figure 6-18). As a result of the drought in 2012, herbaceous cover in the control plots declined by over 80% from 2010. Although 2012 was a drought year, fuel-reduction treatments successfully increased herbaceous cover relative to the control in all seeded fuel-reduction treatments ($P < 0.05$; Figure 6-18). In the absence of seeding, only the broadcast burn had significantly greater increases in herbaceous cover relative to the control ($P = 0.005$; Figure 6-18).

The understory plant communities were significantly differentiated among fuel-reduction treatments two growing seasons following treatment ($P = 0.001$; Figure 6-19). The top ranking species contributing to the dissimilarity between fuel-reduction treatments and the control plots were two common shrubs, *Artemisia* (*A. tridentata and A. nova)* and *A. utahensis,* and a common perennial graminoid, *P. fendleriana,* which were all negatively affected by the fuel-reduction treatments (Figure 6-19). This shift in community composition following fuel-reduction treatments altered the relative cover of perennial graminoids and annual forbs ($P < 0.0001$; Figure 6-20), but did not affect annual graminoid or perennial forb cover ($P > 0.3$). All fuel-reduction treatments increased annual forb relative cover ($P < 0.04$; Figure 6-20), particularly in the broadcast burn (Figure 6-21). This increase was primarily due to the increase in *Chenopodium fremontii* S. Watson (Fremont’s goosefoot), a native species, and *Sisymbrium altissimum* (tall tumblemustard), an invasive species. In addition, the broadcast burn reduced perennial graminoid relative cover compared to the control ($P = 0.001$; Figure 6-20).

The relative density and cover of invasive species was also strongly affected by fuel-reduction treatments ($P < 0.001$; Figure 6-22). Relative cover of invasive species was significantly greater in the broadcast burn (28%) and mastication (11%) compared to the control (0%) (Figure 6-22a). All fuel-reduction treatments had a greater relative density of invasive species when compared to the control (Figure 6-22b), with the highest density in the broadcast burn and mastication treatments (Figure 6-22b). This shift to a more invasive community following fuel-reduction treatments was primarily due to the increase in three invasive annual forb species, *Lactuca serriola* L. (prickly lettuce), *Salsola tragus* L (prickly Russian thistle), and *S. altissimum* (Figure 6-18; Figure 6-22).

