

University of Nevada, Reno

Landscape analysis of post-burn succession in a Great Basin pinyon-juniper woodland

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science in Natural Resource and Environmental Science

by

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Abstract

Plant succession following fire is complex as the post-fire landscape is heterogeneous with respect to propagule availability and environmental conditions. Environmental conditions are influenced by variation in abiotic factors such as topography, climate, and soil. However, important biotic legacy effects associated with site history are difficult to quantify. This study examines the driving factors underlying plant community composition six years following a wildland fire in Wall Canyon of the Toiyabe Range of the central Great Basin. It also examines the direct and indirect influences of various abiotic and biotic factors on the distribution and abundance of two species of particular interest, *Bromus tectorum* and *Artemisia tridentata* ssp. *vaseyana*.

Direct and indirect ordination methods were used to describe post-fire plant community composition according to underlying gradients reflecting the physical environment, pre-burn vegetation structure, anthropogenic disturbances, and proximity to potential seed sources. The strongest abiotic influences on plant community composition included solar radiation, likely reflecting a soil moisture gradient, and soil pH. Biotic influences on community composition, in order of importance, were proximity of unburned patch edge within the burn, pre-burn canopy cover and distance from the burn perimeter. Each of these predictors favored species with particular life history traits. Increased solar radiation favored drought avoiding species such as *Bromus tectorum* and *Descurania sophia*. High values of soil pH, possibly indicating areas of high burn severity or reduced soil development, favored annual, widely dispersing species such as *Lactuca serriola* and *Salsola tragus*. A few native species were favored by simultaneous increases in pre-burn canopy cover and influence of unburned patches that could provide

seed sources: *Astragalus purshii*, *Cryptantha torreyana*, and *Senecio multibalatus*.

Increased distance from the burn perimeter favored widely dispersing species such as *Crepis acuminata* and *Gnaphalium palutre*. Abiotic controls accounted for 11.3% of the variance in species composition and biotic interactions accounted for 7.1% with an interaction of 1.4%. Plant species distributions following fire in Wall Canyon were largely driven by abiotic factors, especially soil moisture, with biotic factors also playing a significant role in determining the availability of plant propagules.

Principal components regression models of *B. tectorum* and *A. tridentata* ssp. *vaseyana* distributions revealed species-specific environmental preferences. *B. tectorum* preferred xeric sites with gentler slopes, lower pre-burn canopy cover, more acidic soils, and higher concentrations of ammonium ($R^2_{\text{adj}} = 0.153$). *A. tridentata* ssp. *vaseyana* preferred more mesic sites with deeper soils ($R^2_{\text{adj}} = 0.296$). Structural equation models identified causal pathways predicting the abundance of *A. tridentata* ssp. *vaseyana* that included a positive effect of soil depth and a negative effect of pre-burn canopy cover. Direct pathways predicting the abundance of *B. tectorum* included a positive effect of solar radiation. Structural equation models also identified negative direct effects of topographic convergence index, TCI, and percent coarse fragment on pre-burn canopy cover.

Plant community development following fire in pinyon-juniper woodlands represents the interaction of the three successional mechanisms proposed by Connell and Slatyer (1977): stress tolerance, facilitation, and inhibition. Annual species such as *B. tectorum* tolerate the environmental stress of low soil moisture and impose stress on other plant species. *B. tectorum* uses available soil moisture before the growing season of

native plant species, inhibiting the establishment of natives. Shrub species, once established, modify the physical environment by increasing available soil moisture and thereby facilitating the establishment of *Pinus monophylla* and *Juniperus osteosperma*. Without the prior establishment of shrubs, soil moisture is too low for these tree species to establish. Once established, these arborescent species inhibit the establishment of understory species through increased canopy cover, extensive rooting systems, and domination of available soil moisture.

Although abiotic factors strongly influence species distributions following fire, pre-burn vegetation modifies these conditions. My findings indicate that effective restoration must consider the pre-burn conditions of the system. Pre-fire restoration efforts should focus on woodlands whose understory vegetation has not been completely reduced by increasing tree canopy cover and that can therefore recover following fire. Post-fire restoration efforts should focus on sites that are dry, have high pre-burn canopy cover, or are at greater distances from unburned patches as these conditions collectively favored invasion of non-native species.

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Background

Pinyon-juniper woodlands have been defined by West and Young (2000) as communities dominated by scattered *Juniperus* species and cembroid pines, with junipers being more widespread in regards to elevation and geography. Over the last 130 years, these woodlands have expanded their range and increased in density at rates exceeding that of anything that has occurred in the last 5,000 years (Tausch 1999). Pinyon-juniper expansion is widely believed to result from favorable climatic conditions for tree establishment and reduced fire return intervals due to domestic grazing. Grazing reduces fine fuel loads, so that the vegetation is not capable of carrying fire through the landscape. It also reduces competition with grazed species (Burkhardt and Tisdale 1976, Miller and Rose 1995, Miller and Rose 1999, Soule et al. 2003 and Soule et al. 2004).

Understory vegetation cover in pinyon-juniper woodlands is inversely related to tree canopy cover. Rapid losses of many shrub and perennial grass species occur as tree dominance exceeds a threshold level (Tausch and Tueller 1990). As woodland canopy cover increases, biomass and seed production of understory species decreases (Koniak and Everett 1982, Tausch and Nowak 1999, Miller et al. 2000). This is due to overstory modification of microclimates and competition for soil water and nutrients (Breshears et al. 1993, Breshears et al 1997).

