

University of Nevada, Reno

Long-term vegetation response to treatments of prescribed fire and chaining in Great Basin pinyon-juniper woodlands

A thesis submitted in partial fulfillment of the requirements for the degree of
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By

Nathan A. Bristow

Peter J. Weisberg/Thesis Advisor

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NATHAN BRISTOW

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Peter Weisberg, Advisor

Robin Tausch, Committee Member

Robert Nowak, Committee Member

Wendy Calvin, Graduate School Representative

Marsha H. Read, Ph. D., Associate Dean, Graduate School

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Abstract

Treatments of prescribed fire and chaining have been widely applied across the Great Basin since the mid 20th century in an effort to reduce pinyon and juniper cover and stimulate understory growth. Treatment efforts often result in altered vegetation structure and composition relative to untreated areas. A few studies have examined short-term effects of chaining and prescribed fire treatments, but this study examined long-term changes in vegetation cover, tree survivorship, and tree establishment multiple decades after historical treatments. This study revisited sites of woodland treatments that were originally sampled over 30 years ago. An emphasis was placed on tree recovery because it is an easily interpretable measure of treatment success.

Changes in vegetation composition were evaluated by collecting vegetation cover, soil depth, and soil texture data at plots within four chaining sites treated in 1958, 1962, 1968, and 1969 and originally sampled in 1971. The same data were collected at five prescribed burn sites treated in 1975 and originally sampled in 1976. In 2008, tree cover at chaining treatment sites was much greater than at burned sites, where it was nearly absent. Absolute increases in tree cover at chaining sites were comparable to absolute increases in tree cover occurring in corresponding control areas. Relative to original tree cover in 1971, however, increases in tree cover at chaining treatments were greater than relative tree cover increases at controls.

At all sites, cover of herbaceous species decreased and cover of woody species increased. Relationships between site overstory and understory cover values were fit with a negative exponential curve, and the parameters were interpreted in the context of

understory response to treatment. Finer-textured, shallower soils were the most predictive environmental conditions for rapid tree recovery following chaining. Tree dominance has recovered at a much faster rate following chaining treatments than prescribed fire. Tree infilling in untreated areas is also occurring at a rapid rate, similar to tree recovery at chaining sites. Forty years after chaining, sites are again tree-dominated with limited understory vegetation. Burned sites, however, continue to be dominated by shrub and herbaceous species 33 years after treatment.

Analysis of post-treatment tree age structures helps to clarify species-specific processes of tree survivorship and establishment. Tree age data were collected at every chaining and prescribed fire plot by sampling increment cores and stem cross sections. Tree-ring data indicated that all chaining sites experienced greater juniper survival than pinyon survival. Chaining sites with higher overall tree survival following treatment also experienced the greatest amount of new tree establishment. During the interval between treatment and 2008 sampling, approximately four more trees $\text{ha}^{-1} \text{y}^{-1}$ established following chaining than following fire. Post-treatment establishment was dominated by juniper at prescribed fire sites. At chaining sites, post-treatment establishment was dominated by juniper for the first 15 years; however, by 15 to 40 years following chaining treatment, pinyon establishment greatly exceeded juniper establishment. The greatest density of newly established trees occurred in control (untreated) plots, indicating that both prescribed fire and chaining treatments decreased tree establishment. However, eventual relative dominance of pinyon is a probable long-term effect of

chaining treatment. Prescribed fires applied at relatively infrequent intervals may favor extended dominance of juniper over pinyon.

Although prescribed fires more closely met resource management goals of the mid 20th century, managers may find the practice too risky when considering current environmental conditions and management concerns. Prescribed burning was more successful than chaining for removing trees, maintaining understory communities, and causing reduced post-treatment tree establishment. However, cheatgrass (*Bromus tectorum*) was present at prescribed fire sites and not chaining sites. The great increases of tree cover in the untreated areas of this study indicate fuel loads are much larger than when the prescribed fires were conducted in 1975. The risk of an escaped fire becoming a conflagration has increased since then, as has the risk of cheatgrass invasion.

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Table of Contents

Abstract.....	i
Acknowledgements.....	iv
Table of Contents.....	v
List of Tables.....	vi
List of Figures.....	vii
Background.....	1
Thesis Overview.....	4
Study Area and Site Descriptions.....	4
Literature Cited.....	8
Chapter 1: Long-term Vegetation Recovery in Pinyon and Juniper Woodlands after Chaining and Prescribed Fire.....	10
Abstract.....	10
Introduction.....	11
Methods.....	16
Data Collection.....	16
Historical Data.....	16
Study Design.....	17
Field Data Collection.....	18
GIS-Derived Data.....	19
Data Analysis.....	20
Results.....	23
Effect of Treatment Type on Current Plant Community Composition.....	23
Site Observations.....	23
Treatment Effects on Plant Functional Types.....	26
Increasing Woody Species Cover over Time.....	27
Changes in Vegetation Type Cover.....	27
Species Compositional Shifts within Sites.....	31
Environmental Effects on Tree Recovery in Chaining Sites.....	35
Discussion.....	39
Effect of Treatment Type on 2008 Plant Community Composition.....	39
Increasing Woody Species Cover over Time.....	41
Changes in Tree Cover.....	41
Species Compositional Shifts within Sites.....	44
Chained Site Resource Utilization Curves.....	45
Environmental Effects on Chained Tree Recovery.....	46
Implications for Management.....	47
Literature Cited.....	50
Chapter 2: Tree Establishment Following Chaining and Prescribed Fire Treatments in Singleleaf Pinyon and Utah Juniper Woodlands.....	53
Abstract.....	53
Introduction.....	54

Methods.....	61
Data Collection.....	61
Data Analysis.....	62
Results.....	63
Discussion.....	71
Effects of Treatments on Rates and Mechanisms of New Tree Establishment.....	71
Differences in Establishment of Pinyon and Juniper Trees Following Treatment.....	74
Influences of Management on Woodland Tree Species Composition.....	79
Literature Cited.....	81
Appendix I.....	84

List of Tables

Chapter 1

Table 1. Number of marked plots discovered during resampling.....	17
Table 2. Fixed effects ANOVA results of prescribed fire (n = 13) and chaining (n = 26) treatments on 2008 mean aerial covers of vegetation types, with time since treatment included as a covariate.....	27
Table 3. Paired T-Test for mean differences in tree cover between 2008 and the time of initial sampling.....	28
Table 4. Species used in NMS ordination and correlations with axes.....	32
Table 5. Mean cover of dominant species by site and year.....	34
Table 6. Parameter estimates of the fit curves for each of the chaining sites.....	37
Table 7. The nine best LME models for describing percent increase in tree cover between 1971 and 2008. Depth = soil depth, TCI = topographic convergence index, coarse = soil % coarse fragment, years = time since disturbance, fine = soil % fine fragment	38
Table 8. Akaike weights and effect directions of the 5 most important variables.....	38

Chapter 2

Table 1. Expected effects of prescribed fire and chaining treatments on proposed important mechanisms of establishment. + indicates greater relative to the other treatment and - indicates less.....	55
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Table 2. Life history traits of pinyon and juniper expected to affect establishment after chaining and prescribed fire. + indicates greater relative to the other species, - indicates less than the other species, AM indicates arbuscular mycorrhizal fungi, and EM indicates ectomycorrhizal fungi.....58

Table 3. Mean number of trees establishing per hectare per year and fixed effects ANOVA results for prescribed fire (n = 5) and chaining (n = 4) treatments on post treatment pinyon and juniper establishment.....64

Appendix

Table i. Correlations between explanatory variables (coarse, fine, depth, TCI, Solar, elevation, and years) and with the response variable (tree).....84

Table ii. Mean absolute percent cover of all species at treatment sites.....84

Table iii. Coefficients (β), weighted coefficients ($w\beta$), and p values for the five most important variables of the LME models.....88

List of Figures

Chapter 1

Figure 1. Map of chaining and prescribed fire study sites in Eastern Nevada.....5

Figure 2. Timeline of chaining and prescribed fire treatments and sampling.....7

Figure 3. Hypothesized effects of chaining and prescribed burning on understory-overstory cover relationships. The solid line represents the resource utilization curve, the dashed line represents deviations caused by chaining, and the dotted line represents prescribed fire.....12

Figure 4. Plot layouts for Spruce Mountain and Blythe Springs (left) and North Kern East, South Kern, and the White Pine prescribed fire sites (right).....18

Figure 5. Photo pair of the center of the North Kern East Chaining. 1971 left, 2008 right. Photographs taken by Robin Tausch.....24

Figure 6. Photo pair of the southern end of South Kern. 1971 left, 2008 right. Photographs taken by Robin Tausch.....25

- Figure 7. Photo pair of the eastern side of Blythe Springs. 1971 left, 2008 right.....25
- Figure 8. Air photo of Blythe Springs and patches that were chained once and twice....26
- Figure 9. Change in absolute percent tree cover at chaining sites between initial sampling and 2008 for treatment and control plots. Error bars represent standard error and * denotes differences between control and treatment plots ($\alpha < .05$).....28
- Figure 10. Absolute percent cover of vegetation types at chaining and prescribed fire treatment sites. Control plot data are also displayed for tree cover (top left). Sites are arranged by treatment age from oldest (left) to most recent (right). Error bars represent standard error and letters denote differences in absolute cover within a site ($\alpha > .05$)....29
- Figure 11. Cover of vegetation growth forms at the Blythe Springs once-chained, twice-chained, and control macroplots.....31
- Figure 12. Graph of mean NMS ordination centroids for each site based on vegetation cover in 1971 and 2008. Bars represent the 95 % confidence limits in each of the directions along axes 1 and 2. Arrow vectors represent the amount of change at each site.....33
- Figure 13. Graphs of understory and overstory curves for the chaining sites. Lines were fit with the open circles (2008 treatment data) and the open triangles (2008 control plot data). Closed circles represent the 1971 treatment plot data, which were not used to fit the curves. The X symbol in the Blythe Springs graph is the 2008 once-chained plot.....36
- Figure 14. Overstory-understory curves for the chaining sites. Curves were taken from the 2008 and control plot data in Figure 12.....37
- Figure 15. Increasing tree cover in adjacent untreated woodlands from photo pairs of Blythe Springs 1971 (a) and 2008 (b) and North Kern East 1971 (c) and 2008 (d). Extracted and blown up from Figures 4 and 6.....43

Chapter 2

- Figure 1. Number of trees establishing before and surviving treatment and number of trees establishing after treatment for five sites in Eastern Nevada.....64
- Figure 2. Number of trees establishing and surviving after chaining or prescribed fire. Bars represent five-year bins of establishment and vertical dashed lines represent years of treatments.....66
- Figure 3. Density of juniper establishment relative to pinyon establishment for 5-year bins of time since treatment.....67

Figure 4. Density of pinyon and juniper trees of basal diameters in 1-cm diameter size classes for control plots (left) and treatment plots (right) in 2008.....69

Figure 5. Density increases in pinyon and juniper trees for treated and control sites at four locations between 1971 and 2008. Positive values indicate an increase in density and negative values indicate a loss of density.....70

Figure 6. WRCC annual precipitation data for Ely, Nevada between 1958 and 2008....78

Background

Pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) woodlands and sagebrush (*Artemisia tridentata*) shrublands occupy a majority of the productive regions of the Great Basin. Over the past century, woody species dominance has increased considerably throughout the Intermountain West, with much of the increase attributed to expansion of pinyon and juniper woodlands beyond their 19th century range (Burkhardt and Tisdale 1976, Miller and Rose 1999, Miller and Tausch 2001). A major focus of Great Basin research has been to better understand mechanisms behind the widespread shift from shrubland to woodland, and effects of restoration efforts (Romme et al. 2009).

Due to negative effects of woodland expansion on the extent of sagebrush shrubland and herbaceous understory vegetation, pinyon and juniper are often considered invasive native species (Tausch et al. 1981, Miller et al. 2000, Ansley and Rasmussen 2005). The shifting ecotone between these two vegetation types has generated concerns regarding human interests, wildlife, plant community diversity, and disturbance regimes. Loss of sagebrush communities often results in reduction of forage and habitat for popular game, livestock, and sagebrush obligate species. Increased volume of live woody biomass and accumulated dry shrub skeletons associated with recent woodland expansion can also greatly contribute to fuel loading and risk of large catastrophic fire (Miller and Rose 1999, Romme et al. 2009).

Woodland expansion is thought to have begun in the late 1800s, coinciding with a variety of simultaneous environmental and anthropogenic changes. Milder, wetter climatic conditions at the beginning of the 20th century and increasing atmospheric CO₂

concentrations are believed to have favorably altered the Great Basin for woodland establishment and growth (Swetnam et al. 1999, Miller and Tausch 2001, Miller et al. 2008). Increased CO₂ is favorable for plant growth, and wet conditions are favorable for pinyon and juniper seedling establishment. European settlement of the Great Basin occurred at approximately the same time. Settler activities may have altered disturbance regimes through active suppression of wildfire and indirect reduction of fire through overgrazing of fine fuels (Burkhardt and Tisdale 1976, Miller and Tausch 2001). It is also possible that settler alterations of disturbance regimes have not contributed to woodland expansion because fire return intervals for Great Basin woodlands were long enough that relatively recent settler activity would have had little effect (Baker and Shinneman 2004).

Although temperature and moisture regimes confine pinyon and juniper woodlands to particular regions, fire has historically been important in controlling woodland distribution as well. Frequent, low intensity surface fires are believed to be important in maintaining seral pine species dominance in many of the forest systems of the West, but the same forest fire model does not apply to pinyon and juniper woodlands (Swetnam et al. 1999). Great Basin woodland fine fuel structure is typified by dispersed bunch grasses. If fire can spread along the ground, there is high probability of coming in contact with low-stature tree and shrub crowns, which burn entirely when ignited (Baker and Shinneman 2004, Romme et al. 2009). In pinyon and juniper woodlands, fire is often extensive, high intensity, and infrequent, returning to some areas after longer than 400 years (Baker and Shinneman 2004, Bauer and Weisberg 2009, Romme et al. 2009).

Prescribed fire and mechanical tree removal by chaining are two common methods used to counter effects of expansion woodlands. Prescribed fire is often applied by drip torch during early spring or late fall (Everett and Ward 1984). Chaining is accomplished by dragging a large anchor chain (15-25 lbs/link) between two tractors to rip large shrubs and pinyon and juniper trees out of the soil (Ansley and Rasmussen 2005).

The intensity of treatment and immediate effects on vegetation can vary greatly for chaining treatments. A chaining treatment can differ by size or style of the chain used, whether the chain was dragged in only one direction or both, and by characteristics of post-treatment seeding. Different chaining treatment processes often result in varying degrees of tree and shrub mortality, but within a chaining treatment, intensity is frequently uniform across the entire area treated. Because shorter-statured, more-flexible vegetation has higher chaining survival, woody vegetation mortality increases with vegetation maturity (Cole 1968, Tausch and Tueller 1977).

Immediate post-treatment effects are expected to differ between prescribed fire and chaining, with prescribed fire resulting in higher tree mortality. Prescribed fire treatments can differ by post-treatment seeding practices as well as heat intensity or patchiness of the fire. Fire patchiness and intensity usually vary with fuel moisture at time of burning and available fuels (Bruner and Klebenow 1979, Miller and Tausch 2001). When trees in persistent woodlands are burned, a vast majority are killed, especially pinyon trees and trees less than 3 m tall (Barney and Frischknecht 1974, Ward 1977, Miller and Tausch 2001, Romme et al. 2009). Immediate effects of treatment,

whether prescribed burning or mechanical methods such as chaining, have lasting consequences for realizing long-term goals of restoring sagebrush steppe communities.

Thesis Overview

Long-term monitoring of Great Basin woodland treatment projects furthers our understanding of ecological processes and can inform future management decisions. The first chapter of this thesis addresses changes in vegetation composition at chaining sites between 39 and 60 years after treatment and 33 years after burning at prescribed fire sites. Changes in cover data are compared between prescribed fire and chaining treatment types to evaluate their effectiveness in achieving management goals. Influential environmental variables are identified for tree recovery at chaining sites.

Age structures of trees establishing after chaining treatment are examined in the second chapter. Average rates of species establishment ($\text{ha}^{-1} \text{yr}^{-1}$) at chaining and prescribed fire sites are provided for the period of time between treatment and sampling in 2008. The densities of pinyon and juniper size classes were examined for untreated woodland. Measuring species-specific processes of tree survivorship and establishment will help to predict treatment effects on eventual woodland structure and how treated woodland structure will compare to the structure of untreated woodland.

Study Area and Site Descriptions

The study sites are located in mountain ranges and oriented north-south along the eastern side of Nevada (Fig.1). Gradual slopes of mostly open woodlands with understory

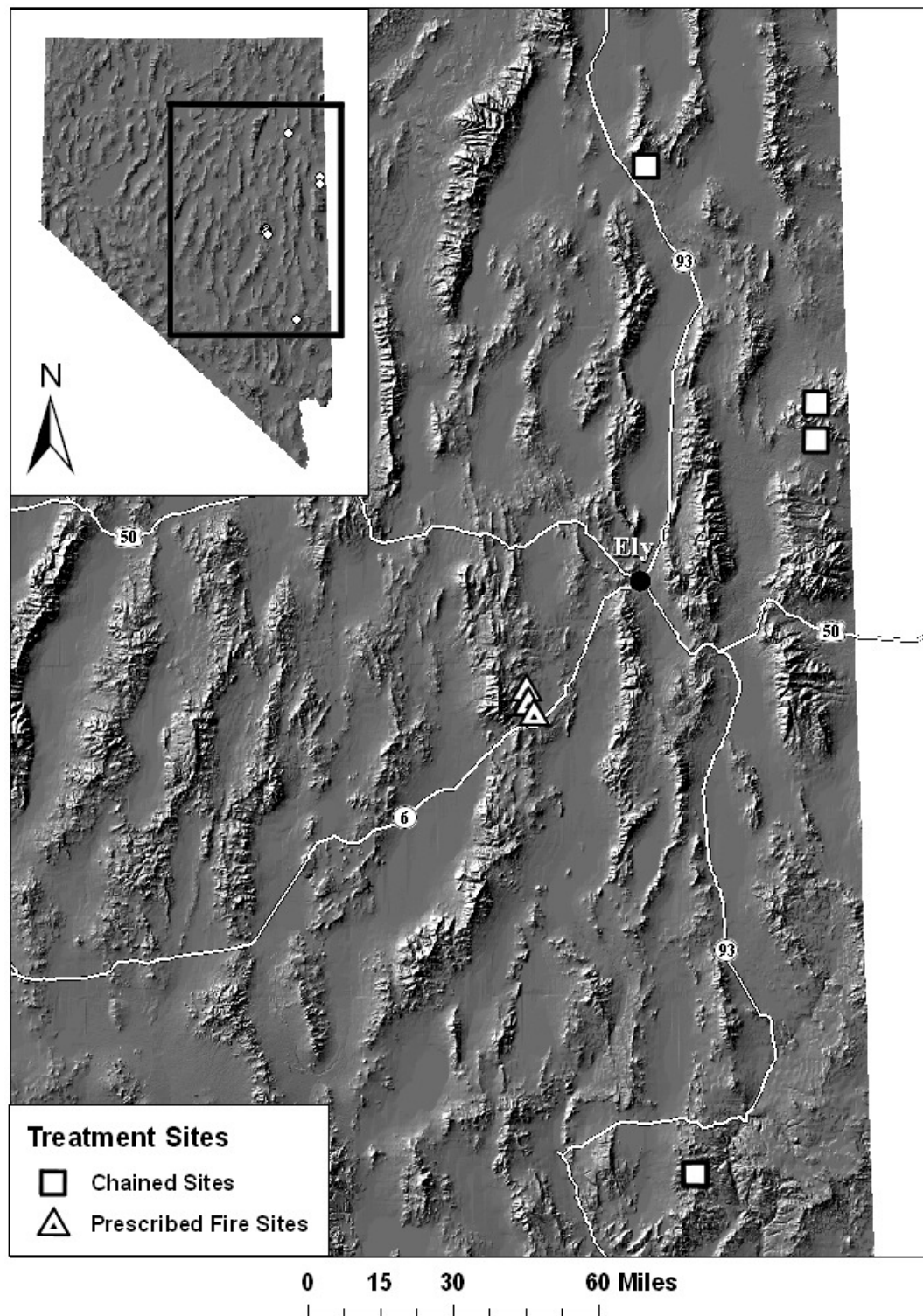


Figure 1. Map of chaining and prescribed fire study sites in Eastern Nevada.

mosaics of sagebrush shrubs and perennial bunchgrasses characterize the area. All sites are on public lands managed by either the U.S. Bureau of Land Management or the U.S. Forest Service.

The oldest and southern-most chaining treatment is the Blythe Springs Chaining (March, 1958) (Fig. 2). It is located on the west side of the Delamar Mountains in south-central Lincoln County, NV (Fig.1). Approximately 500 ha (1200 ac) was chained one way with a 19 lb/ft smooth chain and seeded to crested wheatgrass the next fall. During sampling it became apparent that two age distributions of surviving trees were present and the BLM Caliente Field Office confirmed that approximately 78 percent of the site had been treated a second time in 1985. After the second treatment the site was seeded to bitterbrush, saltbrush, clover, alfalfa, pubescent wheatgrass, and crested wheatgrass. Volcanic soil is characteristic of the Blythe Springs area, which receives approximately 13 inches of precipitation per year (Cole 1968).