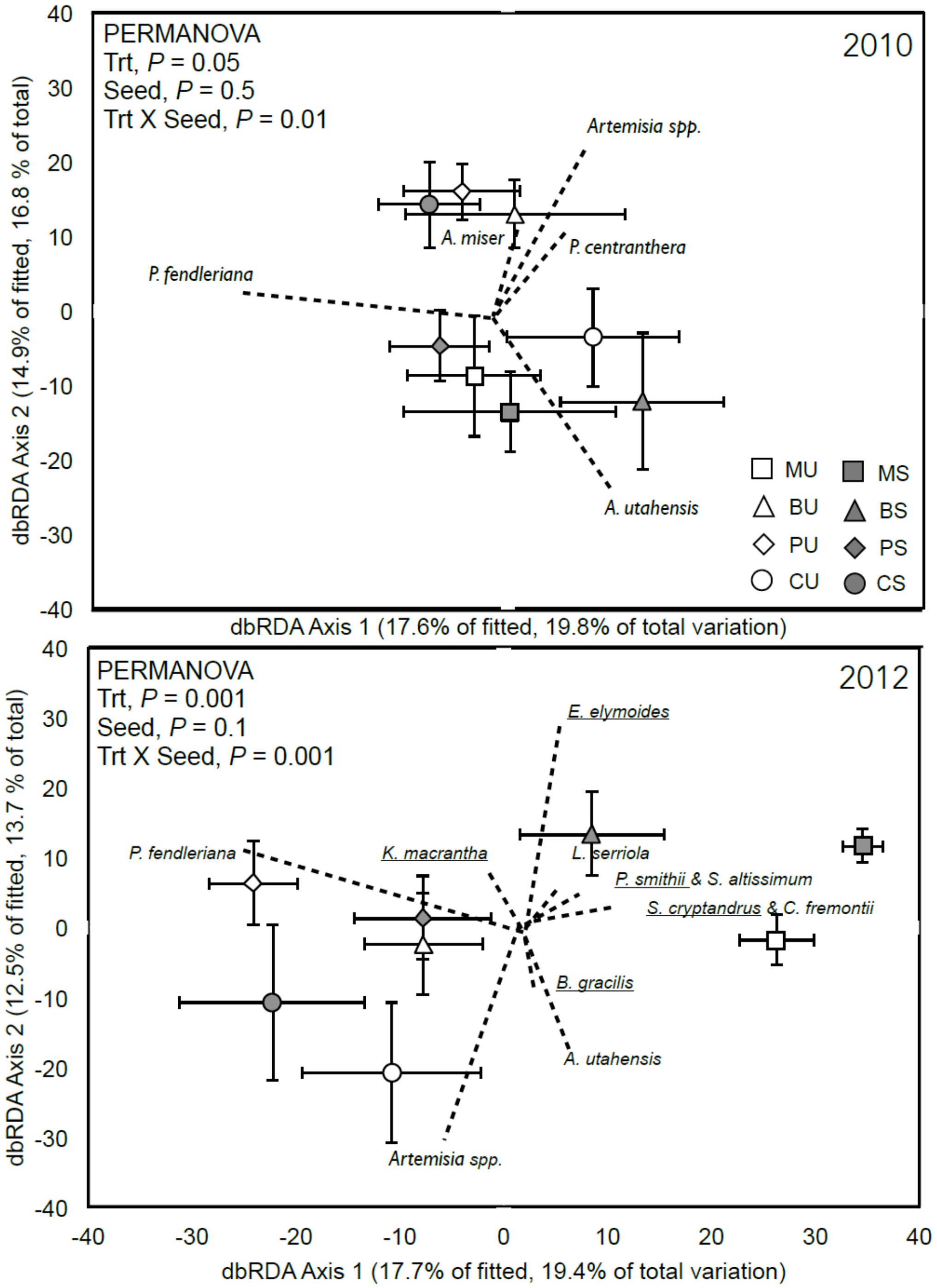


Figure 6-19. Distance-based redundancy analysis (dbRDA) plot in 2010 and 2012, illustrating the contribution of the species driving the differentiation among fuel-reduction (control [C], mastication [M], broadcast burn [B], and pile burn [P]) and seeding (unseeded [U] and seeded [S]) treatments. The axis scores were averaged by treatment and the averages are plotted with brackets indicating ± 1 SE. The length of the species vector indicates the strength of the change in relative cover of that species and vector direction along each axis indicates the direction of change in relative cover. Species that were seeded are underlined.