Spruce Mountain, northern-most of the chainings, is located in Elko County, NV near the Pequop Mountains. The Spruce Mountain Chaining (Late Fall, 1962) treated approximately 1100 ha (2700 ac) by chaining one way with a 56 lb/ft chain drawn by two D-8 Caterpillar tractors. Soils on the southwestern side of Spruce Mountain are primarily volcanic and receive between 12 and 15 inches of precipitation per year (Tausch 1973). About 60 miles south and 30 miles east of Spruce Mountain are the Kern Mountain chainings, which are located in northeast White Pine County, NV (Fig.1). The North Kern East Chaining (October 1969) is on the north side of the Kern Mountains and at this location about 160 ha (400 ac) were double chained using the Ely Chain, which has

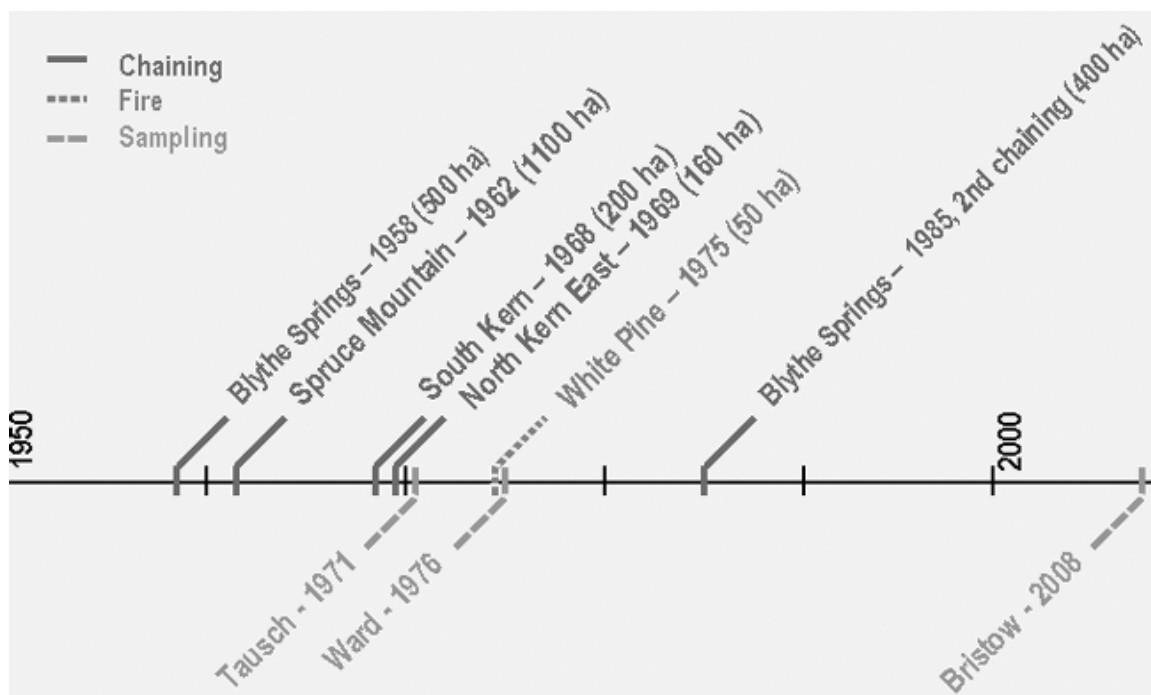


Figure 2. Timeline of chaining and prescribed fire treatments and sampling.

welded cross pieces of railroad track on every other link. The site was seeded between chainings. The South Kern Chaining (October, 1968) is on the south-central base of Kern Mountain and directly across the valley from the north end of the North Snake Range. Here 200 ha (500 ac) were double chained using the Ely chain with seeding between chainings. Both of these sites are characterized by shallow calcareous soil and receive about 13 inches of precipitation per year (Tausch 1973).

The five prescribed fire sites that were resampled are located on the east side of the White Pine Range, southwest of Ely, NV (Ward 1977, Everett and Ward 1984). All five were burned during spring or early summer of 1975. The areas treated are approximately 10, 8, 12, 7, and 5 ha for burns 1 through 5. The original sampling of these sites included data collection both immediately before prescribed burning treatment and in spring and fall of the first two years following treatment.

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Chapter 1: Long-term Vegetation Recovery in Pinyon and Juniper Woodlands after Chaining and Prescribed Fire

Abstract

This study examined long-term changes in vegetation cover multiple decades after historical treatments of prescribed fire and chaining. An emphasis was placed on pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) recovery because it is an easily interpretable measure of treatment success. Vegetation cover, soil depth, and soil texture data were collected at plots within 4 chaining sites treated in 1958, 1962, 1968, and 1969 and originally sampled in 1971. The same data were collected at 5 prescribed burn sites treated in 1975 and originally sampled in 1976. In 2008, tree cover at chaining treatment sites was much greater than at burned sites, where it was nearly absent. The absolute increase in tree cover at the chaining sites was comparable to the increase in tree cover occurring in corresponding control areas. Relative to the original tree cover in 1971, however, the increases in chaining treatment tree cover were greater than the relative tree cover increases at the controls. At all sites, cover of herbaceous species decreased and cover of woody species increased. At prescribed burn sites, post-fire forb communities were replaced by sagebrush-bunchgrass communities. At chaining sites, plant associations dominated by big sagebrush, surviving trees, and seeded grass species were replaced by tree-dominated communities with some understory shrubs. Relationships between site overstory and understory cover values were fit with a negative exponential curve, and the parameters were interpreted in the context of understory response to

treatment. Finer-textured, shallower soils were most predictive of rapid tree recovery following chaining. Tree dominance has recovered at a much faster rate following chaining treatments than prescribed fire. Tree infilling in untreated areas is occurring at a rate similar to tree recovery at chaining sites. Forty years after chaining, sites are again tree-dominated with limited understory vegetation. Burned sites, however, continue to be dominated by shrub and herbaceous species 33 years after treatment. Prescribed fire more successfully removed trees and maintained understory communities; however, cheatgrass (*Bromus tectorum*) had invaded the sites and untreated areas have become much denser with fuel. Chaining only produced short-term success with understory restoration, but did not experience cheatgrass invasion and tree cover in treated areas remained less than in untreated areas.

Introduction

The competitive superiority of pinyon and juniper trees over big sagebrush has lead to displacement of sagebrush communities throughout the Great Basin (Tausch et al. 1981, Tausch and West 1995). At the end of the 19th century, a majority of woodland was confined to rocky ridges with shallow soil and sparse vegetation, but now dense woodland occurs in sites with deeper productive soil (Burkhardt and Tisdale 1969, Miller and Rose 1999). Pinyon and juniper compete heavily with most understory species for soil moisture, the limiting resource of the Great Basin (Noy-Meir 1973, Fowler 1986, Melzoga and Nowak 1991). Through prolific creation of duff and litter layers, overstory

trees also create an environment not suitable for recruitment of many understory species (Everett et al. 1983).

A negative relationship exists between tree overstory cover and corresponding understory cover (Tausch 1973, Tausch et al. 1981, Pieper 1990, Tausch and Tueller 1990, Miller et al. 2000). When plotted against each other, the cover values of understory and overstory vegetation in the Great Basin form a resource utilization curve (Tausch and West 1995, Miller et al. 2000) (Fig. 3). The solid line in Figure 3 represents the amount of understory and overstory vegetation cover the site can support with

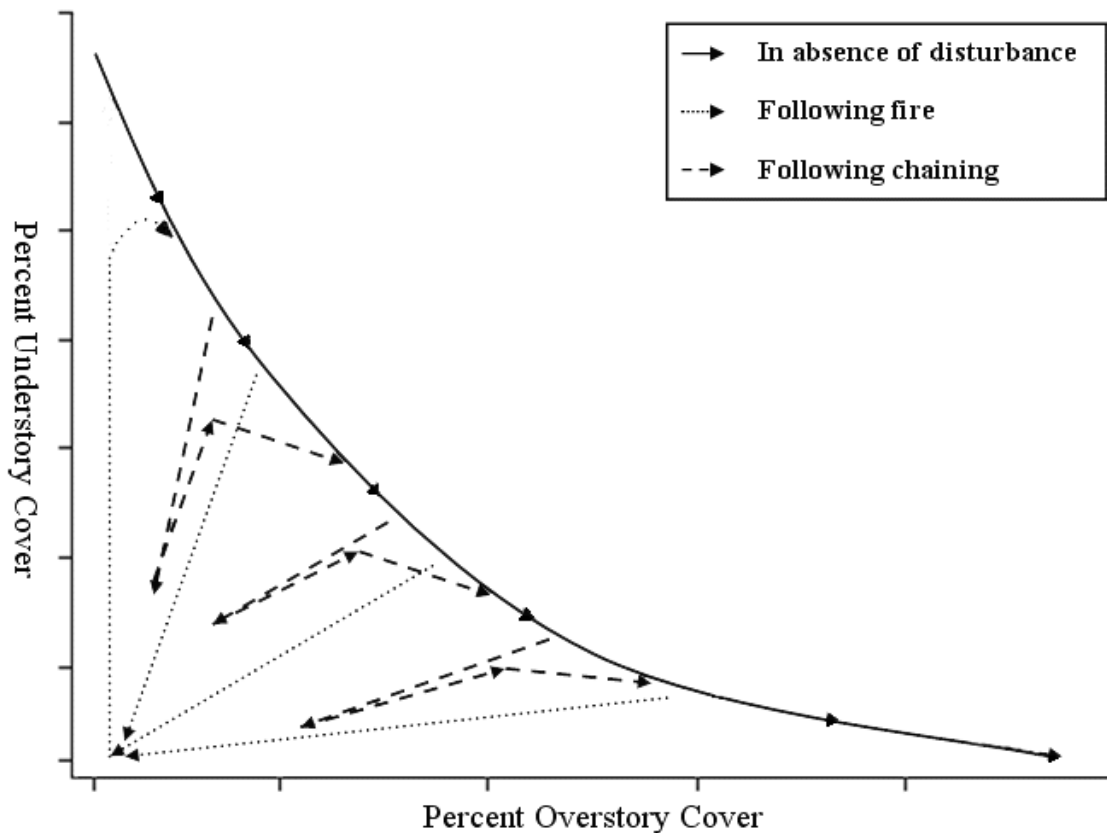


Figure 3. Hypothesized effects of chaining and prescribed burning on understory-overstory cover relationships. The solid line represents the full resource utilization curve, the dashed line represents deviations caused by chaining, and the dotted line represents prescribed fire.

complete utilization of limiting resources. With complete site resource utilization, movement along the curve only occurs when either overstory or understory exploits and incorporates resources previously utilized by the other. In absence of disturbance and resource fluxes, the site will proceed along a successional trajectory from left to right along the curve with increasing tree cover.

The resource utilization curve has been observed to follow a negative exponential relationship because of understory resource partitioning (Tausch 1973, Miller et al. 2000). Sagebrush comprises a majority of the understory cover and the rapid decline of the line at low levels of tree cover is a reflection of sagebrush sensitivity to competition from trees (Tausch and West 1995, Miller et al. 2000) (Fig. 3). The negative slope of the line becomes less steep at moderate levels of overstory cover as remaining sagebrush, bunch grasses, and other sensitive understory vegetation becomes displaced (Everett et al. 1983, Tausch and West 1995, Miller et al. 2000). Some herbaceous understory species, such as *Poa secunda*, *Elymus elymoides*, and *Descurainia pinnata*, are relatively unaffected by woodland closure and cause the slope of the line to reach a lower asymptote with high overstory cover (Everett et al. 1983, Pieper 1990, Tausch and West 1995).

Disturbances release resources formerly utilized by vegetation and cause deviations from the full resource utilization curve. Chaining and prescribed fire cause initial understory mortality, but prescribed fire causes greater loss of overstory and understory cover than chaining, and thus causes greater deviation from full resource utilization. In high fuel situations, such as dense pinyon and juniper woodlands, fire will

often kill most vegetation (Everett and Ward 1984, Baker and Shinneman 2004, Romme et al. 2009). Reestablishment of mature trees following fire has been observed to take longer than 90 years (Barney and Frischknecht 1974, Callaway et al. 1996). Fire causes understory and overstory cover to decrease to near the origin in Figure 3, before gradual increases in understory cover over many years return trajectories to the resource utilization curve (Barney and Frischknecht 1974, Baker and Shinneman 2004).

The effect of chaining on vegetation cover is less severe and the return of the site to the resource utilization curve is expected to be more rapid than following fire. As a result of younger trees having shorter stature and greater flexibility, they are more likely to survive chaining (Cole 1968, Tausch and Tueller 1977). Tree seedlings may continue to grow relatively slowly in the understory of shrubs for upwards of 40 to 50 years and have potential to provide a substantial amount of advance regeneration following chaining (Tausch 1973, Miller and Rose 1999, Miller and Tausch 2001). When chained, both overstory and understory cover are reduced but not completely eliminated, sometimes experiencing survival as high as 50% (Tausch 1973, Tausch and Tueller 1977). After proceeding toward the origin of Figure 3, the site increases in both overstory and understory cover to return to the resource utilization curve more quickly than following fire. Rapid vegetation recovery associated with chaining causes it to be more similar to other Great Basin disturbances, such as beetle kill or drought.

Ward (1977) sampled the five prescribed fire sites used in this study one year after burning. The burns were conducted to convert woodland to an earlier seral stage, considered more valuable for forage, wildlife habitat, and watershed capabilities (Ward

1977). The objective of Ward's study was to measure the impact of fire treatment on vegetation and determine the usefulness of fire as a management tool. The initial changes observed 1.5 years after fire were quite drastic. Trees and nonresprouting shrubs were completely eliminated, while grasses and resprouting shrubs remained in very low quantities, and forbs dominated all sites (Ward 1977).

Tausch (1973) sampled four chainings that had been treated 13, 9, 3, and 2 years previously. The motivation for this study was to evaluate the success of chaining by quantifying persistence of seeded grasses, determining deer use of those grasses, and measuring the growth releases of surviving trees (Tausch 1973). Seeded grass species still persisted at chaining sites, especially at the most recently chained sites, and deer use of a site was most commonly correlated with native (non-seeded) vegetation (Tausch 1973). Survivor trees were experiencing accelerated growth that was beginning to diminish at older sites.

This study examined changes that occurred in overstory and understory dynamics in the 37 years following the initial sampling of the chainings and 32 years following sampling the prescribed fires. Thirty-three years had passed since the prescribed fire treatments were conducted and approximately 40 to 50 years had passed since the chaining treatments. While other studies have examined overstory-understory relationships at sites with ranges of tree dominance (Tausch et al. 1981, Pieper 1990, Tausch and Tueller 1990, Miller et al. 2000), there has been a scarcity of comparisons of long-term changes in vegetation composition at treated woodlands. I explored the effectiveness of historical prescribed fire and chaining woodland treatments for

accomplishing long-term goals of maintaining sagebrush-dominated communities.

Specifically I addressed the following research questions:

- 1) Is current tree cover at chaining sites greater than at prescribed fire sites?
- 2) Is species composition at treated sites currently more dominated by trees than it was at initial sampling?
- 3) Is the resource utilization curve useful for interpreting site changes?
- 4) How is tree recovery at chained treatment sites influenced by environmental variability and site productivity?

Methods

Data Collection

Historical Data

In 1971, Tausch sampled the chaining treatment areas for vegetation recovery and deer utilization. His data collection design utilized a stratified random sampling technique for within site plot determination to capture variation in slope, aspect, elevation, and soil type. At each treatment plot, he collected understory plant cover and density data from randomly located transects along a 250 or 500-foot baseline (Tausch 1973). At treatment and control plots, tree density and cover were determined by measuring every tree in two 1/5-acre subplots. Plot locations were marked using fence posts and rebar.

In 1975 and 1976, Ward (1977) performed a vegetation succession study following five small (5 – 12 ha) prescribed burns. His design consisted of systematically orienting 30 m transects from randomly located starting points within each of the five

prescribed burns. Plant species cover and density data were collected in microplots along the 30 m transects. After treatment, the initial study found no live trees present for measuring. Plot locations were marked using fence posts and rebar.

Study Design

Macroplots were located as close as possible to original plot locations to maintain consistency. This required locating original rebar and fence posts, which was achieved with variable success (Table 1). When unable to relocate an original macroplot, the plot was placed in the general location of the original, which was determined by examining hand drawn maps and air photos. Burned and control macroplots were placed on original locations but chaining macroplots were located immediately adjacent to original positions. Chaining macroplots were relocated to adjacent areas of the same vegetation type, soils, slope, and aspect because the original sampling caused tree mortality.

	Blythe	Spruce	South Kern	North Kern East	White pine
Expected	13	13	10	17	?
Located	2	0	5	12	8

Table 1. Number of marked plots discovered during resampling.

The same basic plot layout was employed as Tausch (1973) with distances converted to metric units at both chaining and fire treatment sites (Fig 3). The same sampling approach was used for re-sampling and equivalent data were collected.

Field Data Collection

Due to the relatively large area chained at Spruce Mountain and Blythe Springs, baselines had lengths of 160 meters. For all other chaining sites and prescribed fire sites, baseline lengths were 80 meters (Fig. 4). Four 20-m transects, perpendicular to the baseline, were positioned in a stratified random manner, with one transect located in each quarter of the baseline. Ocular estimations of macroplot aerial cover of shrub species were conducted in 2-m² plots along the four randomly located transects. Ocular estimates of grass and forb basal cover by species were made in 0.2-m² nested plots along the same

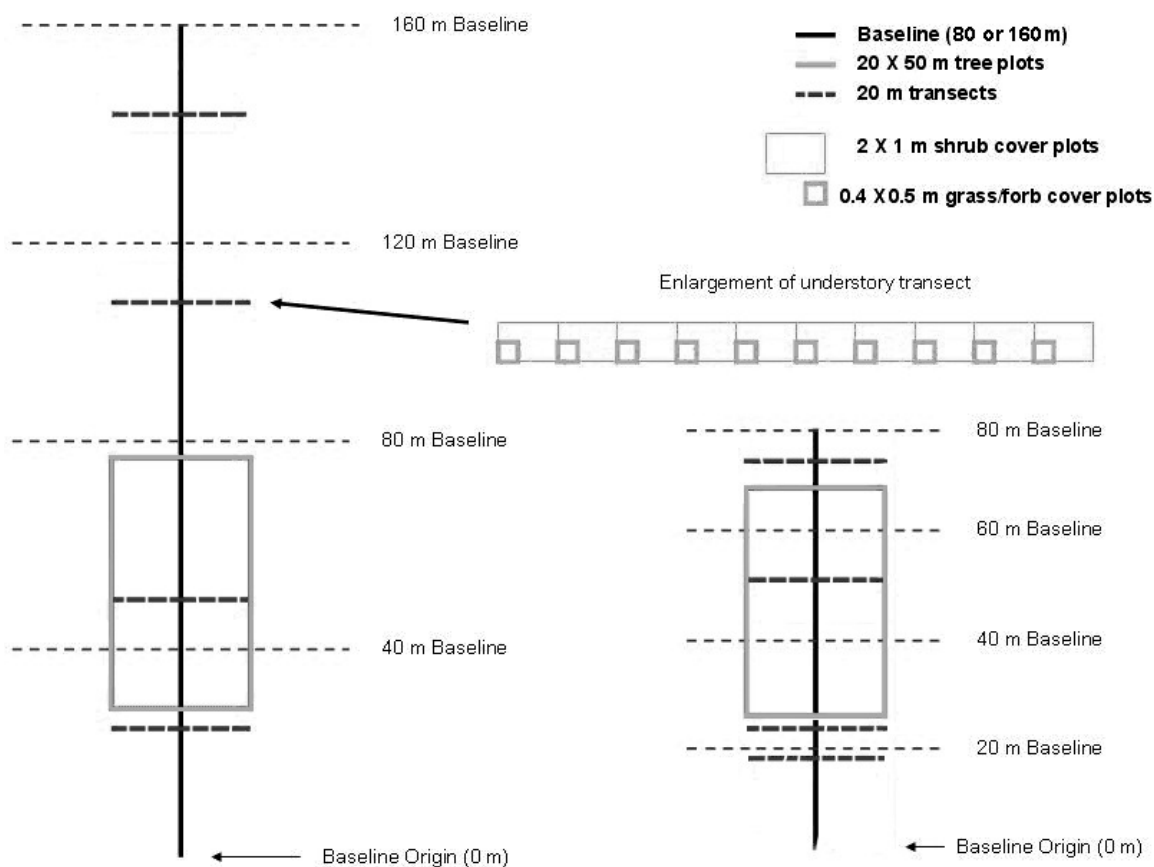


Figure 4. Plot layouts for Spruce Mountain and Blythe Springs (left) and North Kern East, South Kern, and the White Pine prescribed fire sites (right).

transects. Macroplot tree cover by species was measured in a randomly located 0.1-ha tree plot by summing individual tree crown areas for all trees. The longest crown diameter (d_1) and the perpendicular diameter (d_2) were measured to the nearest decimeter using measuring poles. Diameters were later used to estimate aerial coverage (A) of each individual tree by assuming an elliptical crown using Equation 1 below.

$$\text{Equation 1: } A = (\pi * d_1 * d_2) / 4$$

Soil depth was measured at 16 regularly spaced locations along the baseline using a 50-cm aluminum soil probe (0.5-cm diam). Depth was recorded when the probe was obstructed from being thrust any further into the soil by a hard surface (Harner and Harper 1976). Soil samples of the upper four inches were collected at four random locations along the baseline to be tested for texture. Samples were first sieved for coarse fragments (> 2mm) and then further classified using the hydrometer method into classes of percent each of sand, silt, and clay.