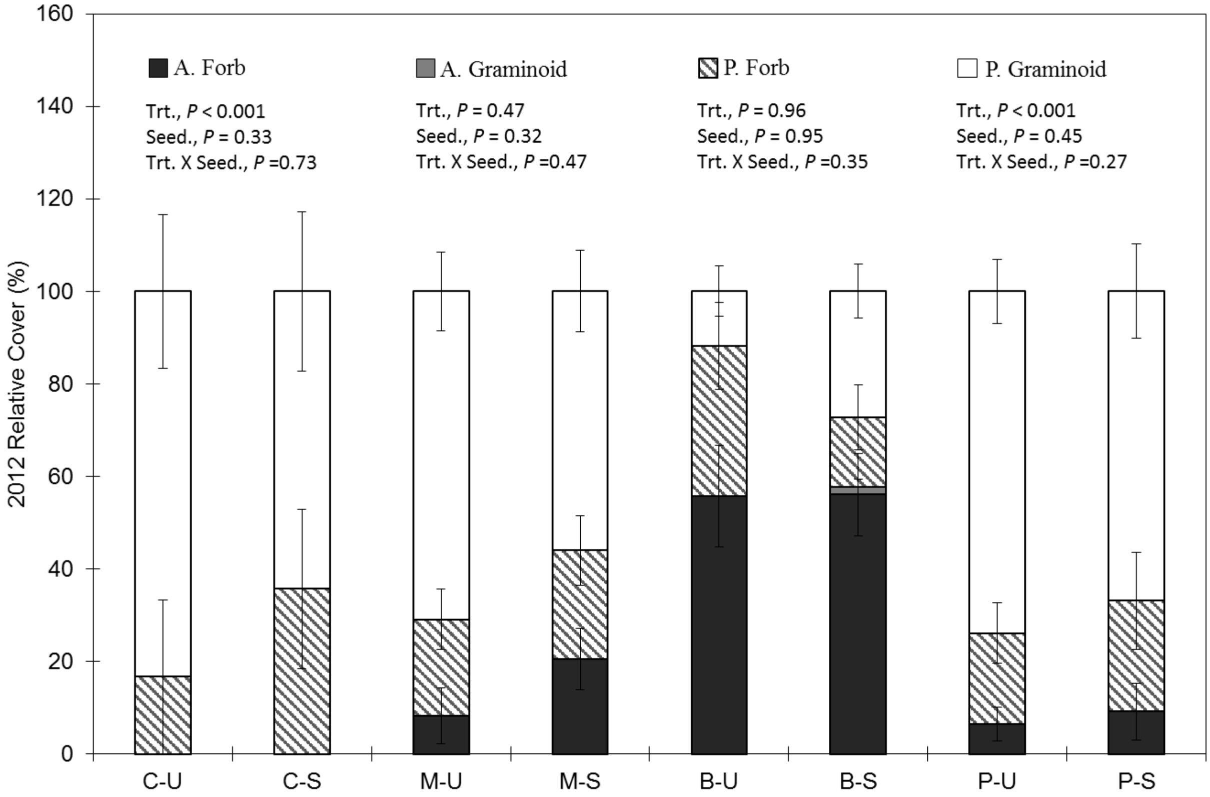


Figure 6-20. Relative cover in 2012 (two growing seasons following treatment) of annual (A) and perennial (P) forbs and graminoids across all fuel reduction (control [C], mastication [M], broadcast burn [B], and pile burn [P]) and seeding (unseeded [U] and seeded [S]) treatments. Results of the two-way ANOVA are given for each functional group. Data are means ± 1 SE.