GIS-Derived Data

Topographic variables were derived using 10-meter digital elevation models (DEMs). Using ArcGIS 9 software, the DEMs were clipped to the general watershed area of each site and converted to topographic convergence index (TCI) and solar radiation layers. TCI was calculated using the following formula (Equation 2), in which a = area of the upstream contribution and b = slope in radians (Beven and Kirkby 1979).

$$\text{Equation 2: } TCI = \ln (a / \tan b)$$

High TCI values occur in areas that have lower runoff and are considered areas of higher potential for soil moisture. Annual solar radiation was calculated using the Area Solar Radiation function (ArcGIS 9 software). Macroplot polygons representing the baseline and the area sampled for vegetation were constructed in ArcMap using 2 GPS points per macroplot that were collected during field sampling. The polygons were used to extract macroplot average values of elevation, TCI, and solar radiation.

Data Analysis

Tree cover was defined as the absolute percent aerial cover of pinyon and juniper trees. Mean values of the cover in 2008 by trees, shrubs, forbs, and seeded and native grasses were compared between chaining and burning treatment types. Fixed effects ANOVA was used to determine if treatment effects on vegetation type covers were significantly different. The number of years since treatment was included as a covariate to control for the effect of time in comparing differences among treatments. Because repeated chaining was not a treatment considered in the design, the data from the twice-chained Blythe Springs treatment were not used in between-site comparison analyses. Blythe Springs plot data were useful, however, for examining site changes between original and 2008 sampling.

Two-sample t-tests were used to compare changes in tree cover between treated and control sites. Plots that were identified from NAIP imagery and GIS layers as differing in vegetation type, soil type, or topography between 2008 and the time of original sampling were removed from the analysis. Paired t-tests were used to determine

if treated site mean tree cover in 2008 differed significantly from mean tree cover at the time of the original sampling. Because understory data were not collected from control sites in 1971, understory comparisons were not made.

A Nonmetric Multidimensional Scaling (NMS) ordination analysis was used to interpret magnitude and direction of changes in vegetation composition. Macroplot cover data were transformed to normality using the arcsine square root transformation. The Sorenson (Bray-Curtis) distance measure was used for the ordination, which was rotated to maximize axis correlations with woody vegetation cover. Macroplot centroids for each plot were displayed as the mean site score with 95 % confidence interval bars.

Nonlinear regression curves were fit to macroplot understory and overstory cover values using the negative exponential function (Equation 3):

$$\text{Equation 3: } Y = a * e^{-bX}$$

where Y is understory cover, X is overstory cover, and a and b represent two fitted parameters. Macroplot 2008 treatment and control data were used to fit the curves. 1971 treatment understory and overstory cover data were plotted with the regression lines to examine their location in relation to the curves. Estimates for parameters a and b represent constraints on the site's understory cover. The y-intercept parameter (a) represents the maximum understory cover the site can support. The value is sensitive to limiting resources of the site such as soil depth or texture, which both limit available moisture. Greater values of parameter b cause greater curvature in the line. Ecologically, larger values of b indicate higher sensitivity of understory cover to increases in overstory

cover. Sensitivity of understory cover to increases in overstory cover may be influenced by understory composition.

Mixed effects regression models incorporating site as a random effect were compared to determine the influence of macroplot-specific environmental variables on tree recovery at the Spruce Mountain and Kern Mountain chainings. Many variables were grouped by site, which created high multicollinearity among explanatory variables due to pseudoreplication (Appendix I, Table i). Mixed effects models are powerful tools for studies with a grouped or clustered sampling design, where observations are not independent but are structured in a predictable way (Pinheiro and Bates 2000). The tree recovery response variable was calculated as change in tree cover at each macroplot between 1971 and 2008. In the regressions, site was included as a random effect, whereas all environmental variables were treated as fixed effects. Environmental variables included GIS-derived elevation, TCI, and solar radiation topographic variables as well as field-collected soil variables. Soil percent silt and percent clay texture classes were combined into a percent fine category. Percent fine, percent coarse fragment (> 2 mm), and average soil depth were included in analysis.

Regression model selection was performed utilizing the second order Akaike's Information Criterion (AIC_c) (Burnham and Anderson 2002). AIC_c scores in combination with AIC_c differences (Δ_i), Akaike weights (w_i), and effect sizes (β) were used to compare and rank models and variables. Models with Δ_i between 1 and 3 have substantial support, between 3 and 7 have considerably less support, and models greater than 10 have virtually no support (Burnham and Anderson 2002).

AIC scores are used to select the best models from a set; however, calculated ranks are only relative to the other models. The selection process does not provide information about how well a model actually fits the data, as does a correlation coefficient. Nagelkerke's R^2 was calculated for each model to determine how well it fit the data. Nagelkerke (1991) developed Equation 4 below to calculate R^2 for situations in which residual variance is not easily defined. $L(\theta)$ and $L(0)$ represent the log likelihoods of the fitted and the null models respectively.

$$\text{Equation 4: } R^2 = 1 - \{ L(0) / L(\theta) \}^{2/n}$$

Results

Effect of Treatment Type on Current Plant Community Composition

Site Observations

At the White Pine prescribed fires (spring of 1975), which were the most recently treated sites, my initial observations in 2008 revealed dense understory vegetation. Robust Indian ricegrass (*Achnatherum hymenoides*), Thurber's needlegrass (*Achnatherum thurberianum*), and Great Basin wild rye (*Leymus cinereus*) occurred in the interspaces of expansive patches of sagebrush and bitterbrush (*Purshia tridentata*). Occasional burnt skeletons of juniper trees were scattered throughout the sites. Aside from two surviving juniper trees at one burn, the fire treatments completely killed all trees across all sites. A few scattered post-treatment tree seedlings and saplings occurred at all of the burn sites, the majority of which were juniper. The burn sites exhibited varying levels of cheatgrass invasion that was occasionally quite dense. At the eastern

ends of two burn treatments, patches of crested wheatgrass were barely persisting in the presence of shrubs, but thriving in rodent exclosures that were devoid of shrubs.

The North Kern East chaining (1969) was dense with juniper trees (Fig. 5). In some places trees were too dense and large to distinguish the treatment boundary. The most densely treed areas had few shrubs and grasses. Crested wheatgrass was the most prevalent grass. In a few smaller areas along the east side and southern end of the chaining, tree cover was sparser, trees were shorter, and a greater cover of sagebrush existed. Cheatgrass was not present.



Figure 5. Photo pair of the center of the North Kern East Chaining. 1971 left, 2008 right. Photographs taken by Robin Tausch.

At the South Kern chaining (1968), trees in general were larger but less dense than those at North Kern East (Fig 6). Relative abundance of juniper and pinyon was similar, understory vegetation was sparse, and interspaces were mostly dominated by sandy soil. Remaining seeded grasses at the site included crested wheatgrass, smooth brome, and intermediate wheatgrass, although only crested wheatgrass was widespread. The bitterbrush that remained was heavily browsed and cheatgrass was not present.

At the Spruce Mountain chaining (1962), plots were arranged along an elevational gradient. Plots located at the lower end of the gradient, which were also furthest east,



Figure 6. Photo pair of the southern end of South Kern. 1971 left, 2008 right. Photographs taken by Robin Tausch.

exhibited the least amount of tree cover and the most continuous sagebrush cover. Lower elevation plots also had the greatest ratio of juniper cover to pinyon cover. Shrubs were still relatively abundant, especially at lower elevation plots. Seeded grasses were absent and cheatgrass cover was sparse but occasional throughout the entire site.

At Blythe Springs (1958), the area chained was also very large (500 ha). The shrub cover was dense and tall. Some small, scattered trees existed throughout the chaining as well as low cover of herbaceous understory (Fig. 7). All seeded vegetation from the first and second treatments were entirely absent from the site.



Figure 7. Photo pair of the eastern side of Blythe Springs. 1971 left, 2008 right.

Seven of the treated plots were treated twice (1958 & 1985), one of the control plots had been treated once (1958), and five of the control plots were never treated (Fig.

8). Because repeated chaining was not a treatment considered in the design, and only one plot sampled at the site was chained once, the Blythe Springs data were not used in between-treatment comparative analyses.

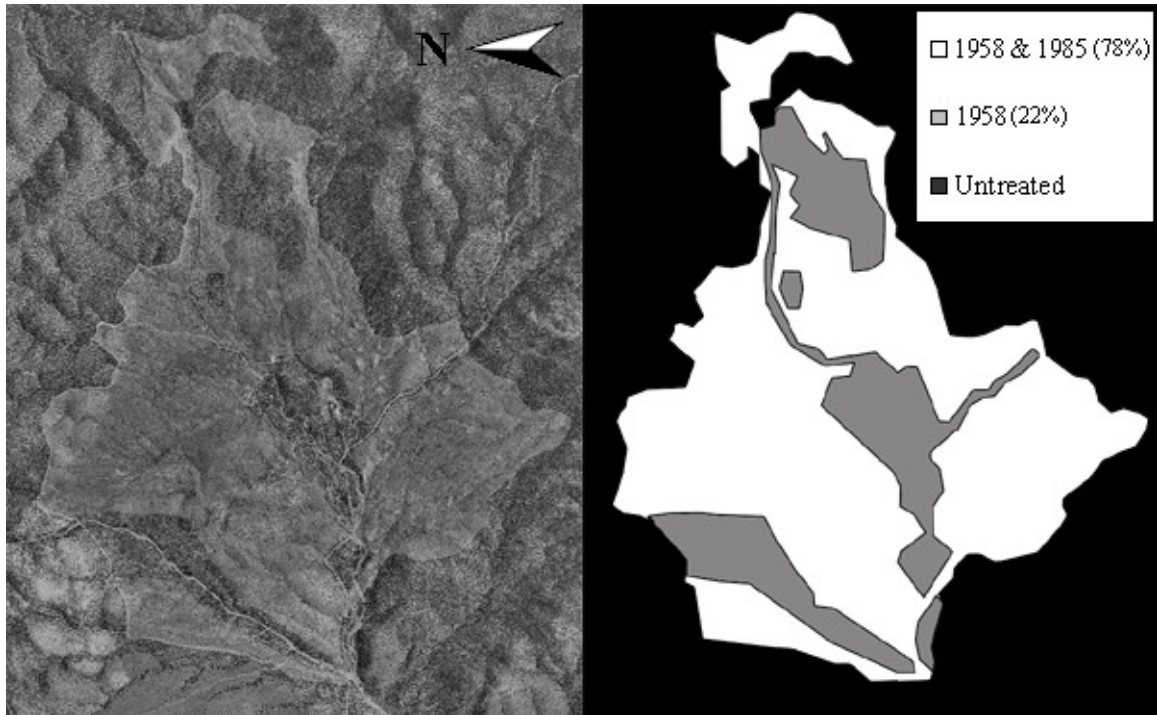


Figure 8. Air photo of Blythe Springs and patches that were chained once and twice.

Treatment Effects on Plant Functional Types

All sites exhibited high variation in species composition (Appendix I, Table ii). The effect of treatment was significant ($\alpha \leq .05$) for the 2008 cover of all vegetation types except forbs (Table 2). The number of years since treatment had significant effects on mean 2008 shrub and forb cover. Mean tree cover at chainings was 71 times greater than mean tree cover at prescribed fires (Table 2). In contrast, mean shrub cover was nearly 3 times greater at prescribed fire sites. There was more than twice as much grass cover at

the prescribed fire sites, but the forb cover was virtually the same at the burned and chaining sites.

Vegetation Type	Chaining	Fire	Difference	Treatment		Time	
	Treatment	Treatment		F Value	P Value	F Value	P Value
Trees	23.44	0.33	23.12	109.84	<.01 *	3.06	0.09
Shrubs	5.76	15.98	-10.22	39.37	<.01 *	12.51	<.01 *
Grass	1.02	2.75	-1.73	17.82	<.01 *	0.80	0.38
Forbs	0.65	0.65	0.00	0.00	1.00	7.95	0.01 *

Table 2. Fixed effects ANOVA results of prescribed fire (n = 13) and chaining (n = 26) treatments on 2008 mean aerial covers of vegetation types, with time since treatment included as a covariate.

Increasing Woody Species Cover over Time

Changes in Vegetation Type Cover

Tree cover increased from the time of original sampling at most treated sites (Fig. 9). At three of the four chaining sites, Spruce Mountain, South Kern, and North Kern East, there was greater than a 10 percentage point increase in percent tree cover (Fig. 9, Table 3). The fourth chaining, Blythe Springs, which was chained twice, had not experienced a significant change in tree cover since 1971 (Table 3). At the prescribed fire sites there was a statistically significant increase in tree cover between 1976 and 2008, but the increase was only from 0 to 0.2% (Table 3).

The magnitude of increases in absolute tree cover at chaining controls was comparable to the tree cover increases observed at the chaining treatments. The increases in treatment tree cover at North Kern East and South Kern were not significantly different from those observed in the untreated areas (Fig. 9). At Spruce Mountain, the increase in

tree cover at the control plots was significantly greater than the increase in tree cover at the treatment plots, but the control sample size was small (Fig. 9).

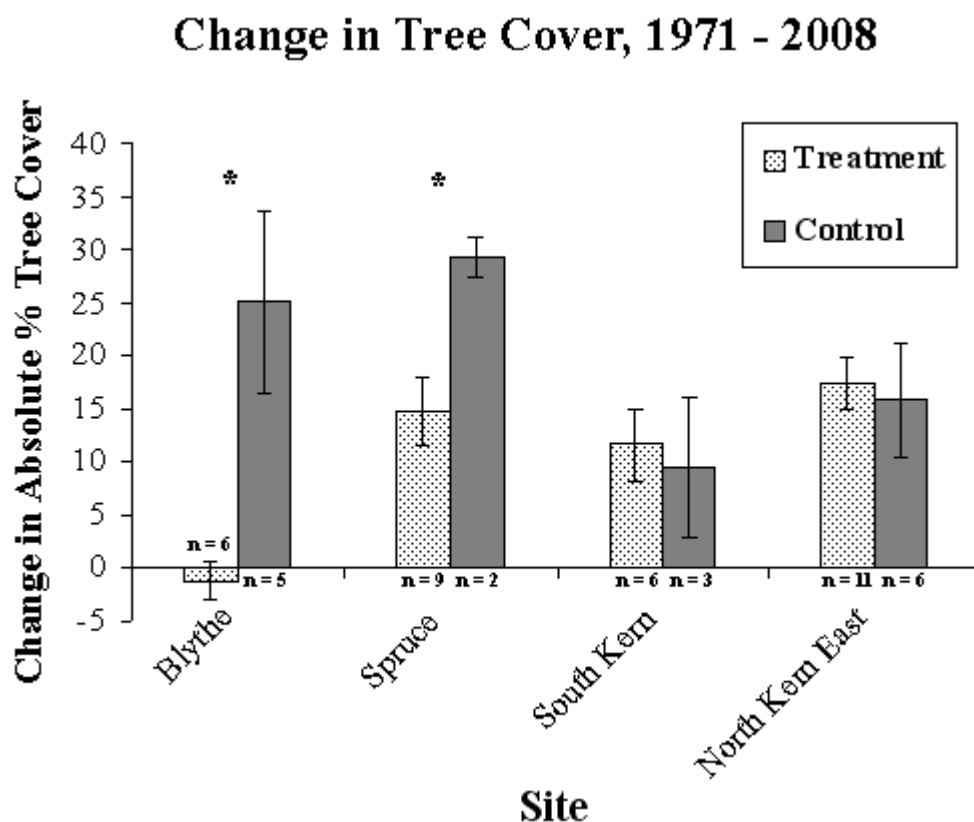


Figure 9. Change in absolute percent tree cover at chaining sites between initial sampling and 2008 for treatment and control plots. Error bars represent standard error and * denotes differences between control and treatment plots ($\alpha < .05$).

Site	2008 - 1971	P - Value
North Kern East	17.34	<.01 *
South Kern	11.64	0.01 *
Spruce Mountain	14.70	<.01 *
Blythe Springs	-1.29	0.49

Site	2008 - 1976	P - Value
White Pine	0.22	<.01 *

Table 3. Paired T-Test for mean differences in tree cover between 2008 and the time of initial sampling.

Relative increases in tree cover at control plots did not exceed relative increases in tree cover at treated plots (Fig. 10). For Spruce Mountain, the 2008 treated plot tree cover was about 2.9 times greater (from 7.7% to 22.4%) and the control plot tree cover was 2.4 times greater (from 27.4% to 67.1%) than in 1971 (Fig. 10). The treatment tree cover at South Kern increased by 3.1 times (from 5.5% to 17.1%) and the control tree

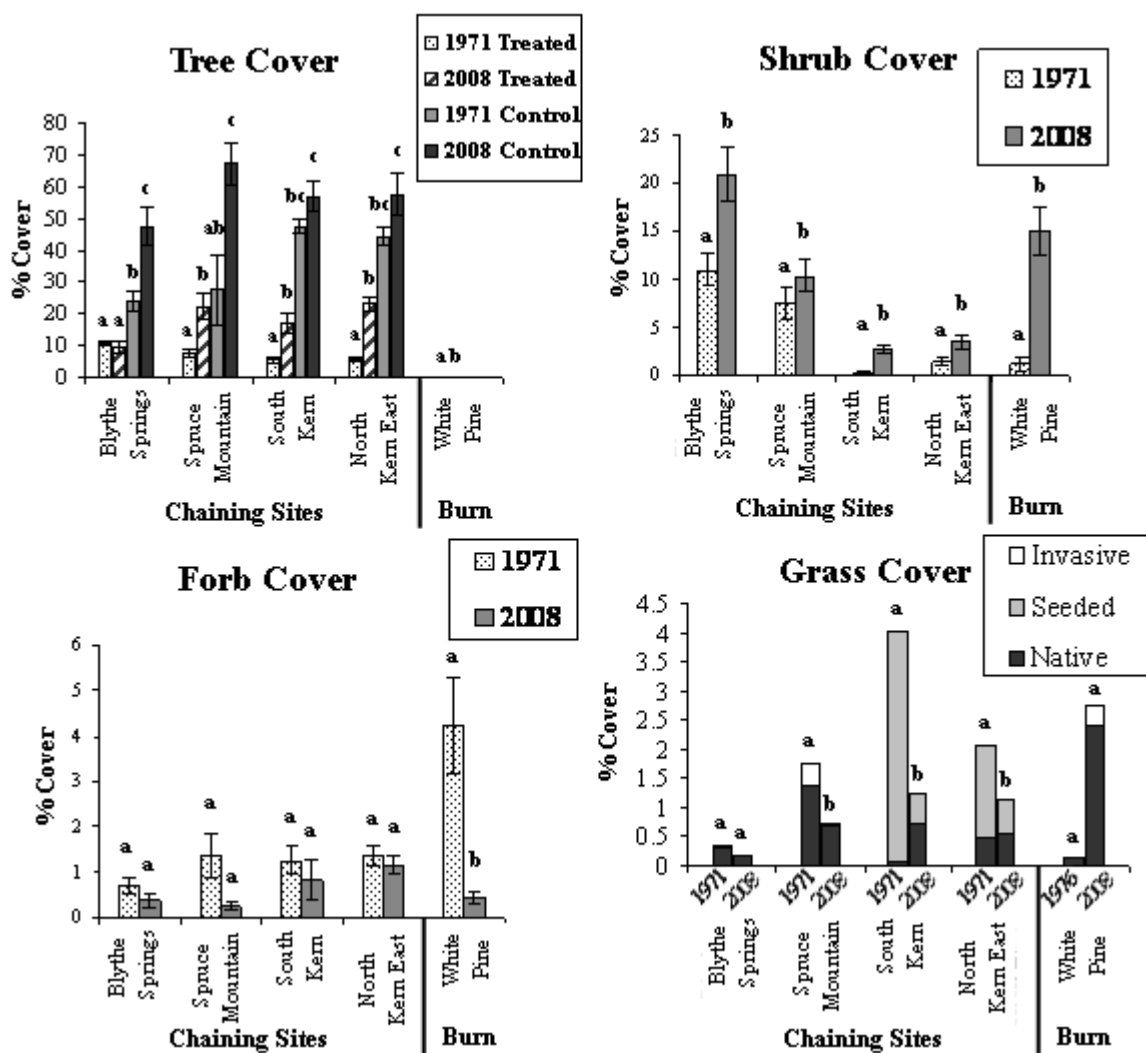


Figure 10. Absolute percent cover of vegetation types at chaining and prescribed fire treatment sites. Control plot data are also displayed for tree cover (top left). Sites are arranged by treatment age from oldest (left) to most recent (right). Error bars represent standard error and letters denote statistically significant differences in absolute cover within a site ($\alpha > .05$).

cover increased by 1.2 times (from 47.5% to 57.0%). At North Kern East, the treatment tree cover quadrupled (from 5.8% to 23.2%), while the control tree cover increased by 1.3 times (from 44.2% to 57.6%) (Fig. 10).

Shrub cover increased for all treatments (Fig. 10). Shrub cover increased most on sites with lower tree cover increases, increasing by about 10 percent at the Blythe Springs twice-chained plots (from 11% to 20.9%) and about 14 percent at the White Pine prescribed fires (from 1.1% to 15.2%) (Fig. 10). Shrub cover rose by more than two percentage points at Spruce Mountain (from 7.5% to 10.4%), South Kern (from 0.2% to 2.8%), and North Kern East (from 1.4% to 3.5%). Seeded grass cover decreased significantly only at South Kern (from 3.9% to 0.5%) and North Kern East (from 1.6% to 0.6%). Change in percent cover of native grasses was inconsistent at chaining sites, but increased by about two percent at the prescribed fire sites (from 0.1% to 2.4%) (Fig. 10). At chaining sites, decreases in forb cover were close to one percent at Spruce Mountain (from 1.4 to 0.3%) and insignificant at the other sites. At prescribed fire sites, the decrease in forb cover was close to four percent (from 4.2% to 0.4%).