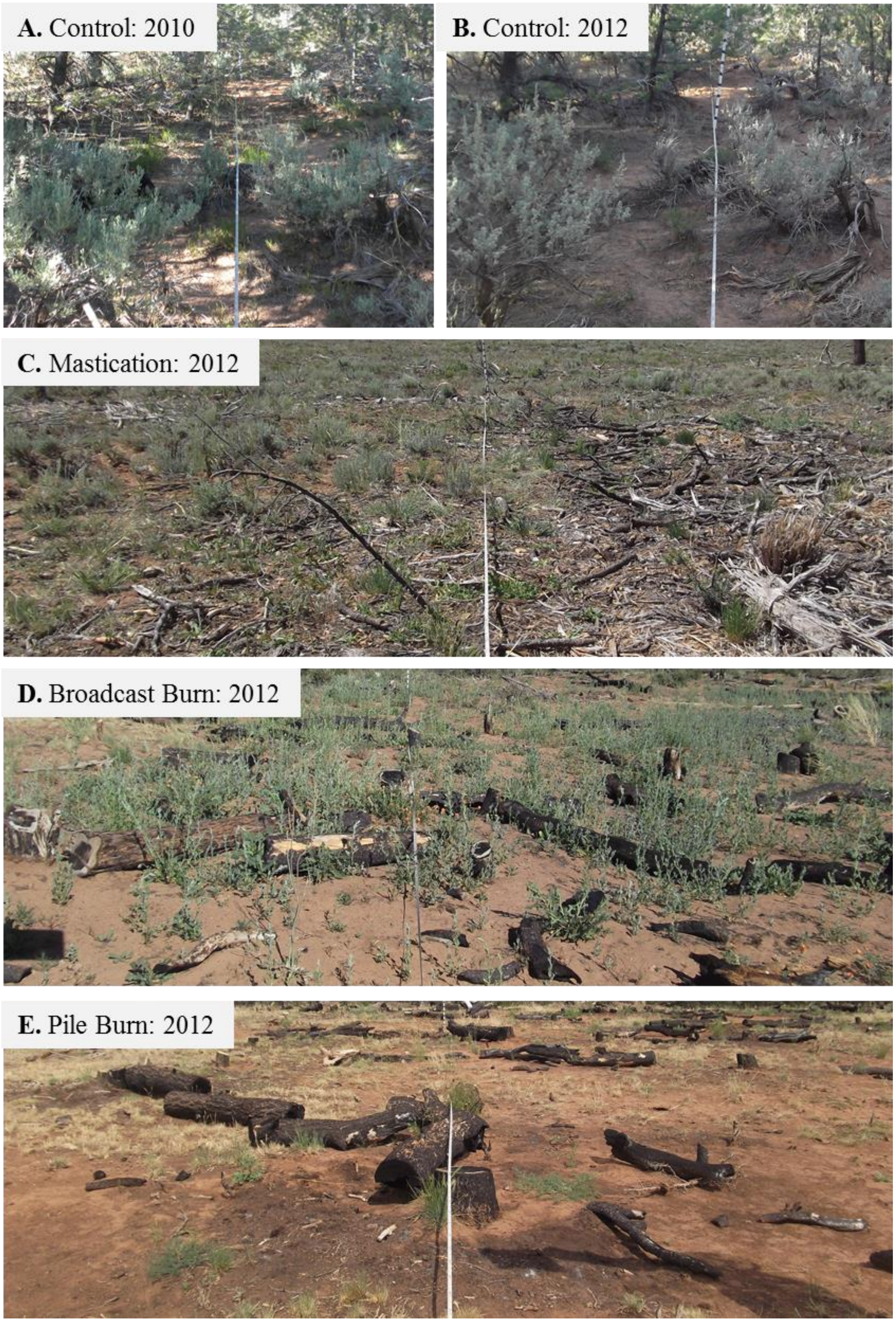


Figure 6-21. Photos illustrating the effect of fuel-reduction treatments and climate on understory vegetation. Top figures show the change in vegetation from 2010 (A.) to 2012 (B.) in the control, unseeded site. Middle and bottom figures show the effects of fuel-reduction treatments two-growing seasons post-treatment (2012) in the mastication (C.), broadcast burn (D.), and pile burn (E.) unseeded treatments.

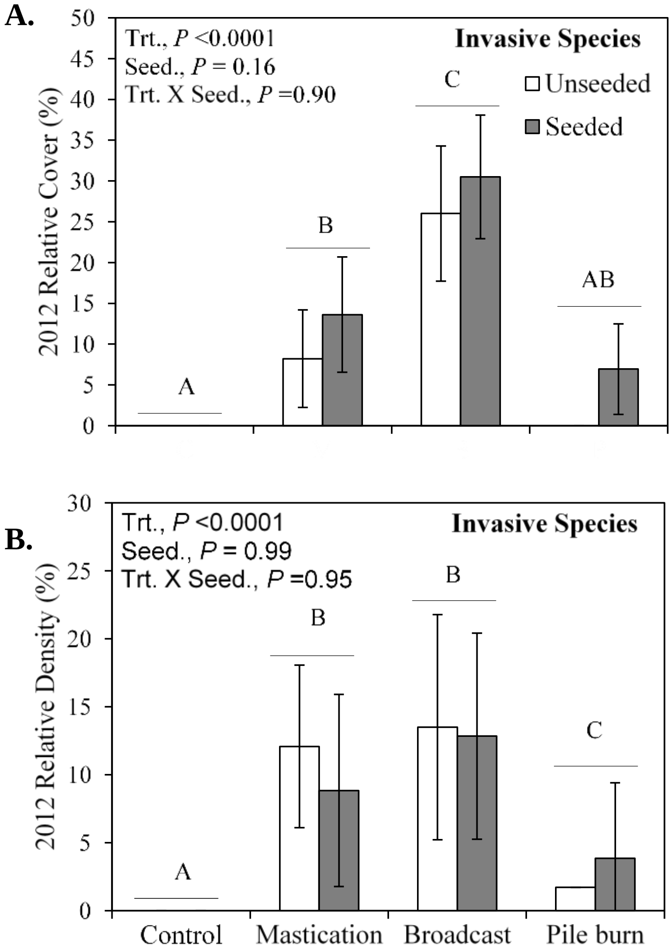


Figure 6-22. Relative cover (top) and stem density (bottom) among invasive herbaceous species two growing seasons following treatment. The three most common invasive species, which comprised over 90% of invasive cover and density, are Lactuca serriola, Salsola tragus and Sisymbrium altissimum. Data are means ± 1 SE, and different letters denote significant differences (α= 0.05) between treatments.

Plant species diversity was positively affected by the three fuel-reduction treatments two growing seasons post-treatment (*P* < 0.0001; Figure 6-23). All fuel-reduction treatments had significantly higher species richness and species heterogeneity when compared to the control (*P* < 0.001; Figure 6-23). In addition, mastication had higher species heterogeneity than the broadcast burn and pile burn treatments (*P* < 0.04; Figure 6-23).