The chaining and repeated chaining treatments at Blythe Springs yielded similar herbaceous species cover values (Fig. 11) but differed in cover of woody species. By 2008, both treatments resulted in almost no herbaceous plant cover. The once-chained macroplot had tree and shrub cover values that were intermediate in relation to the twice-chained and control macroplots (Fig. 11), but were more similar to the control plots.

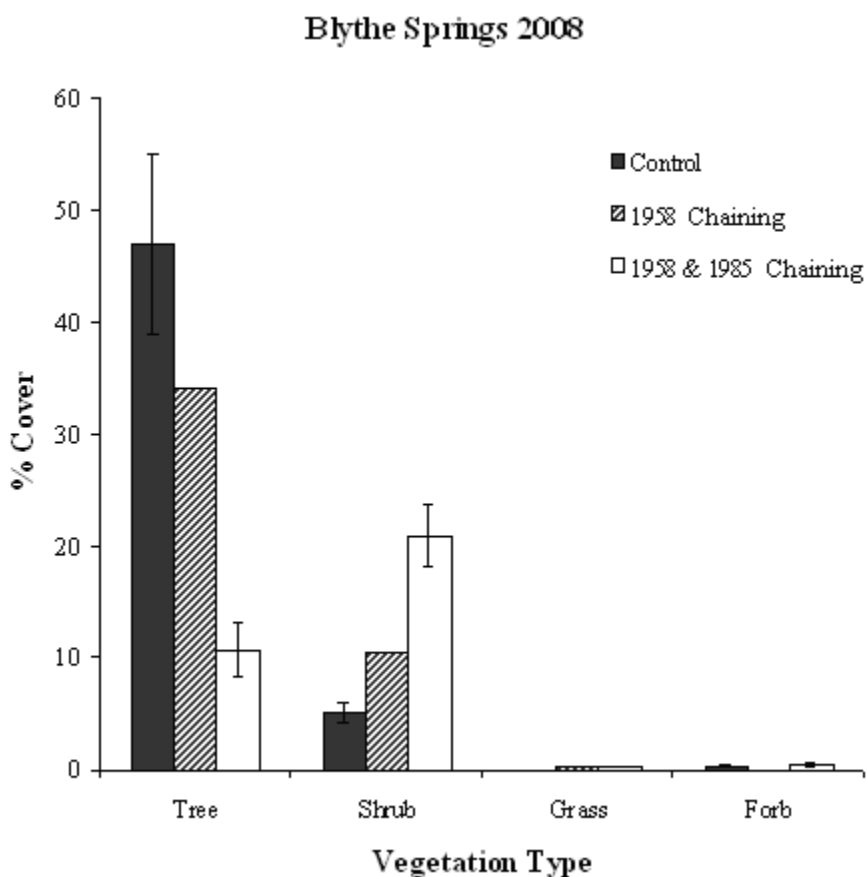


Figure 11. Cover of vegetation growth forms at the Blythe Springs once-chained, twice-chained, and control macroplots.

Species Compositional Shifts within Sites

An NMS ordination was used to describe species compositional shifts, representing successional trajectories from the treatment year to 2008. When all of the treated plots were combined into a single matrix, the resulting NMS ordination yielded a two-dimensional solution with a relatively high final stress of 13.5. Stress in the range of 10 to 20 is considered satisfactory for an ordination describing ecological community data; however, not much reliance should be placed in details of the plot (McCune and Grace 2002). Axis 1 mostly represents tree-dominated cover and axis 2 represents high

sagebrush cover with some cover of other shrubs and low cover of seeded grasses and forbs (Table 4, Fig. 12).

	Axis 1	Axis 2
% Variance Explained (R ²)	0.514	0.374
Vegetation	R	R
Tree	0.824	0.193
<i>Artemisia</i>	0.311	0.882
<i>Purshia tridentata</i>	0.21	0.482
Miscellaneous shrub	-0.419	0.463
<i>Achnatherum nevadensis</i>	0.031	0.102
<i>Achnatherum hymenoides</i>	-0.117	-0.255
<i>Agropyron cristatum</i>	0.246	-0.652
<i>Bromus inermis</i>	0.189	-0.509
<i>Bromus tectorum</i>	-0.166	0.248
<i>Elymus elymoides</i>	-0.026	0.409
<i>Poa secunda</i>	0.287	0.038
<i>Psuedoroegneria spicata</i>	0.176	0.285
<i>Thinopyrum intermedium</i>	0.158	-0.431
Total forb	-0.513	-0.601

Table 4. Species used in NMS ordination and correlations with axes

In the ordination, most of the vectors proceed in the same direction, increasing along both axes, progressing from herbaceous to more woody vegetation (Fig. 12). While the two treatments share vector direction, they differ in the ordination space they occupy and the magnitude of their changes. Both treatments span most of axis 2 (increasing sagebrush cover) but occupy two distinct ranges along axis 1 (increasing tree cover). The vectors of both treatments converge in 2008 on a smaller area than the area the same plots occupied in 1971 or 1976. This is evident in the reduced size of the 95% confidence bars in 2008 and indicates greater similarity between per-plot plant community compositions within the site. The one exception was Blythe Springs, where the second chaining created more divergent 2008 communities. The vectors are much

longer at the burned sites, indicating greater change having occurred along the axes of sagebrush and tree cover.

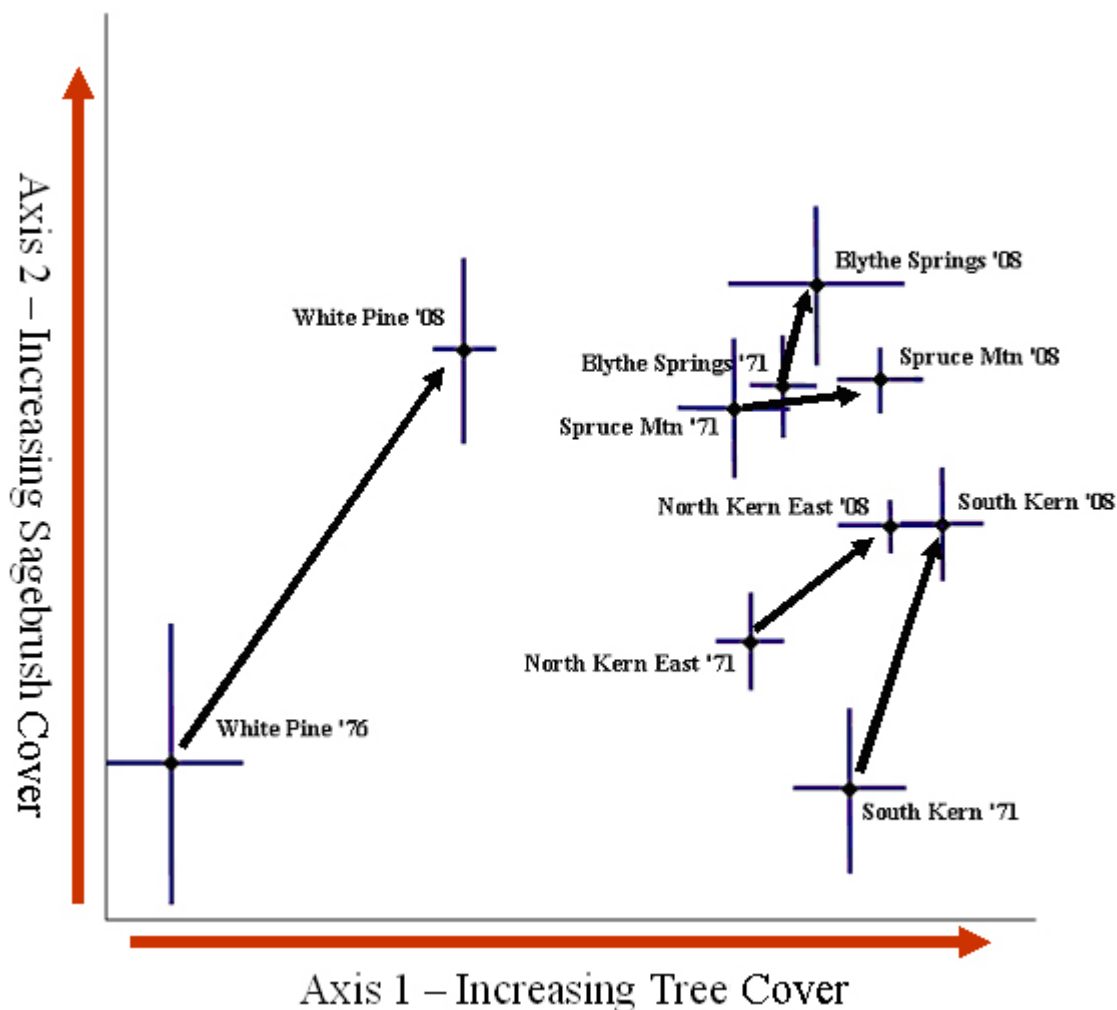


Figure 12. Graph of mean NMS ordination centroids for each site based on vegetation cover in 1971 and 2008. Bars represent the 95 % confidence limits in each of the directions along axes 1 and 2. Arrow vectors represent the amount of change at each site.

These same trends are discernable in the dominant species cover data (Table 5).

At all of the sites there was greater cover of shrubs and trees in 2008 than there was at initial sampling. In general, there was less cover of herbaceous vegetation at chaining sites as a result of seeded grasses (*Thinopyrum intermedium*, *Bromus inermis*, *Agropyron*

Scientific name	Common name		Blythe Springs		Spruce Mountain		South Kern		North Kern East		White Pine	
			1971	2008	1971	2008	1971	2008	1971	2008	1976	2008
NA	Total tree	Mean	10.67	9.38	7.66	22.36	4.90	19.37	5.83	23.17		0.22
		SD	1.44	4.40	3.28	11.53	1.87	5.82	2.08	7.68		0.04
<i>Artemisia species</i>	Sagebrush	Mean	7.82	10.69	7.32	9.27	0.24	2.72	1.05	3.02		4.63
		SD	3.27	6.63	5.16	4.52	0.49	1.19	1.12	2.40		2.71
<i>Purshia tridentata</i>	Bitterbrush	Mean	1.73	9.18	0.17	1.53	0.05		0.05	0.31		5.24
		SD	1.29	2.34	0.12	1.58	0.05		0.06	0.75		2.78
NA	Other shrub	Mean	1.45	1.02	0.19	0.47			0.30	0.20	1.08	5.33
		SD	1.38	1.50	0.13	0.62			0.45	0.20	1.66	2.20
<i>Achnatherum thurberianum</i>	Thurber's needlegrass	Mean	0.03	0.04				0.04	0.22	0.08		0.16
		SD	0.03	0.04				0.04	0.02	0.15		0.20
<i>Achnatherum hymenoides</i>	Indian ricegrass	Mean			0.25	0.08	0.04		0.15	0.13		0.13
		SD			0.27	0.08	0.02		0.17	0.18		0.17
<i>Agropyron cristatum</i>	Crested wheatgrass	Mean	0.04				1.60	0.38	1.59	0.59		
		SD	0.06				0.48	0.29	0.59	0.29		
<i>Bromus inermis</i>	Smooth brome	Mean					0.98	0.12				
		SD					0.55	0.03				
<i>Bromus tectorum</i>	Cheatgrass	Mean		0.02	0.49	0.03						0.21
		SD		0.01	0.89	0.03						0.14
<i>Elymus elymoides</i>	Squirreltail	Mean	0.33	0.20	0.39	0.28	0.03		0.14	0.01		0.29
		SD	0.33	0.20	0.39	0.28	0.03		0.14	0.01		0.29
<i>Poa secunda</i>	Sandberg bluegrass	Mean			0.11	0.19	0.02	0.24	0.15	0.28		0.20
		SD			0.06	0.14	0.02	0.12	0.14	0.26		0.26
<i>Pseudoroegneria spicata</i>	Bluebunch wheatgrass	Mean			1.84	0.44		0.87				
		SD			1.22	0.29		0.82				
<i>Thinopyrum intermedium</i>	Intermediate wheatgrass	Mean					1.63	0.49				
		SD					0.59	0.56				
NA	Total forb	Mean	0.69	0.36	1.36	0.25	1.33	0.91	1.35	1.16	4.22	0.44
		SD	0.47	0.42	1.53	0.23	0.86	1.30	0.68	0.70	2.37	0.33

Table 5. Mean cover of dominant species by site and year.

crisatum), native grasses (*Achnatherum thurberianum*, *Achnatherum hymenoides*, *Elymus elymoides*, *Poa secunda*, *Psuedoroegneria spicata*), and forbs becoming more sparse over the 30-year period. Loss of forb cover alone accounted for the decrease in herbaceous cover at prescribed fire sites, but a variety of native grass species replaced them (Table 5). The dominant invasive grass, cheatgrass, increased in cover from zero to 0.21 % at the White Pine fires. Cheatgrass did not occur at the Kern Mountain sites, increased from zero to 0.02 % cover at Blythe Springs, and decreased from 0.49% to 0.03% at Spruce Mountain (Table 5). Although few dominant species were completely lost, reduction in cover of diverse herbaceous understory species contributed to 2008 species composition being defined primarily by trees and shrubs.

Environmental Effects on Tree Recovery in Chaining Sites

Resource utilization curves can potentially model loss of understory and tree recovery. The parameters of the curves are related to the influence of site environmental characteristics on tree recovery. If it is assumed that by 2008 the vegetation has resumed fully utilizing the available resources, the plots should once again fall along the resource utilization curve (Fig. 3). Because the data of this study form a curve with a negative exponential shape when overstory and understory cover values are plotted against each other (Fig. 13), the data support the proposed curve of Figure 3. Although trajectories could not be tested with data from only two points in time, the shape of the curves are consistent with vegetation having resumed fully utilizing the site resources.

With the exception of South Kern, all the 1971 treated plots of all the sites fell below the understory and overstory curves (Fig. 13). At North Kern East, South Kern, Spruce Mountain, and the Blythe Springs once-chained plot, the treated plots primarily increased in overstory cover, occupying a range of understory cover similar to that of 1971. The second chaining at the Blythe Springs plots caused the understory to increase in cover while the range of overstory cover values remained constant. Chaining twice further delayed movement down the curve toward overstory dominance.

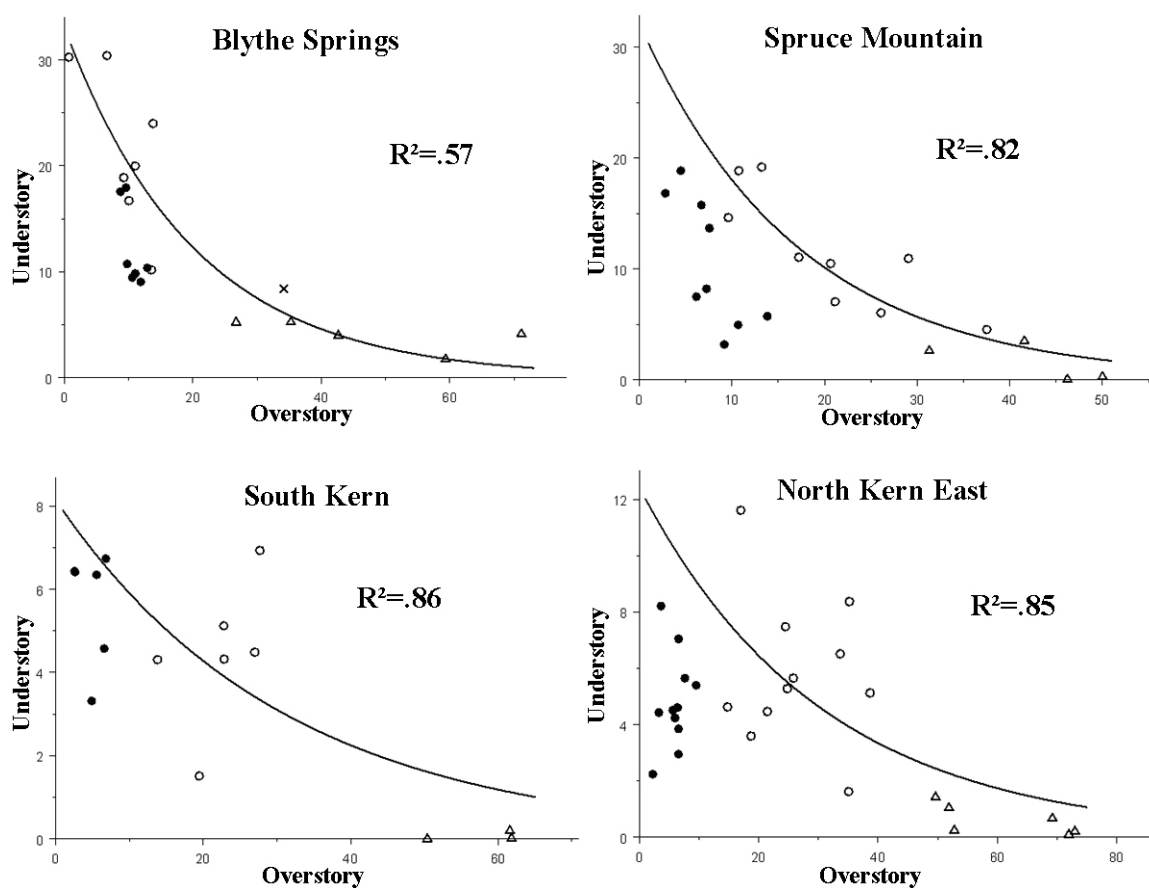


Figure 13. Graphs of understory and overstory curves for the chaining sites. Lines were fit with the open circles (2008 treatment data) and the open triangles (2008 control plot data). Closed circles represent the 1971 treatment plot data, which were not used to fit the curves. The X symbol in the Blythe Springs graph is the 2008 once-chained plot.

	<i>a</i>	<i>b</i>
Blythe Spring	33.0514	0.0495
Spruce Mountain	32.1322	0.0578
North Kern East	12.4177	0.0329
South Kern	8.1492	0.0322

Table 6. Parameter estimates of the fit curves for each of the chaining sites.

Overstory-understory curves for chaining sites vary in slope (*b*) and intercept (*a*) with site productivity for sagebrush. The most productive sagebrush sites (Blythe Springs and Spruce Mountain) have the highest *a* values and support the greatest amount of understory with low overstory cover (Table 6, Fig. 14). At Spruce Mountain and

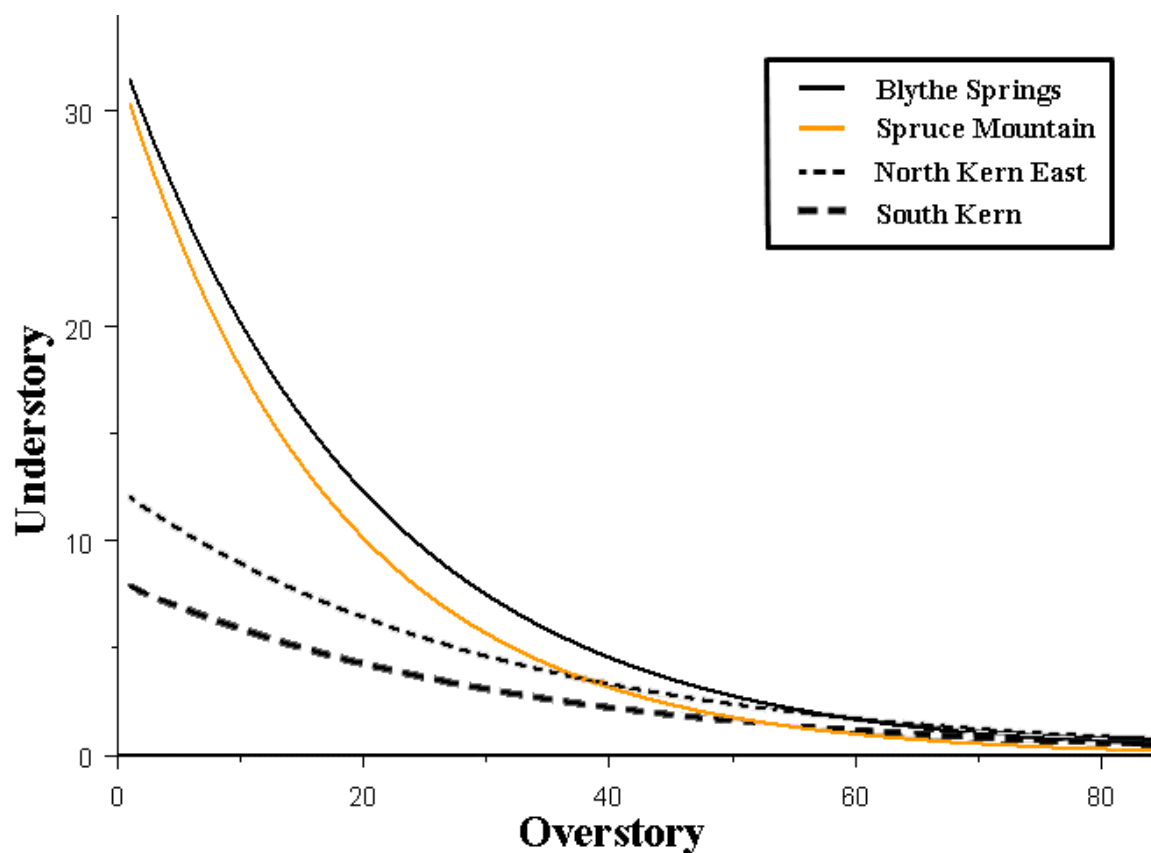


Figure 14. Overstory-understory curves for the chaining sites. Curves were taken from the 2008 and control plot data in Figure 12.

Blythe Springs, shrub cover was higher and herbaceous cover was lower than at North Kern East and South Kern (Fig. 10; Appendix I, Table ii).

The soil depth and soil percent coarse fragment variables appeared most frequently and were most important in the models for predicting tree cover increases in chaining sites. The best linear mixed effects (LME) model produced an Akaike weight (w_i) of 0.363 and nine other models were reported because they produced AIC_c scores within 7 of the best model ($\Delta_i \leq 7$) (Table 7). The average soil depth and percent coarse soil fragment variables appeared in all four models with substantial support ($\Delta_i \leq 3$) and they produced the highest Akaike weights (w_+) (Table 7) (Table 8). The other variables

	Nagelkerke R ²	AIC _c Score	Δ_i	w_i
- depth - TCI - coarse	0.47	158.74	0.00	0.363
- depth - TCI - coarse - years	0.48	159.89	1.15	0.204
- depth - coarse	0.38	160.63	1.89	0.141
- depth - coarse + years	0.40	161.56	2.82	0.089
- depth - TCI	0.33	162.34	3.60	0.060
- depth - TCI - years	0.36	163.04	4.30	0.042
- coarse - years	0.30	163.32	4.58	0.037
- depth - TCI - coarse - years + fine	0.45	163.37	4.63	0.036
- depth - coarse + fine	0.34	163.85	5.11	0.028

Table 7. The nine best LME models for describing percent increase in tree cover between 1971 and 2008. Depth = soil depth, TCI = topographic convergence index, coarse = soil % coarse fragment, years = time since disturbance, fine = soil % fine fragment.

Variable	Effect	
	w_+	Direction
depth	0.963	-
coarse	0.898	-
TCI	0.705	-
years	0.408	-
fine	0.064	+

Table 8. Akaike weights and effect directions of the 5 most important variables.

appearing in the most supported models include, in order of decreasing weight: mean topographic convergence index, number of years between treatment and first sampling, and percent fine soils. Soil depth and coarse fragment had the only two significant coefficients ($P < 0.01$ and $P = 0.02$, respectively) (Appendix I, Table iii).

Discussion

Effect of Treatment Type on 2008 Plant Community Composition

Although an important process in defining woodland distribution, natural fire regimes in the highly diverse landscapes of the Great Basin are difficult to reconstruct and remain ambiguous (Miller and Tausch 2001, Baker and Shinneman 2004). Fire rotations are believed to have been highly variable and can be longer than 400 years (Baker and Shinneman 2004, Bauer and Weisberg 2009). When fires occur in fuel-rich persistent woodlands they tend to kill or top-kill all the trees and shrubs present (Baker and Shinneman 2004, Romme et al. 2009). This pattern was evident at the burned sites in this study. The burned site observations and cover data revealed huge increases in understory cover and virtually no tree recovery over a 33-year period.

Changes in long-term vegetation composition following chaining were dissimilar to those following prescribed fire, but may resemble compositional changes resulting from other Great Basin disturbances. Pinyon and juniper woodland distribution and density are likely regulated by complex interactions of multiple disturbance types (Romme et al. 2009). In many persistent pinyon and juniper woodlands minor disturbances of insects, disease, and meteorological events are more prevalent in driving

stand dynamics than any major disturbance such as fire (Romme et al. 2009). As with chaining, tree recovery and resumption of full site resource utilization will be rapid following these types of disturbances. Large mature pinyons are most susceptible to severe drought mortality and pinyon Ips (*Ips confusus*), and are also most likely to be killed by chaining (Mueller et al. 2005, Greenwood and Weisberg 2008). In extreme cases, these natural disturbances will cause tree mortality at a magnitude that is comparable to that reported for chaining treatments (Tausch 1973, Mueller et al. 2005).

At Blythe Springs, the examination of tree cover alone might suggest that chaining woodland twice results in vegetation type composition that is intermediate to chaining and burning. However, understory composition varied greatly between the two treatment types. Diverse shrub and grass communities were pervasive 33 years after burning the prescribed fire sites. Extremely dense shrub cover with virtually no herbaceous component dominated the understory 23 years after the second chaining at Blythe Springs. The considerable reduction of trees from the first treatment, and the potentially ample seed source with high cover of shrubs prior to the second treatment, may have altered the site conditions to be conducive to the quick establishment of a closed canopy shrubland (Tausch 1973).

Although calculated differences between chaining and prescribed fire treatments were immense and highly significant, plots were not true replicates and the analysis is subject to a variety of confounding factors. The method used by managers to select treatment sites could have contributed to the greater understory cover and lower tree cover measured at prescribed fire sites. The prescribed fire sites were selected for deep

productive soils with high potential to produce shrub-bunchgrass communities and dry meadows (Bruner and Klebenow 1979), whereas the chaining treatment sites were selected for maximum conversion area, which was limited by the type of terrain suitable for D-8 Caterpillars (Tausch 1973). Future comparisons of differences in long-term vegetation response to chaining and burning treatments should implement the use of paired plots within paired treatments to reduce confounding factors. A design of adjacent control, burn, and mechanical treatments such as that utilized by the Joint Fire Sciences SageSTEP would be ideal for long-term monitoring (McIver et al. 2005).

Increasing Woody Species Cover over Time

Changes in Tree Cover

At all treated sites, there was significantly more woody plant cover in 2008 than at the time of the initial sampling. It was expected that tree cover at chaining sites would increase at a rapid rate. The earlier study (Tausch 1973) predicted a more rapid rate of tree recovery at the chaining sites than what was observed by 2008. Tausch (1973) used a series of prediction equations based on annual basal diameter growth from Blythe Springs to estimate that the South Kern and North Kern East sites would have 20.4 and 28.6 percent tree cover respectively by the year 1984. While the tree recovery at those sites has been rapid, the cover at the South Kern and North Kern East sites had not yet reached those levels by 2008, having 17.1 and 23.2 percent tree cover respectively. The overestimation of regrowth by Tausch and Tueller's (1977) prediction equations appears related to calculating them based on the early growth release and did not account for a

more gradual reduction of growth once the resources released by treatment were fully utilized.

The large increases in tree cover at control sites adjacent to chainings were surprising, being of similar to or greater magnitude than the treatment sites. Pinyon and juniper have increased in density in many other sites throughout the Great Basin (Bauer 2006, Weisberg et al. 2007, Romme et al. 2009). Juvenile trees usually exhibit the most rapid growth (Barney and Frishnecht 1974, Miller and Tausch 2001). For the control tree cover to have increased at such a rapid rate, it is likely the result of a surge of tree establishment occurring in the early 20th century (Miller et al. 2008). By mid-century, a cohort of juvenile trees were primed for accelerated growth beginning shortly before initial sampling in 1971. The phenomenon of tree canopy growth in adjacent untreated areas is clearly evident in the backgrounds of the photo pairs for Blythe Springs and North Kern East (Fig. 15). This infilling has implications for the rate and extent of fuel load increases across Great Basin woodlands.

Tree recovery in treatment plots was slower at sites described as mature closed or old growth at the time of treatment. Tausch (1973) reported that the North Kern East site represented expansion woodland with a high density of young to mature trees, which had only just reached canopy closure before treatment. In contrast, almost the entire South Kern chaining could be described as old closed canopy woodland, nearly devoid of understory at the time of chaining (Tausch 1973). Although Tausch's cover data indicated similar tree cover at the two sites in 1971, the tree density at North Kern East was nearly twice the density at South Kern. The primarily old growth site responded less

vigorously than the neighboring mixed young tree site indicating that younger expansion trees are likely to have higher survival of the treatment and then recover at an accelerated rate. The Spruce Mountain plots spanned a range of expansion and old closed woodland stands. This site demonstrated tree recovery intermediate to the old growth and young expansion site (Tausch 1973).

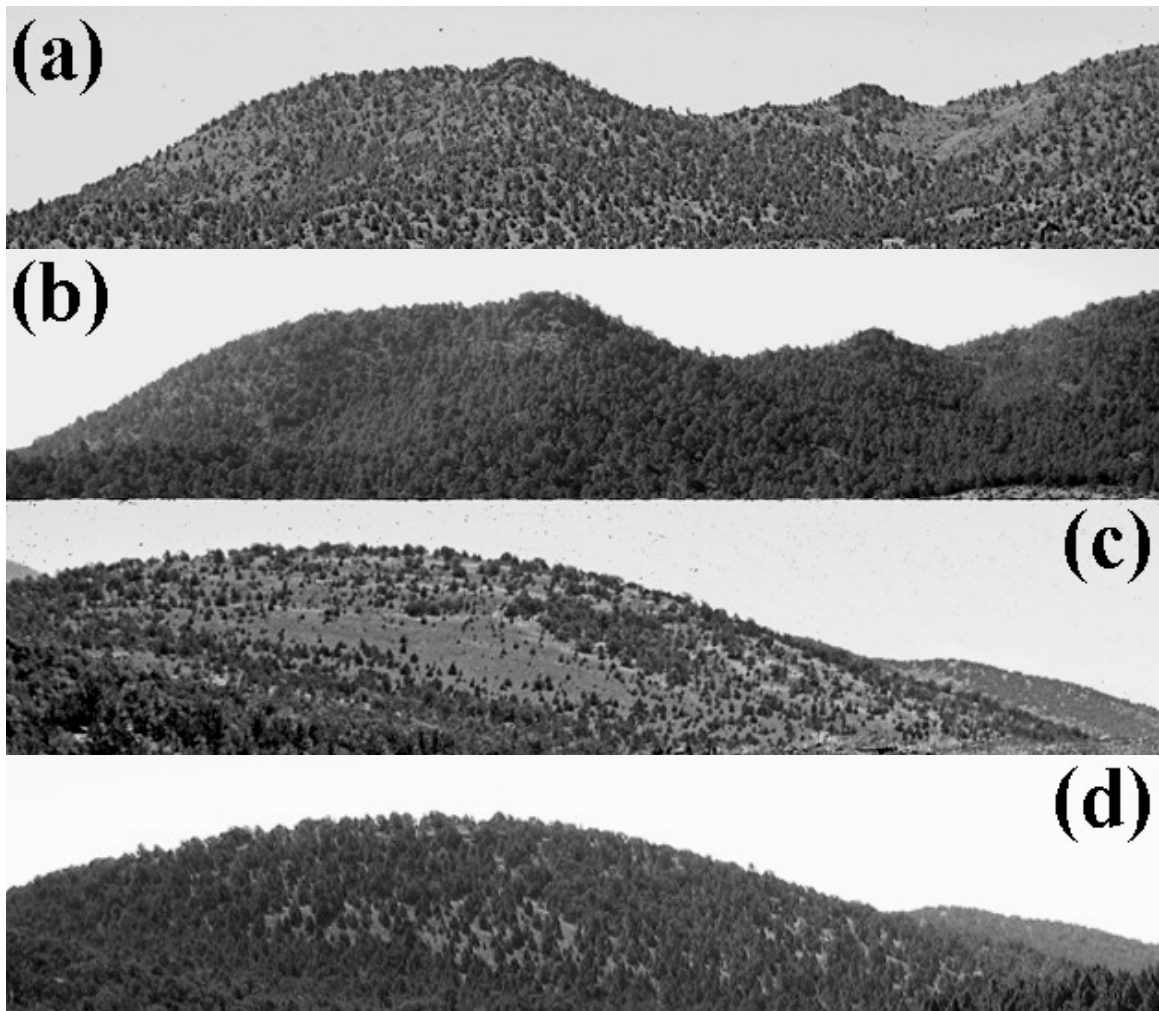


Figure 15. Increasing tree cover in adjacent untreated woodlands from photo pairs of Blythe Springs 1971 (a) and 2008 (b) and North Kern East 1971 (c) and 2008 (d). Extracted and blown up from Figures 4 and 6.

Although unreplicated, the Blythe Springs once-chained treatment plot represented the most extreme case of tree recovery. The tree cover increase not only

exceeded the Blythe Springs twice-chained plots by 25 percentage points, but also was about 10 percentage points higher than the average percent tree cover of the treated North Kern East plots. Intensity of treatment and time since treatment were likely two factors that influenced the relatively quick recovery of woodland. The first Blythe Springs chaining was conducted longest ago (1958), using a 19-lb link smooth chain, and it was chained in only one direction. The 19-lb link chain was the lightest used on all of the sites in this study. This likely resulted in high tree survivorship and high post-treatment tree densities (Tausch 1973).

At prescribed fire sites, shrubs were the dominant woody species. The robust increase in shrub cover and scarcity of trees at burned sites suggests multiple decades are required for burned sites to return to woodland. The prolonged recovery of pinyon and juniper after fire is the basis for proposed fire return intervals of a few centuries in persistent woodlands (Baker and Shinneman 2004, Romme et al. 2009). If fires were occurring more frequently than pinyon and juniper could recover, the area would be dominated by other plant species (Baker and Shinneman 2004).

Species Compositional Shifts within Sites

Species composition on chaining sites converged to a less variable plant community composed of trees, shrubs, and shade tolerant grasses (Fig. 12). At all the chaining sites, the plots differed in the relative amount of tree and sagebrush cover at initial sampling due to differing local mortality caused by the chain. At sites that were initially sampled within a year or two of treatment, a high diversity of forbs existed that

did not persist to 2008. Germination of seeded grasses also varied by plot at most sites and caused further divergence. By the second sampling the plots all had converged on more similar communities dominated heavily by trees and sagebrush, with some native grasses that were common to most of the plots. Changes in composition are oversimplified when represented by data from only two points in time (Fig. 12) and trajectories of change would likely have been nonlinear if fit with data from multiple sampling years.

Chained Site Resource Utilization Curves

The resource utilization curves have value for predicting understory response to increasing overstory cover at treated sites that are now undergoing succession. Creating productive, diverse, and persistent understory communities is a common justification for treatment of pinyon and juniper woodlands (Tausch 1973, Ward 1977). The shapes of the curves and the parameters provide information about understory resource partitioning, site potential for understory response to treatment, and eventual understory sensitivity to increases in overstory cover. Sites with high values of parameter a have high potential for an understory growth response and high values of parameter b indicate high understory sensitivity to increasing tree cover. Chainings are more likely to produce a vigorous understory that persists for a relatively long time on sites where parameter a is high and parameter b is low.

High values of parameter a may not co-occur with low values of parameter b for Great Basin woodland vegetation. In this study, sites that could support dense shrub

cover with low or absent overstory cover had high values of a , while sites with low shrub and high cover of seeded grasses had low values of a (Table 6, Fig. 10, Fig. 14). Shrub cover declines greatly with slight increases in tree cover and consequently high values of a will most often occur with high values of b in pinyon and juniper woodlands (Tausch and West 1995, Miller et al. 2000). At sites not productive for shrub growth, where grasses dominate the understory vegetation, understory cover is generally lower than at shrub-dominated sites. Consequently, a will be lower where grasses are dominant. Some grass species are less sensitive to tree cover than shrubs and will persist for longer with increasing overstory cover. Thus grass-dominated composition will likely exhibit low values of b . It is possible that parameters a and b are often inversely related.

Environmental Effects on Tree Recovery at Chaining Sites

Soil depth and percent coarse fragment were the most important variables for determining the magnitude of tree cover at chaining sites. Tree cover increased the most between 1971 and 2008 at sites with the least coarse and most shallow soil. Coarser soils generally have lower potential for holding soil moisture and sites with coarse soil will often have low cover of sagebrush and other understory species (Burkhardt and Tisdale 1969). It is possible that denser vegetation existed on plots with finer soils. As a result chaining removed more competitors on finer soils that were exploiting soil moisture required for the growth of small surviving trees. Heavier competition with sagebrush and existing mature trees before chaining may have suppressed tree growth in seedlings and saplings less than 6 feet tall on sites with finer-textured soil.

The strong relationship between shallow soil and greater tree growth and recovery was not expected. Pinyon and juniper are capable of growth and survival on a variety of soil depths, with older stands existing on shallow soils of ridges and knolls, while newer stands also thrive on deeper well-drained soils (Burkhardt and Tisdale 1976, Miller and Rose 1999, Miller and Tausch 2001). The soil depth variable could be a measure of competition confinement (Miller et al. 2000). While most pinyon and juniper roots are found in the upper layers of the soil, these species are capable of rooting more deeply than sagebrush and other shrub competitors (Burkhardt and Tisdale 1976, Peek et al. 2006). In shallow soils they would be confined to sharing root space and competing heavily with the surrounding shrubs and mature trees. Miller and others (2000) found that competition with mature trees above a 45-cm restrictive soil layer was much more detrimental to understory herbaceous species than on deep well-drained soils. Tree seedlings and juveniles are also subject to increased competition in restrictive soils and would experience the greatest growth release once the suppressive mature trees and shrubs were removed.

Implications for Management

Common goals of rangeland management in the Great Basin include maintenance of sagebrush-dominated communities in areas recently invaded by trees, to reduce fuel loading, and maintain potential habitat for sagebrush obligate species. Results of this study indicate that prescribed fire more completely removes the overstory, allowing a prolonged persistence of sagebrush and other understory vegetation. The effects of

chaining on expansion woodland sites are short-lived in comparison. As a disturbance, chaining is more similar to natural disturbances such as drought and insect attack than to fire because the preservation of small trees during chaining causes relatively rapid stand regeneration.

Another major concern of woodland managers is increased fuel loading as a result of extensive tree densification in persistent woodlands. Infilling sometimes occurs in less favorable microsites when favorable microsites are already occupied and consequently infilling trees are more susceptible to drought (Greenwood and Weisberg 2008).

Drought, insect outbreaks, and heartrot events are responsible for much of the tree mortality in persistent woodlands and these disturbances can leave a multitude of dry, flammable, dead trees in their wake (Knapp and Soule 1999, Mueller et al. 2005, Soule and Knapp 2007, Greenwood and Weisberg 2008). Untreated woodland tree cover was significantly greater than absolute tree cover of chained woodland. Untreated areas had become quite dense while chained areas exhibited less than half the tree cover, indicating that chaining did successfully reduce fuel loads on the sites. The chaining sites have limited and diminishing understory cover, but if fuel reduction is the major management goal, chaining without retreatment was able to keep fuel loads lower than at control sites for 46 years after treatment.

Managers must consider a series of tradeoffs that hinge primarily on biological legacy effects when choosing a site to chain or otherwise treat using mechanical means. Plant community composition and degree of competition at the time of initial treatment are considerations most important to predicting the resulting vegetation. This

observational study suggests that small surviving trees will have the greatest growth response to overstory removal and tree cover will recover most quickly at sites with shallower, more finely textured soil. Soil depth and soil texture are relatively easy to measure and can provide insight into rates of vegetation change following treatment.

Treatment of old growth woodland should be avoided and not included in management plans because of the low understory response, despite the high likelihood of tree mortality. Old closed stands of woodland also have an important ecological role for a diverse array of animals in the Great Basin (Waichler et al. 2001) and native early seral plants do not respond well once the overstory has been removed (Tausch 1973, Condon 2007). The results of this study suggest that treatments should be confined to open and expansion woodlands. In open and expansion woodlands the chaining treatment can provide a brief period of early seral vegetation dominance that lasts at most about 15 years due to advance regeneration and accelerated succession of young trees. A follow up chaining treatment or a prescribed fire would be necessary to maintain open conditions. By contrast, prescribed burning created early seral communities that have persisted for 33 years, and where stand closure will likely not occur for another 30 to 60 years (Barney and Frischknecht 1974).

Prescribed fire has a more lasting tree removal effect relative to chaining but the trade off is increasing the site's susceptibility to cheatgrass invasion. Cheatgrass was not the focus of this study, but the results indicated that by 2008 little or no cheatgrass existed at the chaining sites (Figure 10, Table 5, Appendix I, Table ii). However, cheatgrass cover increased at the prescribed burns, despite Ward (1977) not reporting any

cheatgrass presence in the year prior to or the year following burning. Although burning might produce the desired effect in regard to reduction of tree dominance, there is a risk of facilitating conversion of native understory species to a cheatgrass dominated community.

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Chapter 2: Tree Establishment Following Chaining and Prescribed Fire Treatments in Singleleaf Pinyon and Utah Juniper Woodlands

Abstract

Treatments of prescribed fire and chaining are widely applied across the Great Basin in an effort to reduce pinyon and juniper cover and stimulate understory growth. Treatment efforts often result in altered woodland structure relative to untreated areas. Analysis of post-treatment tree age structures helps us to understand species-specific processes of tree survivorship and establishment. Tree age data were collected at plots within four chaining sites treated in 1958, 1962, 1968, and 1969 and originally sampled in 1971. The same data were collected at five prescribed burn sites treated in 1975 and originally sampled in 1976. Tree-ring data indicate that all chaining sites had greater juniper survival than pinyon survival. Chaining sites with higher tree survival following treatment also had the greatest amount of new tree establishment. During the interval between treatment and 2008 sampling, approximately four more pinyon and juniper trees $\text{ha}^{-1} \text{y}^{-1}$ established following chaining than following fire. At prescribed fire sites, initial post-treatment establishment was dominated by juniper, but neither tree species established beyond 15 years after treatment. Tree establishment transitioned from being dominated by juniper for the first 15 years, to primarily pinyon between 15 to 40 years following chaining. The greatest density of newly established trees occurred in control (untreated) plots, indicating prescribed fire and chaining treatments decreased tree establishment. Results support an earlier successional role for juniper than pinyon, which

is more dependent upon favorable microsites and facilitation from nurse shrubs. Long-term effects of chaining treatment will likely lead to eventual dominance of pinyon. Prescribed fires at relatively infrequent intervals may favor dominance of juniper over pinyon.