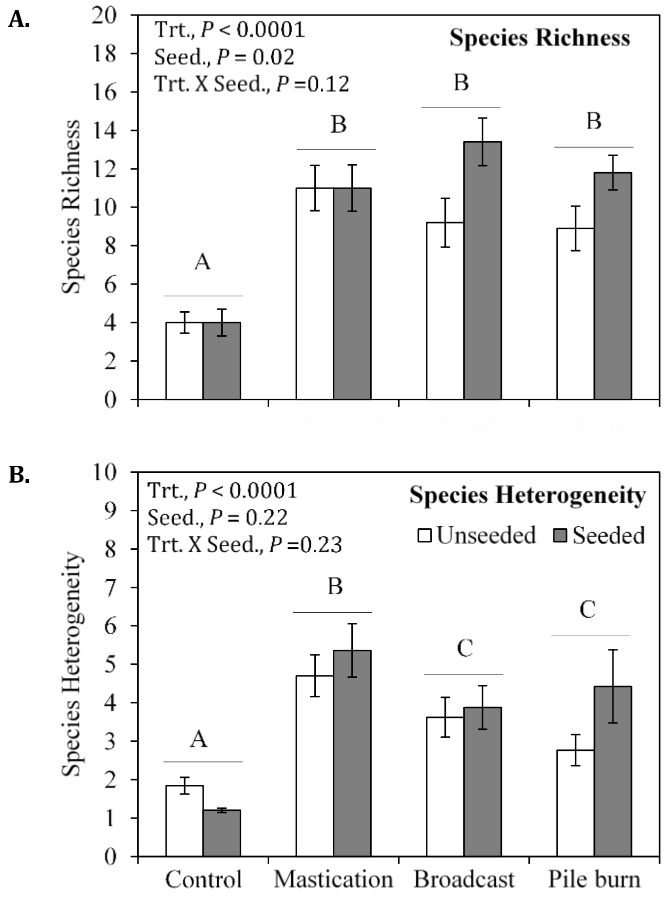


Figure 6-23. Species richness (A.) and species heterogeneity (B.) of the herbaceous plant communities two growing seasons following treatment. Data are means ± 1 SE, and different letters denote significant differences (α= 0.05) between treatments.

Understory plant response to seed applications

I observed no main effect of seeding on understory plant cover and density one growing season post-treatment (*P* > 0.17; Figure 6-18). However, there was weak evidence that seed applications in the mastication and broadcast burn treatments offset the reduction in herbaceous cover in the first growing season (Treatment x Seeding, *P* = 0.08; Figure 6-18). Seeding did have significant positive effects on herbaceous cover and density two growing seasons after treatments (Figure 6-18), but only in the broadcast burn and mastication (*P* < 0.04; Figure 6-18). Seeded plots also had greater herbaceous density within the broadcast burn treatment (*P* = 0.004; Figure

6-18). The higher herbaceous cover and density in the broadcast burn seeded treatment suggests seeding enhanced plant recruitment in this treatment in particular.

Seedling altered the understory plant communities two growing seasons after treatment (Treatment X Seeding, $P = 0.001$; Figure 6-19). Seeding increased the relative density of seeded species (*B. gracilis*, *E. elymoides, K. macrantha, P. smithii*, *P. secunda,* and *S. cryptandrus*) in the seeded plots compared to the unseeded plots in the broadcast burn and mastication treatments ($P < 0.05$; Figure 6-24b), but not the pile burn ($P = 0.22$; Figure 6-24b). Seeded species also increased in relative cover in the seeded plots in the broadcast burn treatment ($P < 0.05$, Figure 6-24a). These increases in relative density and cover of seeded species were predominately driven by three seeded species: *E. elymoides*, *P. smithii,* and *S. cryptandrus.*

Seeding had no significant effect on the relative cover of annual and perennial forbs and graminoids ($P > 0.3$; Figure 6-20). There was also no significant seeding effect on invasive species density and cover relative to native species ($P > 0.17$; Figure 6-22). Seeding significantly increased species richness ($P = 0.02$; Figure 6-23), particularly among the broadcast burn and pile burn, but did not affect species heterogeneity ($P = 0.22$; Figure 6-23).

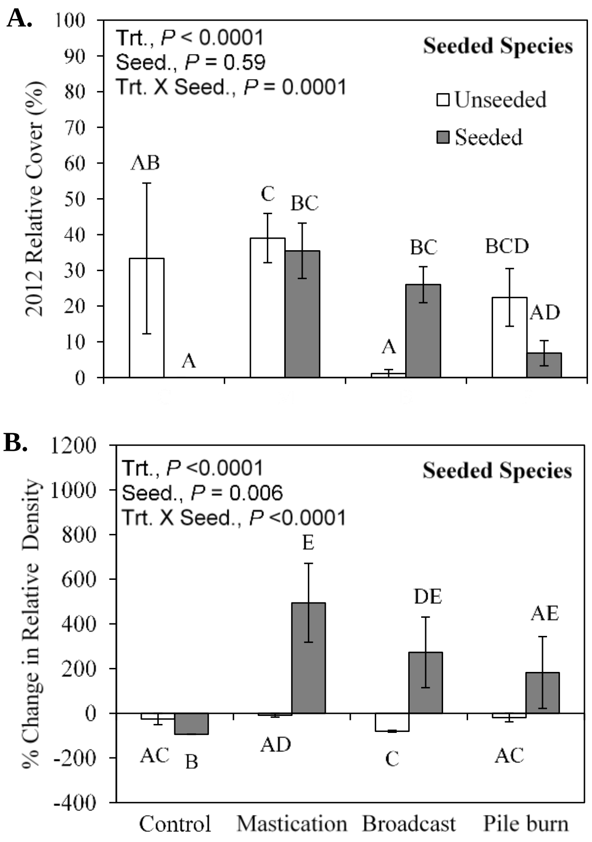


Figure 6-24. (A.) Relative cover among seeded herbaceous species two growing seasons following treatment in 2012. (B.) Percent change from 2010 to 2012 in relative stem density among seeded herbaceous species two growing seasons following treatment. Data are means ± 1 SE, and different letters denote significant differences ($\alpha = 0.05$) between treatments.