Introduction

Since the mid-twentieth century, treatments of prescribed fire and chaining have been widely applied across the Great Basin, with few plans for long-term monitoring. Reduction of tree dominance and enhancement of extent and diversity of understory species have been stated goals of such activities (Tausch 1973, Ward 1977). In the short-term, chaining and prescribed fire treatments successfully reduce tree dominance and stimulate understory growth (Tausch and Tueller 1977, Everett and Ward 1984). However, because sites typically are not retreated, surviving trees quickly grow and new trees establish when site conditions are suitable (Tausch and Tueller 1977, Chambers 2001). Follow-up measurements of treatment effects on tree re-establishment have been rare, but are necessary for evaluating long-term effects of treatments on tree recovery rates and stand composition. The post-treatment environments differ greatly for prescribed fires and chainings, which could potentially affect rates of new tree establishment.

A set of mechanisms identified as important for both pinyon and juniper establishment may be affected by the dissimilar environmental conditions created by treatments of prescribed fire and chaining (Table 1). Seed availability is a factor that

differs in the post-treatment environments of prescribed fires and chainings, which may contribute to different rates of tree establishment. Tree mortality can be higher at prescribed fires than at chainings, which can cause fewer mature trees to exist within burned sites than within chaining sites (Tausch 1973, Ward 1977). Most surviving trees at chainings are small, young, flexible trees, but are also potential seed sources (Tasuch 1973). More seed-producing trees are likely to be present at chaining sites than at prescribed fire sites (Table 1).

Mechanism	Burn	Chaining
Seed source	-	+
Seed dispersal	+	-
Availability of safe sites	-	+
Seed predation	-	+
Competition	+	-

Table 1. Expected effects of prescribed fire and chaining treatments on proposed important mechanisms of establishment. + indicates greater relative to the other treatment and - indicates less.

For seed availability, however, the presence of seed-producing trees may not be as important as dispersal by rodents and birds. Temperature and moisture requirements of seedlings cause emergence to be greatest when seeds are buried between one and three cm (Chambers 2001). Therefore caching by rodents and corvids (nutcrackers and jays) plays an important role in depositing seed at necessary depths for germination (Vander Wall and Balda 1977, Vander Wall 1997). Birds, which cache and disperse a majority of pinyon and juniper seed, can act as effective seed dispersal agents over distances as far as 10 km (Chambers et al. 1999). The interiors of all the treatments studied were well within 5 km of the treatment perimeters, and could therefore be reached by birds and

rodents caching seed from mature trees outside the treated area. Seed dispersal likely occurred at both chainings and prescribed fires, but because the fires studied were much smaller in extent than the chainings, it is possible that more seed was cached in the interiors of the prescribed fires (Table 1).

In addition to seed availability, seedling germination and survival are also important components of tree establishment. Chaining produces a unique environment that may be beneficial to pinyon and juniper seed germination and seedling survival. The first few years following chaining have reduced availability of biotic safe sites because the treatment causes high shrub mortality (Tausch 1973). Nurse plants facilitate tree establishment in the Great Basin, with the greatest emergence occurring under shrubs (Callaway et al. 1996, Chambers 2001). After chaining, few shrub safe sites persist but occasional slash piles composed of coarse woody debris may serve as surrogate safe sites. Slash piles vary in size and composition, but may provide the shading, cooling, and moisture necessary for seedling survival (Jotham Berger, unpublished data).

Prescribed fire likely creates a harsher environment for tree germination and survival than chainings (Table 1). Prescribed fire and chaining can cause varying vegetation mortality depending on treatment intensity, but prescribed fire is often capable of achieving higher mortality than chaining (Tausch 1973, Ward 1977). Fire can remove all of the sagebrush from a site (Ward 1977), leaving a small number of scattered resprouting shrubs as potential safe sites for tree seedlings. The potentially hot, dry, environment created by fire has only sparse sources of shade, which is necessary for the moisture and temperature requirements of tree establishment.

Differential seed predation may also affect seed and seedling survival at treatments. Cache retrieval and predation on seedlings can cause mortality as high as 74 percent (Chambers 2001). Some evidence indicates cache retrieval and cache pilfering by rodents is lower when ash is present due to some loss of olfaction (Briggs and Vander Wall 2004). Lower cache retrieval and seed predation could contribute to greater seed survivorship at prescribed fire sites (Table 1).

Prescribed fire sites may also be poor biotic environments for tree establishment as a result of competition. Competition from early herbaceous colonizers may directly or indirectly restrict tree establishment. Grasses and forbs respond vigorously to the flux of newly available resources released by the fire (Ward 1977). Grasses do not provide the cool and moist microsite conditions required by tree seedlings and may compete with tree seedlings for shallow soil resources. Forbs and grasses may also indirectly reduce seedling germination and survival by competing with and delaying recruitment of potential nurse shrubs. Grass and forb cover was much higher at the prescribed fires than at the chainings, creating greater potential for competition with tree seedlings (Table 1) (Tausch 1973, Ward 1977).

The post-treatment environmental conditions of prescribed fires and chainings may also cause differential species establishment of pinyon and juniper, resulting from species-specific life history traits. Life history traits of pinyon and juniper suggest that each species responds to and recovers from disturbances or woodland treatments in different fashions (Table 2). Tree survivorship, type of mycorrhizal association, duration of seed viability, dispersal distance, sensitivity to drought, and dependence on facilitation

are all species-specific factors that may influence relative establishment of pinyon and juniper after treatment.

Life History Trait	Pinyon	Juniper
Mortality from disturbance	+	-
Type of mycorrhizae symbiont	EM	AM
Duration of seed viability	-	+
Dependence on nurse shrub facilitation	+	-
Drought sensitivity	+	-

Table 2. Life history traits of pinyon and juniper expected to affect establishment after chaining and prescribed fire. + indicates greater relative to the other species, - indicates less than the other species, AM indicates arbuscular mycorrhizal fungi, and EM indicates ectomycorrhizal fungi.

Juniper exhibits greater survivorship than pinyon for most disturbances in the Great Basin, which partially contributes to initial dominance of juniper following disturbance (Table 2). Higher juniper survivorship has been documented for fire, drought, and insect outbreaks (Tausch and West 1988, Mueller et al. 2005, Greenwood and Weisberg 2008). Due to relatively high stem flexibility, juniper has been reported to experience lower mortality than pinyon from mechanical disturbance, such as chaining (Tausch 1973). Because juniper is more likely to survive disturbance, more mature juniper trees will be present and producing seed at chaining sites.

Greater mortality of pinyon at chaining and prescribed fire sites may also cause less mycorrhizal fungi to be available for pinyon root inoculation. Mycorrhizal fungi form associations with fine roots of plants to improve uptake of water and nutrients. The benefits of symbiosis for capitalizing on available soil moisture can be critical for germination (Haskins and Gehrig 2004). Pinyon pine forms associations with ectomycorrhizal (EM) fungi, but juniper and most other Great Basin plant species are

hosts of arbuscular mycorrhizal (AM) fungi. High tree mortality can reduce EM availability for pinyon seedling root inoculation (Neary et al. 1999, Swaty et al. 2004, Hart et al. 2005, Hubert and Gehrig 2008). Complete pinyon tree mortality and soil exposure to heat occurred at prescribed fire sites (Ward 1977), which may delay pinyon reestablishment. High pinyon tree mortality relative to juniper mortality occurred at chaining treatments (Tausch 1973), which could decrease EM availability at chaining sites as well (Table 2). EM inoculation of germinating pinyon roots occurs 6 times less frequently and extent of root inoculation is more reduced in juniper-dominated zones than in pinyon-dominated zones (Haskins and Gehrig 2004).

The vast majority of understory plants in the Great Basin form associations with AM fungi, and as a result, there is higher probability of AM fungi being available for juniper inoculation in the soil after treatment (Haskins and Gehrig 2005). Many early seral plant species form associations with AM fungi that are also capable of inoculating juniper roots and provide a mycorrhizae reservoir (Haskins and Gehrig 2005). The short-term studies indicated that a host of understory species had returned to treated sites in the first 13 years (Tausch and Tueller 1977, Everett and Ward 1984). The AM forming associations with early seral plants at prescribed fires may provide juniper seedlings a benefit not available to pinyon seedlings. With few other plant species providing EM reservoirs, pinyon roots are less likely to be inoculated (Haskins and Gehrig 2004, Hubert and Gehrig 2008). Pinyon seedlings probably only survive in years of high moisture without mycorrhizal root inoculation, when water uptake efficiency is less critical.

At burned sites, where few mature trees survived within the burned area, viable seed availability was likely another important difference between the pinyon and juniper species. Juniper seed remains viable for up to several years, whereas pinyon seed viability decreases greatly after only one year (Johnsen 1959, Chambers et al. 1999). If fire intensity was not great enough to kill seed in the seed bank, the greater longevity of juniper seed viability would be advantageous for establishment (Table 2).

Post-disturbance tree establishment in the Central Great Basin also differs for the two species because juniper is less dependent upon favorable microsites and nurse shrub facilitation than pinyon (Table 2). Following fire, juniper establishes initially within the first five to 55 years and pinyon arrives later, particularly once a shrub layer has developed (Barney and Frischknecht 1974, Everett and Ward 1984, Tausch and West 1988, Bauer 2006). For mid-elevation woodlands, pinyon density can be greater than juniper density by 60 years after fire. Pinyon can, depending on site conditions, also continue to increase in density over the next century, eventually dominating the stand (Tausch and West 1988).

Because water is often limiting in semi-arid ecosystems, many previously described mechanisms are related in some way to the ability of pinyon and juniper seedlings to acquire water after chaining and prescribed fire treatments (Fowler 1986). It is possible that climate, and specifically drought, can override the effects of the other proposed mechanisms. Mature pinyons have exhibited the highest susceptibility to mortality from drought (Mueller et al. 2005). Other studies have shown that juniper has lower levels of water stress when water is plentiful, juniper has greater capability to

tolerate water stress, and juniper is better able to extract water from canopy interspaces (Barnes and Cunningham 1987, Breshears et al. 1997, Nowak et al. 1999). Under drought conditions, juniper seedlings are more likely to germinate and survive than pinyon seedlings at both treatment types (Table 2).

Differential effects of chaining and prescribed fire treatments on site environment will influence relative species establishment and eventual species composition of the stand. The objective of this study was to use tree-ring analysis to evaluate effects of treatment on density and relative dominance of establishing pinyon and juniper trees 33 years after burning on five prescribed fires in one location and 39 to 50 years after chaining at four locations. The study was designed to address the following questions:

- 1) Do chaining treatments provide a more suitable environment for new tree establishment than burning treatments?
- 2) Does greater juniper establishment occur at burned sites?
- 3) Does greater pinyon establishment occur at chaining sites?

Methods

Data Collection

At each site location originally sampled by Tausch in 1971 (Tausch 1973) or Ward in 1976 (Ward 1977), one to eleven 0.1-ha macroplots were resampled for tree age data. The original investigators used a stratified random sampling design to determine macroplot placement. At each macroplot, tree diameter data were collected from every tree and age data were taken from a random subsample of 24 trees within a 0.1-ha

subplot. Trees with basal diameters larger than eight cm were cored as close as possible to the root collar using an increment borer. At least two cores were taken for each tree. Measurements of coring height above root collar and trunk diameter at coring height were recorded for each sample collected. For trees smaller than eight cm in basal diameter, a cross section was removed just above the root collar.

Increment core samples were processed using standard dendrochronological techniques after sanding using progressively finer grits until tracheids were clearly visible (Stokes and Smiley 1968). Tree ages were adjusted for coring height above root collar using an empirical age-height relationship developed from a destructive sampling of pinyon seedlings and saplings (Bauer and Weisberg 2009):

$$\text{Age Correction} = 24.60 + 0.218 * \text{CH (cm)}$$

where CH is coring height. Age adjustments for cores that miss tree pith used an empirical relationship based on early growth response of singleleaf pinyon, after estimating distance to pith using the concentric circle method (Appelquist 1958, Bauer 2006). Three researchers independently counted and crosschecked every core, and all discrepancies were resolved by recounting until a consensus was reached regarding tree age. Cores were counted to year of establishment for trees that germinated after treatment.

Data Analysis

Increment cores were not consistently taken from root collars and cross-dating was not possible due to complacent rings and relatively short tree-ring chronologies.

Therefore, dates of establishment for tree cores taken from older, larger trees lacked annual precision, but most discrepancies were within three years. Dates of establishment were more likely annually precise for younger, smaller trees from which cross sections were taken. Age structures of the 0.10-ha plots were examined using frequency histograms aggregated to one-year and five-year bins. Mean rates of pinyon and juniper tree establishment (trees $\text{ha}^{-1} \text{y}^{-1}$) were compared between chaining and burning treatment types. Fixed effects ANOVA was used to determine if tree establishment rates for both species, and each species separately, were significantly different between treatments. Because trees were not cored in control plots, stand basal diameter size structures were compared between treatment and control plots. Changes in tree density between 1971 and 2008 were also examined for control and treated plots.

Results

Relative rates of tree establishment differed among treatment types ($F_{1,7} = 5.5$, $p = 0.052$) (Table 3). Over both species, almost four more trees $\text{ha}^{-1} \text{y}^{-1}$ established following chaining than following fire. This effect was primarily due to pinyon establishing at a rate averaging more than 3 trees $\text{ha}^{-1} \text{y}^{-1}$ greater after chaining than after fire ($p = 0.021$). Juniper establishment did not significantly differ among treatments (Table 3).

At chaining sites, both the number of pinyon and juniper trees having established before and surviving chaining and the chronological pattern of post-treatment establishment varied. Because it was chained twice, Blythe Springs had the lowest density of surviving trees that established prior to the first chaining (Fig. 1). At Spruce

	Chaining	SE	Fire	SE	Difference	P Value
Both	5.8609	1.5568	2.0556	0.7732	3.8053	0.0516
Pinyon	3.9045	1.2054	0.6162	0.2850	3.2883	0.0208
Juniper	1.9564	0.4701	1.4394	0.5688	0.5170	0.5213

Table 3. Mean number of trees establishing per hectare per year and fixed effects ANOVA results for prescribed fire (n = 5) and chaining (n = 4) treatments on post treatment pinyon and juniper establishment.

Mountain and South Kern, where chaining only occurred once, close to twice as many surviving trees per hectare had established before treatment than at Blythe Springs (Fig.

1). The current number of surviving trees per hectare at North Kern East, which was also chained only once, is greater than 3 times that of Blythe Springs and nearly twice that of

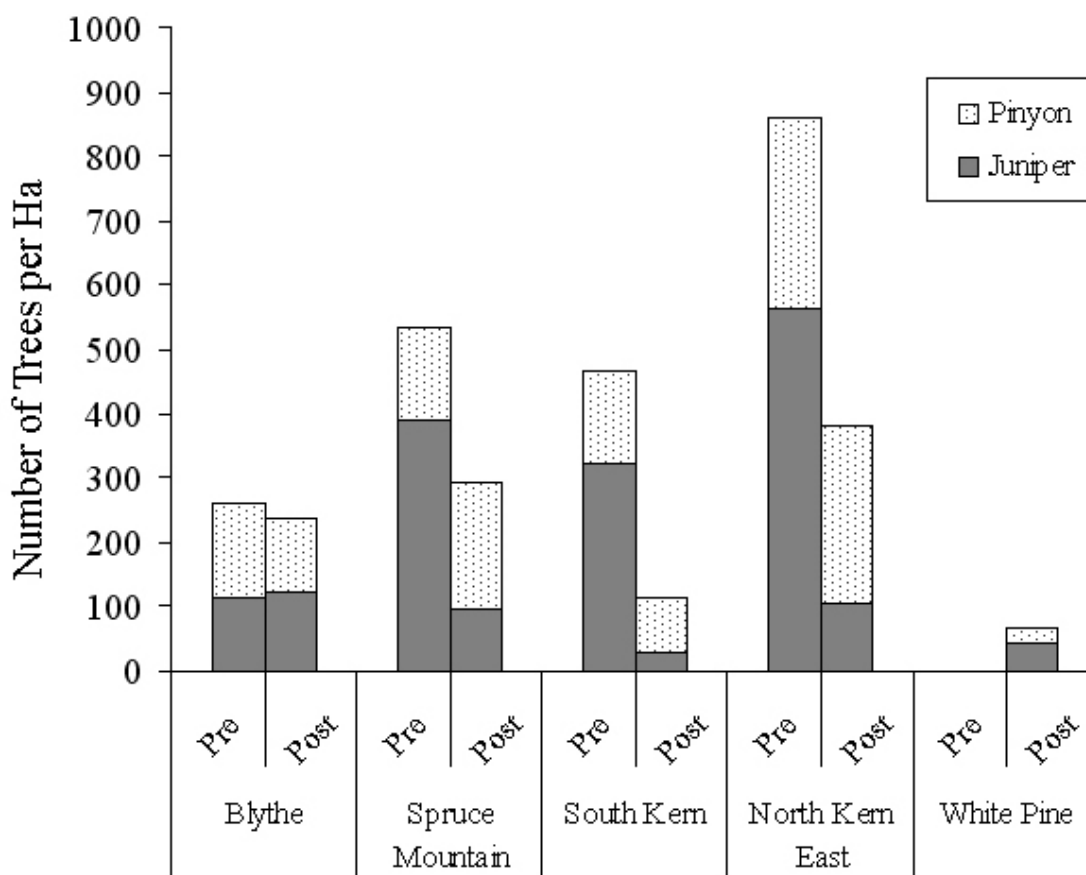


Figure 1. Number of trees established before and surviving treatment (left; pre) and number of trees established after treatment (right; post) for five sites in Eastern Nevada.

the other two sites (Fig. 1). Spruce Mountain, South Kern, and North Kern East had greater densities of surviving juniper than pinyon, but greater pinyon establishment after treatment.

Relatively high rates of tree establishment occurred immediately following treatment at all sites. Juniper establishment was high initially but diminished with time (Fig. 2). Possibly due to the second chaining, establishment at Blythe Springs during the first five years after the 1958 chaining was not greater than any of the following five-year intervals. Trees that germinated after chaining in 1958 may have died during the 1985 chaining, with the earliest germinating (oldest) trees being most susceptible to mortality (Tausch 1973). A small surge of establishment coincided with the second chaining, but quickly dropped to low levels over the next 15 years (Fig. 2). No juniper and very little pinyon establishment occurred between 1998 and 2003. No trees established in the last five years prior to sampling in 2008.

In general, tree establishment at South Kern was very low after chaining, although slightly more juniper established in the first 15 years following treatment than in the last 25 years before sampling (Fig. 2). The same pattern is more evident for Spruce Mountain and North Kern East. Juniper establishment was greater than pinyon establishment during the first 10 years following chaining but dwindled after 15 years (Fig. 3). Pinyon establishment has been much greater than juniper establishment at both sites for the last 30 years, beginning 20 years after chaining (Fig. 2, Fig. 3).

In contrast, pinyon establishment has not increased much at the White Pine prescribed fires. Rather, establishment of pinyon remained relatively constant and low

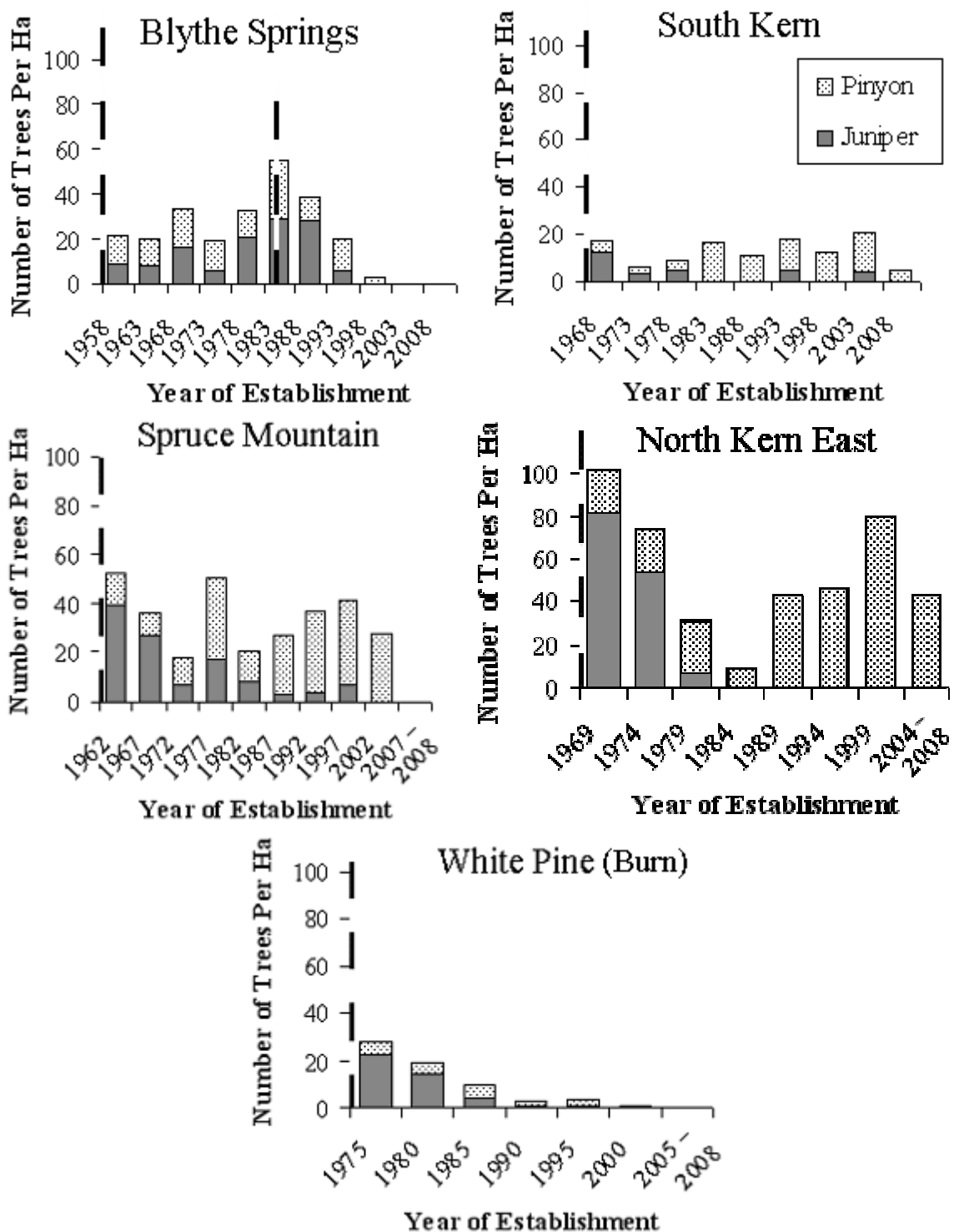


Figure 2. Number of trees establishing and surviving after chaining or prescribed fire. Bars represent five-year bins of establishment and vertical dashed lines represent years of treatments.

for the first 25 years before stopping completely, coinciding with cessation of juniper establishment, at approximately year 2000 (Fig. 2). This pattern is similar to that observed following the second Blythe Springs chaining, and is consistent with a recent, regional scale reduction in tree establishment across the Great Basin (Miller et al. 2008).

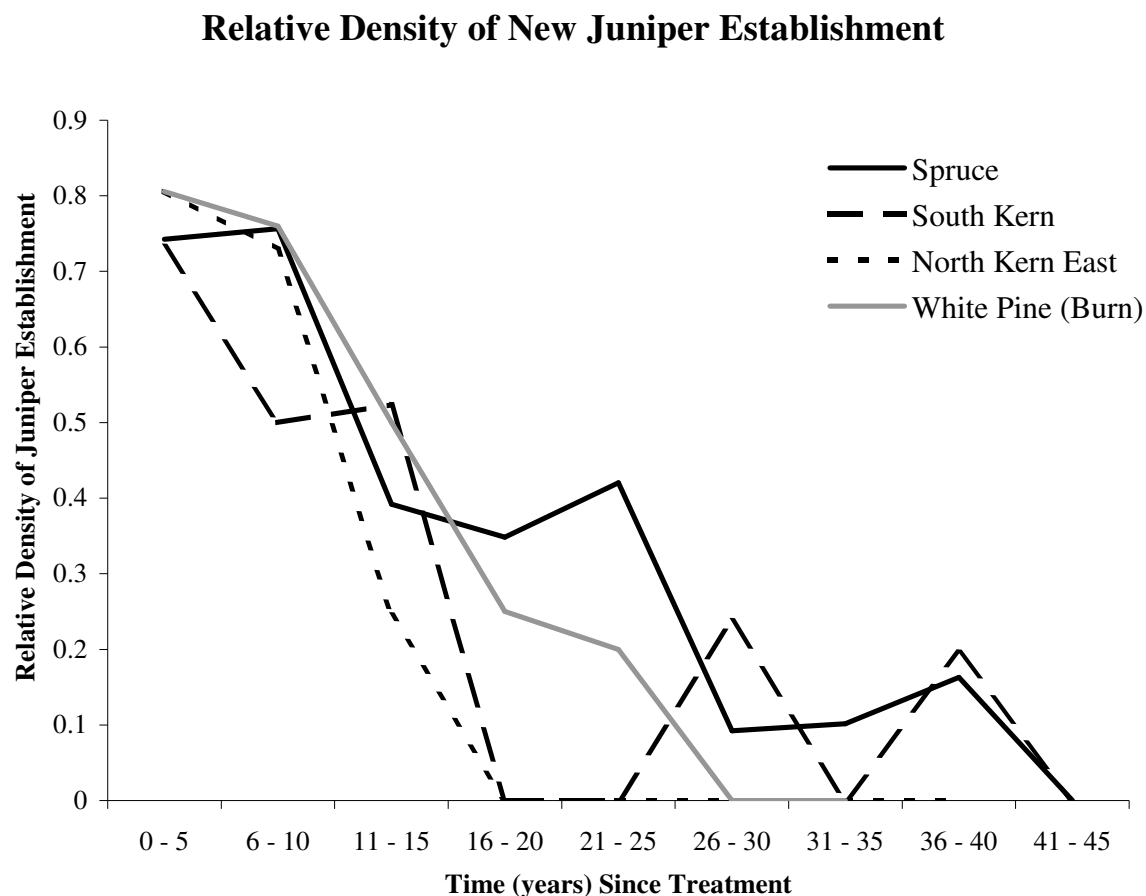
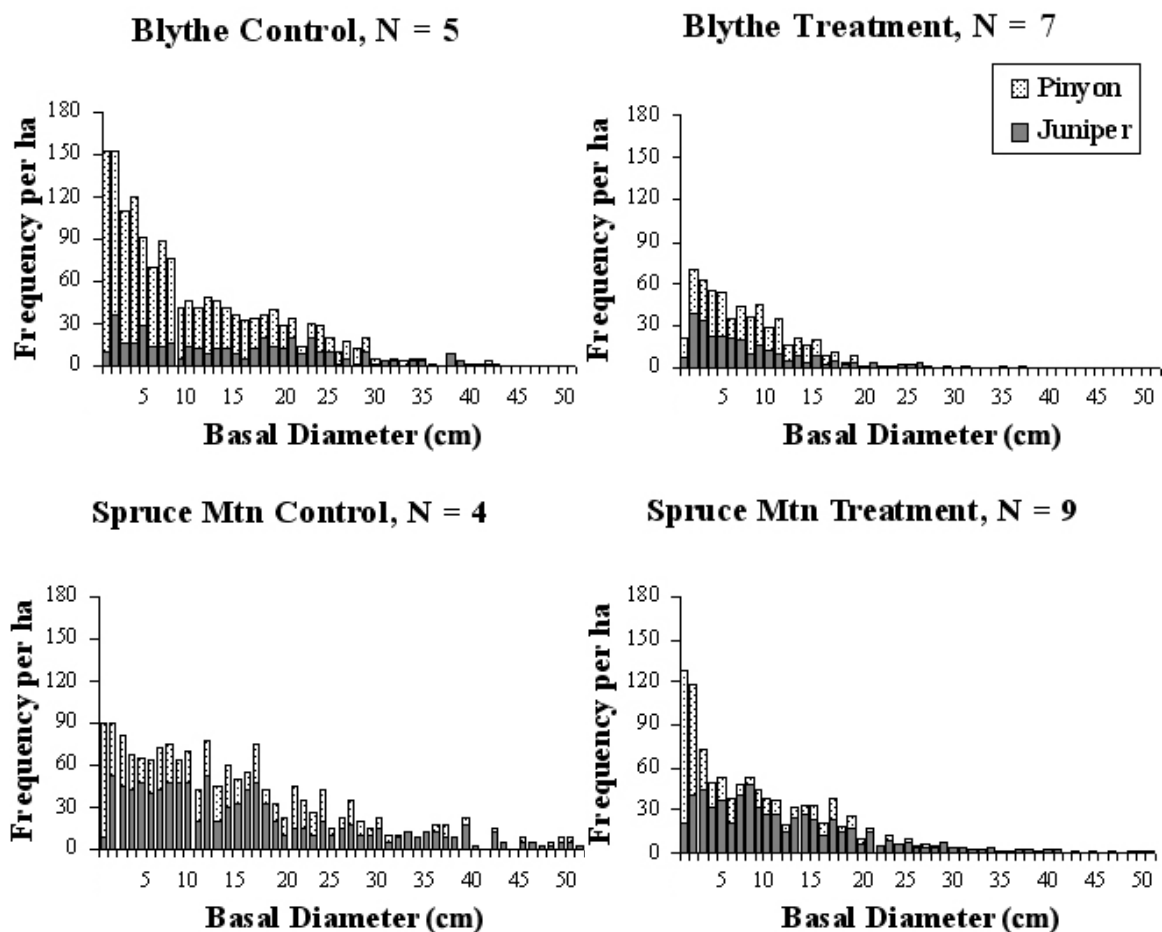


Figure 3. Density of juniper establishment relative to pinyon establishment for 5-year bins of time since treatment.

Although no trees were cored in control plots, basal diameter and density data provide evidence for abundant recent tree establishment, assuming smaller basal diameters often correspond with younger trees. Treatment plots at Spruce Mountain and North Kern East indicate greater density of small size classes than the other sites (Fig. 4),

which corresponds with the relatively high recent tree establishment for the same plots, reflected in their age data (Fig. 2). Blythe Springs exhibited high density of small tree diameters at control plots similar to the density of small tree diameters at treated plots (Fig. 4). South Kern treatment and control plots and White Pine control plots have a high frequency of 1-cm basal diameter trees but have humped distributions of the other size classes (Fig. 4). This suggests that although germination was high, seedling survivorship was low at South Kern and White Pine.

At all treatment sites, there were few juniper trees in smaller size classes. In general, control plots have greater amounts of small trees than treatment plots (Fig. 4),



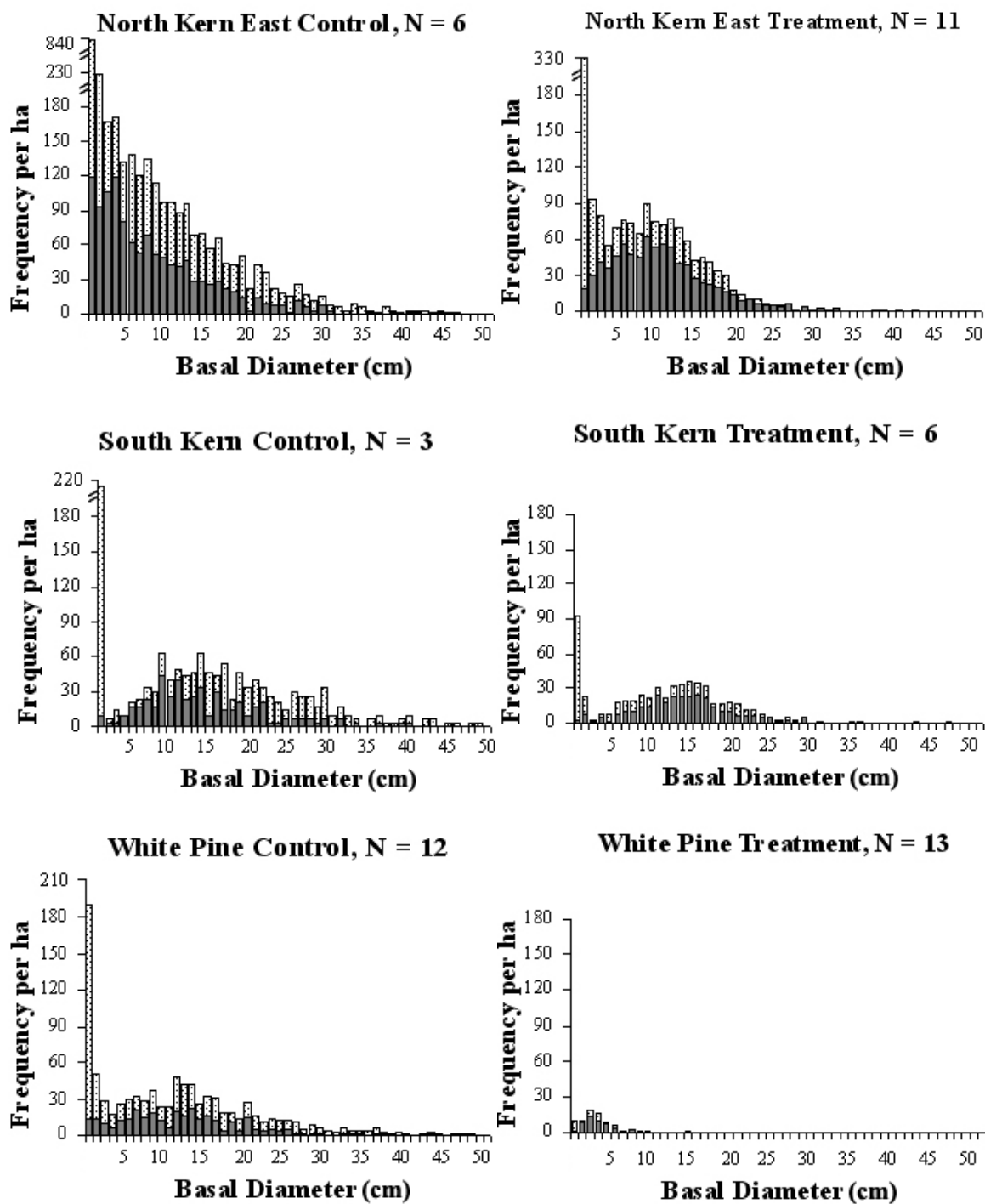


Figure 4. Density of pinyon and juniper trees of basal diameters in 1-cm diameter size classes for control plots (left) and treatment plots (right) in 2008.

suggesting that untreated woodlands are better sites for tree establishment than treated woodlands. Untreated plots had particularly high densities of small juniper trees when

compared with treated plots. Basal diameter data also indicate differential species mortality occurring at chaining sites. Results from Spruce Mountain, North Kern East, and South Kern clearly demonstrate that larger juniper trees exist in higher relative proportions to larger pinyon trees at treatment sites.

At most sites, pinyon and juniper density increased between original sampling in 1971 and resampling in 2008. At every site, increases in control plot tree densities exceeded increases in treatment plot density (Fig. 5). Tree density increased at all control sites and at treatment sites that displayed concave curve shapes in Figure 4 (ie, Spruce Mountain and North Kern East). These size class distributions are consistent with higher

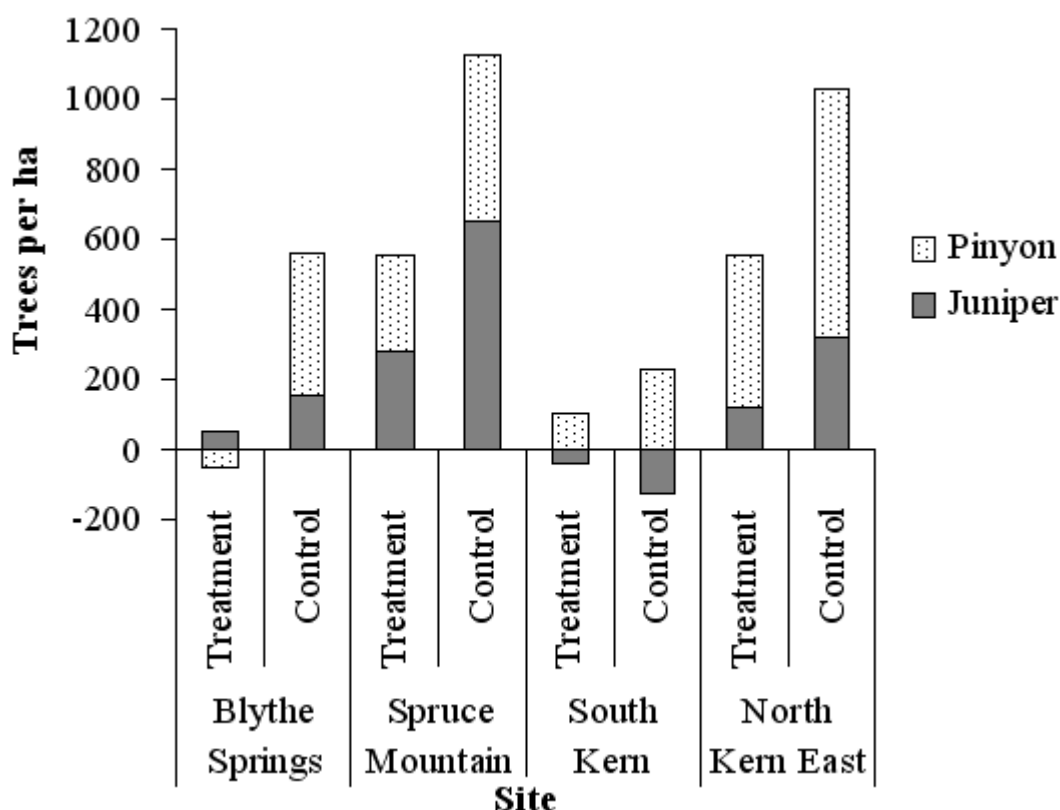


Figure 5. Density increases in pinyon and juniper trees for chaining treatment and control sites at four locations between 1971 and 2008. Positive values indicate an increase in density and negative values indicate a loss of density.

survival of recently germinated trees. Treatment and control plots at North Kern East and South Kern initially experienced additions of pinyon density (Fig. 5). Spruce Mountain had the largest increases in juniper density.

Discussion

Effects of Treatments on Rates and Mechanisms of New Tree Establishment

Chaining and prescribed fire were expected to have differing rates of tree establishment as a result of treatment effects on seed source, seed dispersal, seed predation, nurse plant availability, and competition (Table 1). Concerning tree establishment, the mechanisms of seed dispersal and seed predation could be ruled out by the data of this study. However the expected effects of seed source, nurse plant availability, and competition were consistent with the results. It is possible that these three mechanisms, or a subset, contributed to causing greater tree establishment at chaining sites than at prescribed fire sites.

Greater production of pinyon and juniper seed at chaining sites was expected to contribute to greater tree establishment at chaining sites than at prescribed fire sites. Some trees that survived chaining treatment likely recovered sufficiently to produce seed, whereas burned sites were likely devoid of seed-producing trees. Seed producing trees likely created a greater seed source at chainings, which is a mechanism identified as causing greater tree establishment (Table 1). In this study, tree establishment was higher at chaining sites, which is consistent with the expected effect of seed source.

The expected effects of chaining and prescribed fire on tree establishment, as mediated by seed dispersal differences (Table 1), were not consistent with the findings of this study, given that greater tree establishment occurred at chainings. Pinyon and juniper rely heavily on seed caching birds and rodents for seed dispersal and deposition of seed at necessary soil depths for germination (Vander Wall and Balda 1977, Vander Wall 1997). Dispersers could reach all of the treatment interiors in this study, but because the fires were smaller in extent than the chainings, it is likely that more seed was dispersed into the interiors of the prescribed fires.

Seed predation was another mechanism expected to cause greater establishment at prescribed fire sites (Table 1), which was not supported by the results. Loss of olfaction in some rodents due to presence of ash can cause lower cache retrieval and lower cache pilfering (Briggs and Vander Wall 2004). At burned sites, however, tree establishment was relatively low, indicating that either cache retrieval and cache pilfering continued despite ash interference with olfaction at these sites or other factors were limiting establishment.

Greater availability of nurse plants, or structural equivalents, at chaining sites were predicted to contribute to greater seed germination and survival (Table 1). The predicted effects of this mechanism were consistent with the data. Following chaining, biotic safe sites are reduced because sagebrush, which is the primary nurse plant for Great Basin trees (Callaway et al. 1996), also experiences mortality (Tausch 1973). Slash piles composed of coarse woody debris replace living shrub safe sites on the chained landscape. Slash piles vary in size and composition, but may provide the shading,

cooling, and moisture necessary for seedling germination and survival. Because lower establishment occurred at prescribed fire sites, where there were no slash piles and initial shrub cover was lower, nurse plant availability is a mechanism consistent with the findings of this study.

In addition to having fewer slash piles and shrubs to provide the necessary moisture conditions for tree establishment, seedlings at prescribed fire sites were expected to be subject to intense competition from high herbaceous plant cover (Ward 1977). Greater competition from grasses and forbs at prescribed fire sites may have contributed to lower rates of tree establishment (Table 1). Because lower tree establishment occurred at prescribed fire sites, the competition mechanism is consistent with the results of this study.

Although the results indicate chaining creates a better environment for tree establishment than burning, untreated sites experienced the highest level of new tree establishment. The largest number of small diameter trees was observed in control plots (Fig. 4). The establishment mechanisms identified as being supported by treatment plot data of this study may also have contributed to greater seedlings establishing at control plots. Control plots, having the greatest number of large, mature, seed-producing trees (Fig. 4), have greater seed source than treatment plots and less competition from herbaceous plants (Tausch 1973, Ward 1977). However, nurse shrub availability was likely lower in control sites, indicating nurse shrubs were less important than at least one of the other two mechanisms. With regard to goals of reducing further tree

establishment, managers achieved some success with chaining treatments and more success with prescribed fire, relative to untreated controls.

Differences in chronology of tree establishment at burned and chaining sites will have lasting effects on plant community composition. Tree establishment at burned sites dropped over the first 15 years, and stabilized near zero for the last 18 years prior to sampling (Fig. 2). The total increase in tree density at burned sites was minor in comparison with the relatively regular and moderate increases in density observed at chaining sites. Continued establishment of trees at chaining sites will result in more rapid stand closure and loss of understory species (Tausch et al. 1981, Miller et al. 2000). Understory plant species can persist for a longer duration at burned sites, where initial tree density is low and further tree establishment has been drastically reduced.

Differences in Establishment of Pinyon and Juniper Trees Following Treatment

The life history traits of pinyon and juniper suggested that each species would respond to and recover from woodland treatments of prescribed fires and chainings in different fashions (Table 2). The traits under consideration were tree survivorship, type of mycorrhizal association, duration of seed viability, dependence on facilitation, and sensitivity to drought. These species-specific strategies were expected to influence relative establishment of pinyon and juniper after treatment. As expected, a greater proportion of pinyon trees established at chaining sites and primarily juniper established at prescribed fire sites. Pinyon establishment was lowest at burned sites, but juniper establishment rates were similar for both treatments (Table 3).