Understory plant response to herbivory

Understory vegetation cover was nearly twice as high inside wildlife-exclosure cages (47.4%) as compared to outside (28.3%) two growing seasons following treatment ($P = 0.002$). There was no interaction between wildlife exclosure, seeding, or fuel-reduction treatment on understory vegetation cover ($P > 0.10$). Shrubs and perennial graminoids had significantly higher cover inside the exclosures than outside (paired Student's t-test, both $P < 0.02$; Figure 6-25), but there were no differences in annual or perennial forb cover (Wilcoxon Signed Rank test, both $P > 0.1$; Figure 6-25).

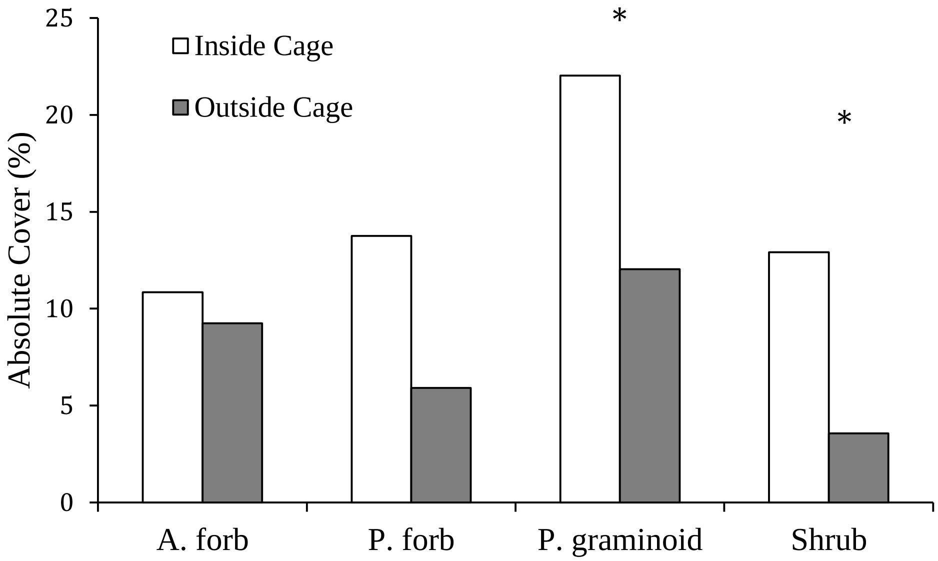


Figure 6-25. Absolute cover in 2012 of annual (A) forbs, perennial (P) forbs, P. graminoids, and shrubs inside cages and in the adjacent controls (outside cages). An asterisk indicates significant differences (α= 0.05) in plant cover between inside the cages and outside the cages.

Discussion

Response to fuel-reduction treatments

All fuel-reduction treatments generally increased the herbaceous understory two growing seasons following treatment, as hypothesized. However, their effects on herbaceous plant community composition differed. The broadcast burn resulted in the greatest increase in herbaceous plant cover and density (Figure 6-18). Yet this treatment shifted the plant community from a perennial grass dominated community to an annual forb dominated community and also increased the relative abundance of invasive species by nearly 30%. This shift to an annual dominated community may increase soil erosion potential (Craddock and Pearse 1938) and reduce resistance to weed invasion (Corbin and D'Antonio 2004; Floyd et al. 2006). However, this shift in community composition may be temporary and other longer-term fuel-reduction studies have found annual forb cover and density return to pre-treatment levels 8-10 years following green chaining treatments (Tausch and Tueller 1977; Skousen et al. 1989).

Mechanical mastication increased herbaceous cover similarly to the broadcast burn, but this increase in cover was not associated with as large of a shift in understory plant community composition. This difference may be due to the high mortality of herbaceous vegetation during the broadcast burn, which showed significant declines in herbaceous plant cover and density in the first year after treatment (Figure 6-18). In contrast, the herbaceous plant cover and density following mastication was similar to the control during the first year after treatment (Figure 6-18). In addition, the enhanced nutrient availability that often occurs following prescribed fire (Neary et al. 1999; Blank et al. 2007; Owen et al. 2009) may have also altered plant community composition in the broadcast burn treatment. Regardless of the mechanism, the shift to a more annual forb dominated community following broadcast burning compared to mastication should be taken into consideration when developing management plans.