Tree survivorship is a life history trait only applicable to the chaining sites, where trees survived, and greater survivorship of juniper was observed (Tausch 1973). Greater juniper survivorship at chaining sites was expected to cause greater abundance of mature, seed-producing junipers than pinyons. Greater juniper seed source likely promotes greater juniper establishment, which was consistent with the findings for the first 15 to 20 years following chaining (Fig. 2, Fig. 3). Establishment became dominated by pinyon and because greater seed source did not likely shift from juniper to pinyon at that period, the data no longer support the expectation. Either higher juniper survivorship became less important than other life history traits after 20 years or the initial greater establishment of juniper resulted from some other trait or combination of traits.

Differing survivorship of pinyon and juniper likely also affected the relative abundance of mycorrhizal fungi types, which was expected to affect efficiency of moisture uptake by seedlings of each species. AM fungi, the type associated with juniper, was expected to be more available to seedlings as a result of higher juniper survivorship and existing mycorrhizal reservoirs from associations with other Great Basin plant species (Haskins and Gehrig 2004, Hubert and Gehrig 2008). Because pinyon pine forms associations with EM fungi, the least common type in the Great Basin, pinyon root inoculation and establishment were expected to be less than juniper (Haskins and Gehrig 2005). For the initial 20 years following treatment, juniper establishment was greater than pinyon establishment at both treatments, and therefore the data are consistent with treatments causing reduction of EM (Fig. 2). The data did not indicate pinyon

establishment decreased or ceased simultaneously at control sites, where other pinyon trees were present, potentially providing an EM reservoir for seedlings (Fig. 4).

The transition from juniper to pinyon establishment at chaining sites may be consistent with trends in shifting plant composition. Pinyon establishment occurred on a smaller scale than juniper establishment at chaining sites for the first 20 years (Fig. 2). As pinyon density slowly increased, EM presence likely increased in unison. Perhaps after 20 years, EM fungi had increased to levels sufficient to support increased pinyon establishment and simultaneously reduce the probability of juniper seedlings encountering AM for root inoculation. Understory cover has been reported to decrease through time at chaining sites with increasing tree cover (Tausch 1973). By nine and 13 years after chaining at Blythe Springs and Spruce Mountain, Tausch (1973) observed relatively low cover of understory species, which may serve as important sources of AM mycorrhizal fungi for juniper. It is possible that shifting from understory dominance to tree dominance and increasing pinyon density caused shifts in relative abundance of mycorrhizae types.

Differences in timing of tree species establishment at treated sites indicated that juniper was more capable of early establishment on the treated sites studied than pinyon. Species-specific differences in reproductive life history traits may have been responsible for observed differences. Juniper seed remains viable for up to several years, whereas pinyon seed viability decreases after one year (Johnsen 1959, Chambers et al. 1999). Viable seed in the seed bank may have been important for juniper establishment for the first few years after chaining and prescribed fire, when proximity to mature trees with

seed was reduced. The data supports the duration of seed viability as an important life history trait for the first few years following treatment.

The difference in initial relative species establishment is consistent with the safe site requirements of pinyon pine (Tausch and West 1988, Callaway et al. 1996, Chambers et al. 1999). Both pinyon and juniper trees establish well in the presence of nurse plants, although improved moisture and shade are primarily limiting for pinyon establishment (Chambers et al. 1999). Juniper trees established in similar densities at burned and chaining sites, which supports the expectation that juniper is less dependent upon nurse shrub presence (Chambers et al. 1999). Pinyon pine established in greater quantities at chaining sites, where a variety of slash material and recovering shrubs provided shading. However, at prescribed fires, pinyon establishment decreased despite nurse shrub availability increasing through time. Dependence on nurse shrub availability was a less important factor at prescribed fires than other mechanisms such as competition.

Although an important life history trait in the Great Basin, the expected effects of differences in drought tolerance between pinyon and juniper are not consistent with the findings of this study. Mature pinyon pine trees exhibit greater sensitivity to water stress and higher susceptibility to mortality from drought than junipers (Barnes and Cunningham 1987, Breshears et al. 1997, Nowak et al. 1999, Mueller et al. 2005). Under drought conditions, juniper seedlings were expected to exhibit higher germination and survival than pinyon seedlings at both treatment types (Table 2). Transitions to greater establishment of pinyon were expected to coincide with transitions from low precipitation to high precipitation. However, Western Regional Climate Center (WRCC) precipitation

data from the Ely WBO station exhibit highly variable periods of drought and wet years (Fig. 6). A few periods exist of higher than average precipitation, when pinyon was

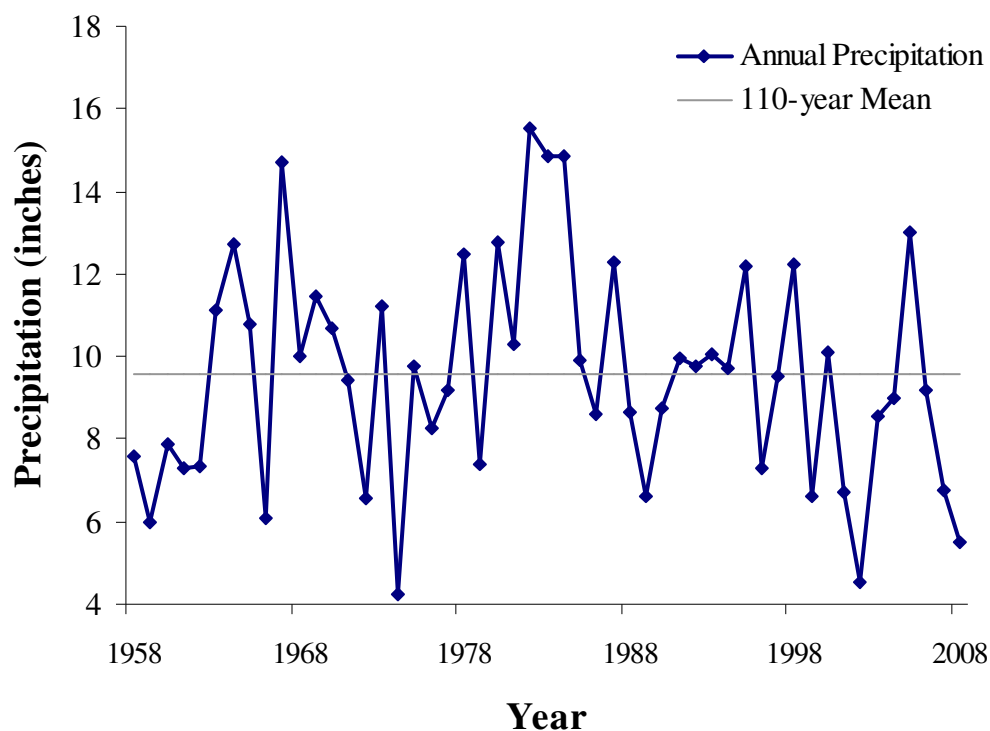


Figure 6. WRCC annual precipitation data for Ely, Nevada between 1958 and 2008.

expected to dominate establishment at a site, but instead higher juniper establishment occurred. More clearly, only two years of above average precipitation occurred between 1998 and 2008, yet pinyon establishment far exceeded juniper establishment for that time period at both of the sites exhibiting the transition (Fig. 2).

Further research is necessary to confirm or disprove the importance of the mechanisms and life history traits discussed. The data collected for this study only measures the response variable of density of establishing trees; however, the proposed explanatory variables are more informative of ecological processes. Ideally a long-term

study could be constructed with paired treatments and controls to examine effects of woodland treatments on site conditions. If the transition between juniper and pinyon establishment were the subject of a follow-up study, useful information might be acquired through annual measurements of density of seed-producing trees, abundance of mycorrhizal fungi types in the soil, and cover of competing and facilitating vegetation. The expected effects of these factors were most consistent with the results of this study.

Influences of Management on Woodland Tree Species Composition

The results of this study are evidence for the need and usefulness of long-term monitoring of treatment sites. Had sites only been sampled within 15 years of treatment, there would have been only evidence of juniper trees reestablishing at all sites (Fig. 2). Sampling multiple decades after treatment captured changes in tree population structure likely to affect long-term composition and structure of woodlands.

That juniper establishment has been more recently replaced by pinyon establishment at chaining sites has implications for future woodland structure, assuming that sites are not re-treated. At the site of a mid-19th century wildfire, Tausch and West (1988) reported that pinyon establishment did not exceed juniper establishment until 60 years following burning. Pinyon establishment at the prescribed fire sites used for this study had not begun to increase by 2008, 33 years after burning. However, pinyon establishment exceeded that of juniper after about 15 years at chaining sites in this study, indicating that pinyon might become the dominant species sooner following chaining than following fire. Chaining treatments that are without follow-up retreatment have

potential to create or amplify landscape-level shifts in tree species composition. Relative to fire disturbances, the rate of re-dominance of the site by pinyon is much faster on chaining sites.

Chaining may not have the same effects on site conditions as more modern mechanical treatments used in the Great Basin. Chaining is often considered out-dated as a mechanical treatment for pinyon and juniper woodland removal, but chaining treatments have been conducted in eastern Nevada and western Utah within the last decade. Newer methods of mechanical treatment, including mastication and bullhogging, are being used with more frequency. The new methods are similar to each other, both targeting and mulching individual trees, and occasionally leaving some trees untreated. Untreated mature trees of bullhogging and mastication are likely to produce more seed than the small surviving trees from chaining. More shrubs are expected to survive bullhogging and mastication, but slash piles, like those resulting from chaining, will not be present. I would speculate that greater tree establishment would occur following bullhogging and mastication than chaining, unless the density of untreated trees was extremely low. The decision to treat pinyon and juniper woodland by prescribed fire, mechanically, or leave untreated requires a long-term perspective incorporating expected responses of treatment on eventual tree population processes.

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Appendix I

Table i. Correlations between explanatory variables (coarse, fine, depth, TCI, Solar, elevation, and years) and with the response variable (tree).

	coarse						
fine	-0.34	fine					
depth	0.09	0.37	depth				
TCI	0.08	-0.71	-0.32	TCI			
solar	-0.06	-0.67	-0.49	0.46	solar		
elevation	0.24	-0.64	-0.68	0.50	0.62	elevation	
years	0.13	0.21	0.82	-0.24	-0.46	-0.65	years
tree	-0.47	0.09	-0.56	-0.03	0.17	0.20	-0.50

Table ii. Mean absolute percent cover of all species at treatment sites.

Scientific name	Common name	Mean Treatment Absolute Percent Cover				
		Blythe	Spruce	S Kern	N Kern E	White Pine
<i>Trees</i>						
<i>Cercocarpus ledifolius</i>	Curl-leaf mountain mahogany	0.031	0.113	1.515	0.396	0.000
<i>Juniperus osteosperma</i>	Utah juniper	5.067	5.751	8.891	10.690	0.051
<i>Pinus monophylla</i>	Pinyon pine	4.221	14.756	11.921	15.274	0.275
TOTAL TREE		9.318	20.619	22.326	26.360	0.326
<i>Shrubs</i>						
<i>Amelanchier alnifolia</i>	Serviceberry	0.014	0.000	0.000	0.000	0.000
<i>Artemisia ludoviciana</i>	White sage	0.000	0.000	0.000	0.000	0.015
<i>Artemisia nova</i>	Black sage	0.000	9.054	0.000	2.922	0.000
<i>Artemisia tridentata v. vasiana</i>	Mountain big sage	0.000	0.000	0.000	0.000	3.911
<i>Artemisia tridentata v. wyomingensis</i>	Wyoming big sage	10.693	0.211	2.721	0.102	0.839
<i>Chrysothamnus nauseosus</i>	Rubber rabbitbrush	0.418	0.389	0.000	0.032	0.318

Scientific name	Common name	Blythe	Spruce	S Kern	N Kern E	White Pine
<i>Chrysothamnus viscidiflorus</i>	Yellow rabbitbrush	0.130	0.015	0.000	0.094	4.594
<i>Cowania mexicana</i>	Mexican cliffrose	1.155	0.000	0.000	0.000	0.000
<i>Ephedra viridis</i>	Morman tea	0.468	0.000	0.000	0.000	0.000
<i>Eriogonum microthecum</i>	Slender buckwheat	0.002	0.001	0.000	0.000	0.000
<i>Eriogonum umbellatum</i>	Sulfur-flower buckwheat	0.000	0.000	0.002	0.020	0.000
<i>Leptodactylon pungens</i>	Granite Gilia	0.000	0.063	0.054	0.050	0.000
<i>Purshia glandulosa</i>	Desert bitterbrush	6.839	0.000	0.000	0.000	0.000
<i>Purshia tridentata</i>	Antelope bitterbrush	1.186	0.678	0.098	0.314	5.325
<i>Rhus trilobata</i>	Skunkbush sumac	0.000	0.000	0.000	0.000	0.400
<i>Ribes cereum</i>	Wax currant	0.000	0.000	0.000	0.000	0.532
<i>Rosa woodsii</i>	Wood's rose	0.000	0.000	0.000	0.000	0.017
<i>Sambucus mexicana</i>	Blue elderberry	0.000	0.000	0.000	0.000	0.015
<i>Tetradymia canescens</i>	Gray horsebrush	0.000	0.000	0.000	0.006	0.013
TOTAL SHRUB		20.905	10.411	2.875	3.540	15.981
<i>Grasses</i>						
<i>Achnatherum hymenoides</i>	Indian ricegrass	0.000	0.046	0.004	0.093	0.192
<i>Achnatherum nevadensis</i>	Nevada needlegrass	0.025	0.000	0.000	0.044	0.000
<i>Achnatherum thurberianum</i>	Thurber's needlegrass	0.000	0.000	0.042	0.039	0.166
<i>Agropyron cristatum</i>	Crested wheatgrass	0.004	0.011	0.317	0.590	0.000
<i>Bromus inermis</i>	Smooth brome	0.000	0.000	0.100	0.000	0.000
<i>Bromus tectorum</i>	Cheatgrass	0.013	0.011	0.000	0.000	0.358
<i>Elymus elymoides</i>	Squirrel tail	0.139	0.285	0.013	0.002	0.204
<i>Hesperostipa comata</i>	Needle and thread	0.000	0.000	0.000	0.000	0.131
<i>Leymus cinereus</i>	Giant Great Basin wild rye	0.000	0.000	0.000	0.000	1.533
<i>Thinopyrum intermedium</i>	Intermediate wheatgrass	0.000	0.000	0.102	0.000	0.000
<i>Pleuraphis jamesii</i>	James' galleta	0.004	0.000	0.000	0.000	0.000
<i>Pascopyrum smithii</i>	Western wheatgrass	0.000	0.000	0.000	0.006	0.000
<i>Poa nevadensis</i>	Sandberg bluegrass	0.000	0.000	0.000	0.000	0.005
<i>Poa secunda</i>	Sandberg bluegrass	0.000	0.172	0.240	0.284	0.107
<i>Psuedoroegneria spicata</i>	Blue bunch wheatgrass	0.004	0.197	0.433	0.000	0.008

Scientific name	Common name	Blythe	Spruce	S Kern	N Kern E	White Pine
TOTAL GRASS		0.188	0.722	1.250	1.058	2.703
<i>Graminoid</i>						
<i>Carex douglasii</i>	Douglas' sedge	0.004	0.000	0.000	0.085	0.050
<i>Forbs</i>						
<i>Antennaria dimorpha</i>	Low pussy-toes	0.000	0.000	0.017	0.013	0.000
<i>Arenaria aculeata</i>	Needleleaf sandwort	0.000	0.013	0.010	0.013	0.000
<i>Arabis holboellii</i>	Holboell's rockcress	0.000	0.001	0.006	0.005	0.000
<i>Astragalus lentiginosus</i>	Speckle-pod milkvetch	0.005	0.003	0.002	0.093	0.004
<i>Astragalus newberryi</i>	Newberry's milkvetch	0.000	0.003	0.000	0.053	0.000
<i>Astragalus purshii</i>	Woolly-pod milkvetch	0.000	0.004	0.000	0.000	0.000
<i>Caulanthus californicus</i>	St. Francis cabbage	0.000	0.001	0.000	0.016	0.000
<i>Castilleja chromosa</i>	Paintbrush	0.000	0.036	0.000	0.008	0.000
<i>Caulanthus crassicaulis</i>	Thickstemmed wild cabbage	0.000	0.011	0.000	0.002	0.000
<i>Calochortus nuttallii</i>	Sego lily	0.000	0.000	0.000	0.011	0.000
	Small-flowered blue-eyed					
<i>Collinsia parviflora</i>	Mary	0.000	0.000	0.002	0.000	0.000
<i>Cordylanthus kingii</i>	King's bird's-beak	0.000	0.001	0.000	0.000	0.000
<i>Crepis acuminata</i>	Tapertip hawkbeard	0.000	0.003	0.000	0.001	0.025
<i>Cryptantha flavoculata</i>	Yellow eyed cryptantha	0.000	0.003	0.004	0.188	0.034
<i>Delphinium andersonii</i>	Desert larkspur	0.000	0.000	0.000	0.001	0.000
<i>Descurainia pinnata</i>	Tansy mustard	0.004	0.001	0.000	0.000	0.014
<i>Erigeron aphanactis</i>	Rayless shaggy fleabean	0.000	0.015	0.000	0.003	0.000
<i>Eriogonum caespitosum</i>	Mat buckwheat	0.000	0.058	0.000	0.000	0.000
<i>Eriogonum ovalifolium</i>	Cushion buckwheat	0.000	0.000	0.000	0.001	0.000
<i>Fritillaria atropurpurea</i>	Checker lily	0.000	0.000	0.000	0.001	0.000
<i>Ipomopsis aggregata</i>	Scarlet gilia	0.000	0.000	0.000	0.009	0.000
<i>Ipomopsis congesta</i>	Ballhead ipomopsis	0.000	0.000	0.023	0.005	0.000
<i>Iva axillaris</i>	Poverty weed	0.000	0.000	0.000	0.000	0.196

Scientific name	Common name	Blythe	Spruce	S Kern	N Kern E	White Pine
<i>Lesquerella kingii</i>	King bladderpod	0.000	0.000	0.000	0.009	0.000
<i>Lomatium sp.</i>	Biscuit-root	0.000	0.000	0.000	0.000	0.002
<i>Lupinus caudatus</i>	Tailcup lupine	0.000	0.000	0.000	0.000	0.064
<i>Lygodezmia spinosa</i>	Skeleton weed	0.000	0.000	0.000	0.000	0.057
<i>Machaeranthera canescens</i>	Hoary tansyaster	0.000	0.000	0.000	0.006	0.000
<i>Mentzelia albicaulis</i>	Whitestem blazingstar	0.000	0.000	0.000	0.000	0.020
<i>Opuntia Polyacantha</i>	Prickly pear cactus	0.002	0.000	0.004	0.000	0.069
<i>Pedicularis centranthera</i>	Dwarf lousewort	0.000	0.000	0.000	0.074	0.000
<i>Penstemon confusus</i>	Owens Valley beardtongue	0.014	0.025	0.210	0.005	0.001
<i>Penstemon janishiae</i>	Antelope Valley beardtongue	0.000	0.000	0.000	0.024	0.000
<i>Penstemon species</i>	Unknown Penstemon	0.000	0.006	0.000	0.011	0.000
<i>Phlox diffusa</i>	Spreading phlox	0.000	0.000	0.017	0.526	0.000
<i>Phlox longifolia</i>	Long-leaf phlox	0.000	0.065	0.015	0.011	0.038
<i>Senecio multilobatus</i>	Lobeleaf groundsel	0.000	0.001	0.000	0.061	0.000
<i>Sphaeralcea munroana</i>	Munro's globemallow	0.016	0.000	0.000	0.000	0.020
<i>Taraxacum officinale</i>	Dandelion	0.000	0.000	0.000	0.001	0.000
<i>Trifolium gymnocarpon</i>	Dwarf clover	0.000	0.000	0.002	0.000	0.000
<i>Zigadenus paniculatus</i>	Foothill deathcamus	0.000	0.000	0.000	0.000	0.002
TOTAL FORB		0.041	0.251	0.313	1.151	0.547

Table iii. Coefficients (β), weighted coefficients (w_β), and p values for the five most important variables of the LME models.

Model	Variables														
	Depth			Coarse			TCI			Years			Fine		
	β	w_β	P Value	β	w_β	P Value	β	w_β	P Value	β	w_β	P Value	β	w_β	P Value
- depth - TCI - coarse	-1.18	-1.14	<.01*	-0.74	-0.66	0.02*	-1.71	-1.21	0.25	-	-	-	-	-	-
- depth - TCI - coarse - years	-1.09	-1.05	0.07	-0.73	-0.65	0.02*	-1.70	-1.20	0.27	-0.13	-0.05	0.87	-	-	-
- depth - coarse	-1.06	-1.02	0.01*	-0.75	-0.67	0.01*	-	-	-	-	-	-	-	-	-
- depth - coarse + years	-1.11	-1.07	0.06	-0.72	-0.64	0.02*	-	-	-	0.03	0.01	0.97	-	-	-
- depth - TCI	-1.28	-1.23	<.01*	-	-	-	-2.06	-1.45	0.23	-	-	-	-	-	-
- depth - TCI - years	-1.19	-1.14	0.08	-	-	-	-1.42	-1.00	0.47	-0.09	-0.04	0.93	-	-	-
- coarse - years	-	-	-	-0.75	-0.67	0.02*	-	-	-	-1.00	-0.41	0.22	-	-	-
- depth - TCI - coarse - years + fine	-1.15	-1.11	0.07	-0.68	-0.61	0.05*	-1.18	-0.83	0.58	-0.09	-0.04	0.91	0.06	0.00	0.73
- depth - coarse + fine	-1.21	-1.17	<.01*	-0.64	-0.57	0.05*	-	-	-	-	-	-	0.14	0.01	0.29