Of all fuel-reduction treatments, I observed the smallest change in herbaceous plant community composition and total herbaceous cover in the pile burn. There was little surface disturbance between piles and therefore much of the herbaceous vegetation remained intact, which may explain the lack of a strong treatment effect on herbaceous plant composition associated with pile burning. Total tree cover was also reduced less with this treatment method, which may have suppressed herbaceous understory development and thus partially explain the lack of a large increase in herbaceous cover. In P-J woodlands in southwestern Colorado, Owen et al. (2009) also found a weak herbaceous cover response to pile burning when compared to mastication, further suggesting that the pile burn may not be as effective at increasing herbaceous cover compared to other fuel-reduction methods.

The magnitude of herbaceous cover increase was lower than the outlined restoration goals (NRCS, 2004) and also lower than reported in other fuel-reduction studies in P-J woodlands in Utah (Ross et al. 2012) and P-J savannas in New Mexico (Jacobs and Gatewood 1999). For this upland P-J woodland in southeastern Utah, perennial forb and graminoid cover should equal approximately 15% to meet target restoration goals (NRCS, 2004), yet perennial herbaceous cover reached up to only 8% two growing seasons after fuel-reduction treatments. Environmental conditions, such as drought during the time period following treatment, may strongly influence plant community responses to treatment (Huffman et al., 2013). Thus, the relatively low herbaceous cover I observed after fuel-reduction treatments was likely the result of the dry years that immediately followed the treatments. During the drought in 2012 (two growing seasons post-treatment), I observed a 60% reduction in herbaceous vegetation cover in the non-treated plots relative to the wetter year in 2010 (pre-treatment), confirming an overall trend of reduced herbaceous cover across the study area, regardless of fuel-reduction treatments. These results are consistent with other fuel-reduction studies that report similar trends when treatments are followed by dry years (Huffman et al. 2013), and highlight the importance of climate in determining restoration success.

Response to seeding treatments

My findings suggest that seed availability limits herbaceous recovery following fuel-reduction treatments in this upland P-J woodland. I found a trend of greater herbaceous cover and density in seeded treatments across all fuel-reduction treatments. Seeding had the strongest effect in the broadcast burn, where herbaceous cover and density were over 1.5 times higher in the seeded treatment compared to the unseeded control. The strength of the seeding effect in the broadcast burn may be because this treatment greatly reduced herbaceous vegetation immediately after treatment (Figure 6-18). The loss in vegetation and soil heating during prescribed burning can increase soil erosion (Neary et al. 1999) and result in seed loss from the seed bank. In addition to seed loss through erosion, there is also a potential for soil heating during prescribed fire to negatively impact the viability of seeds within the seed bank in certain areas (Hare 1961; Jiménez Esquilín et al. 2007). Further, herbaceous cover prior to treatment was relatively low, suggesting that this study site may have had a moderately depleted soil seed bank (Koniak and Everett 1982; Poulsen et al. 1999).

While seeds are often applied to reduce the abundance of invasive species following fuel-reduction treatments, I found no effect of seeding on invasive species cover or density. Other studies in P-J woodlands have found that following fire, seeding reduces the abundance of invasive species, particularly annual grasses but also annual forbs (Floyd et al. 2006; Thompson et al. 2006; Sheley and Bates 2008). The lack of a seeding effect on the abundance of invasive species in this study may be explained by the extreme drought year in 2012. While seeding did increase the abundance of seeded species relative to the control (Figure 6-18), these seeded species still had low abundance in 2012 due to the drought, and their low abundance likely reduced their competitive effect on invasive annual forbs. In addition, this drought likely affected the ability of invasive annual grasses, such as *Bromus tectorum* L. (cheatgrass) to establish following treatment (Mack and Pyke 1983; Miller et al. 2006).

Of the six seeded species, *E. elymoides, P. smithii,* and *S. cryptandrus* had the greatest increase in density. The two cool season perennial grasses, *E. elymoides* and *P. smithii,* are relatively drought tolerant (Ogle et al. 2010), comprised over 70% of the seed mix, and are commonly seeded following disturbances due to their ease of establishment and effectiveness in erosion control (Ogle et al. 2010). Another drought-tolerant species, *S. cryptandrus,* a warm season perennial grass, comprised only 3% of the seed mix, but successfully established following fuel-reduction treatments. These results suggest that seeding these drought tolerant perennial grasses may be especially important in promoting herbaceous recovery during times of drought.

Impacts of wildlife herbivory

Wildlife herbivory reduced understory plant cover by 40% and altered plant community composition following treatments. Wildlife preferentially browsed shrubs and perennial graminoids, which is consistent with browsing preferences of wildlife in this region (Sandoval et al. 2005; Bestelmeyer et al. 2007). Wild ungulates, such as elk and mule deer, commonly eat shrubs and, to a lesser extent, perennial graminoids (Sandoval et al. 2005). In addition, herbivory by jackrabbits has been reported to limit perennial graminoid establishment in desert shrublands (Bestelmeyer et al. 2007). By preferentially browsing perennial graminoids, wildlife herbivory reduced the ability of fuel-reduction treatments to reach the target perennial graminoid cover goal of 10% for this ecological site (NRCS, 2004).

The reduction in understory plant cover by wildlife may be especially high in this study because of the reduced understory plant cover across the study area due to the dry years following treatment. Because herbivory can strongly affect understory plant cover responses to fuel-reduction treatments, my results suggest it may be important to allow the understory vegetation to recover for longer time periods before permitting grazing by livestock. This may be particularly important if fuel-reduction treatments are followed by drought years.

Data Considerations

This study provides important insights into vegetation responses to fuel-reduction and restoration treatments in upland piñon-juniper woodlands of the Colorado Plateau and the information I provide can help guide future management decisions in this area. However, this study was conducted in one piñon-juniper woodland in southeast Utah under significant drought conditions. In addition, treatments were not replicated across the landscape due to difficulties in controlling fire in multiple blocks within the study area. Despite these limitations, many of my results are consistent with other fuel-reduction studies in other piñon-juniper woodlands on the Colorado Plateau (Owen et al., 2009; Huffman et al., 2013).

Management Implications

Increases in tree density, coupled with declines in understory cover over the past century, have led to decreased forage production for livestock, diminished habitat quality for some wildlife species, and increased soil erosion in certain P-J woodlands. These historic changes in the structure and extent of P-J woodlands have placed them at high priority for restoration and fire-mitigation. If the management goal is to enhance understory cover while promoting native species diversity, this study suggests that mechanical mastication may be the most effective treatment strategy in these upland piñon-juniper sites. Seed applications of drought-tolerant, native perennial grasses increased herbaceous cover by over 100% in the broadcast burn and mastication treatments, suggesting that for these two fuel-reduction treatments, seed applications are worth the time investment and cost. Lastly, excluding wildlife nearly doubled understory plant cover during drought. These results highlight how it is important to take into consideration climate and wildlife herbivory following fuel-reduction treatments, as these two factors can strongly influence the vegetation response to treatments.

CHAPTER 7

CONCLUSION

Changing climate and altered disturbance regimes has the potential to dramatically affect vegetation dynamics. Importantly, the effects of these disturbances may vary across the landscape due to differences in local climate, physiography, and biotic interactions. Results of my comparative study (chapter 2) revealed clear declines in piñon pine seed cone production from the 1974 decade (1969-1978) to the 2008 decade (2003-2012). Further, I show that declines in seed cone production were greatest in areas with greater increases in growing season temperatures, which suggests seed cone production may be an important bottleneck to piñon pine regeneration with climate change. In chapter 3, my results indicate that recent, widespread piñon pine mortality did not strongly affect successional trajectories in piñon-juniper woodlands of southwestern Colorado due to advanced regeneration. Accordingly, this landscape appears resilient to recent drought and beetle-induced mortality due to the high densities of juveniles that survived the drought. However, piñon recruitment was positively associated with soil available water capacity and tree and shrub cover, highlighting how physiography and biotic interactions may influence successional trajectories across the landscape.

My findings highlight how tree reduction treatments may strongly affect vegetation and soil erosional processes within pinon-juniper woodlands of the Colorado Plateau. Over 247,000 hectares of piñon-juniper woodlands were treated with tree-reduction treatments between 1950 and 2003 on the Colorado Plateau (chapter 4), representing 6.6% of woodlands managed by the BLM. These tree-reduction treatments may alter herbaceous communities over both the short and long term (chapter 5, chapter 6; Owen et al. 2009; Huffman et al. 2013; Redmond et al., 2013;

Redmond et al., 2014b), tree composition (chapter 6; Redmond et al. 2013), and soil erosional processes (Gifford 1973; Farmer et al. 1999; Pierson et al. 2007; Cline et al. 2010). Further, the array of treatment methods may differentially affect vegetation cover and soil erosion (chapter 6; Owen et al. 2009; Huffman et al. 2013; Redmond et al. 2014b).

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