Areas with reduced understory vegetation are less resistant to exotic plant invasion following fire (Floyd et al. 2006) due to increases in suitable sites for establishment as well as increases in the abundance of nutrients (Davis et al. 2000). Exotic annuals such as *Bromus tectorum* benefit from this increase in nutrients, making

the Great Basin ecoregion particularly vulnerable to invasion following fire. *B. tectorum* facilitates frequent fires by producing abundant, fine fuels (Whisenant 1990, D'Antonio and Vitousek 1992, Brooks et al. 2004). As fuels become more continuous with the establishment of *B. tectorum*, few unburned patches remain to act as seed sources following fire. Additionally, native species of the Great Basin are not adapted to frequent fire (Whisenant 1990, Brooks et al. 2004) or seedling competition for soil moisture with this winter annual species before the onset of the growing season (Harris 1967). The invasion of *B. tectorum* can result in the conversion from native to exotic plant communities (Harris 1967, Whisenant 1990, Brooks et al. 2004).

Declining cover of *Artemisia tridentata* and native perennial bunchgrasses is not only correlated with the invasion of *B. tectorum* but also the expansion of pinyon-juniper woodlands (Miller et al. 1999, Miller and Tausch 2001). The loss of *Artemisia tridentata* is of concern to wildlife biologists, plant ecologists, land managers and ranchers. Loss of sagebrush grassland habitats has been implicated in declining populations of Sage Grouse, Horned Larks, Vesper Sparrows, Brewers Sparrows, and Sage Thrashers (Connelly and Braun 1997, Fisher et al. 1996; Swenson et al. 1987).

To maintain herbaceous grassland and shrub species, prescribed fire is increasingly used to remove pinyon and juniper trees (Wright et al. 1979, Everett 1986, Miller and Tausch 2001). An increased understanding of plant succession following fire in pinyon-juniper woodlands will assist land managers in determining where restoration efforts should be focused, given the threat of *B. tectorum* invasion. I expected that plant community responses to fire in pinyon-juniper woodlands would depend upon local site

conditions in terms of physical environment, pre-burn vegetation structure, and anthropogenic disturbance such as grazing, ATV use, and salvage logging.

Few studies of post-fire succession in pinyon-juniper woodlands have been conducted (Barney and Frischknecht 1974, Wright 1979, Everett 1984, Tress and Klopatek 1986, Whisenant 1990), and there have been even fewer landscape scale studies of understory succession in this vegetation type (Floyd et al. 2006). I examine abiotic and biotic influences on post-burn succession of understory species in pinyon-juniper woodlands. Biotic factors include pre-burn tree canopy cover, distance from the burn perimeter, and proximity to unburned patches that provide sources of propagules. Anthropogenic disturbances, which often select for ruderal species and hence alter plant community composition, were also considered as influences on post-fire succession. Abiotic (soil characteristics, topography) and biotic (pre-burn tree canopy cover, influence of propagule sources) gradients are evaluated to determine the range of conditions over which species occur. My results address understory species responses at the plant community level as well as for two species of particular interest: *Artemisia tridentata* ssp. *vaseyana* and *Bromus tectorum*.

I used life history traits to interpret species-specific responses to the physical environment and proximity to unburned area. Plants with similar life history traits are expected to respond to disturbance in a similar manner (Connell and Slatyer 1977, Noble and Slatyer 1980, Bradstock and Kenny 2003). Ruderal species tend to avoid environmental stress through short life cycles, but often disperse widely. Stress tolerators are longer lived but have lower reproductive output (Pianka 1970, Grime 1977). Ruderal species often increase after moderately severe disturbance, but stress tolerators take

longer to achieve pre-disturbance levels of abundance. Plant species have a range of tolerances for environmental conditions and disturbance. Plant communities, typically, are composed of species with similar tolerances for local conditions. Conditions that are outside the tolerance range of a given species act as an ecological filter to the establishment or growth of that species at a given site. The ability of a species to survive to reproductive maturity is likely to be subject to a different set of filters. I identified major environmental gradients influencing plant species abundance based upon the life history traits of understory species in pinyon-juniper woodlands.

Thesis Overview

This thesis addresses three objectives related to succession in pinyon-juniper woodlands following wildfire.

- (1) Assess whether patches of similar environmental setting, pre-burn vegetation structure and proximity to unburned areas are likely to exhibit similar post-burn species composition
- (2) Contrast the role of each of the post-burn establishment filters (environment and propagule supply) for taxa of particular importance (*Artemisia tridentata* ssp. *vaseyana* and *Bromus tectorum*)
- (3) Develop recommendations for restoration ecologists seeking to use prescribed fire or similar treatment for maintaining native understory composition in pinyon-juniper woodlands

The first chapter examines the response of the plant community six years after a summer wildfire. Abiotic and biotic gradients influencing species composition are identified. The second chapter examines *Artemisia tridentata* ssp. *vaseyana* and *Bromus tectorum* abundance, identifying which site types show higher cover of these species after fire. I statistically model the direct and indirect effects of environmental influences hypothesized to affect the cover of these species. Specific influences modeled include pre-burn tree canopy cover, proximity to unburned patches, soil characteristics, and the physical environment.

Study Area

This study was conducted in Wall Canyon of the Toiyabe Range, south of Austin, Nevada and immediately west of the Great Smoky Valley (Figure 1). A total of 2822 ha burned in July 2000 as the result of a lightning strike. Approximately, 10% of the burn area persisted as unburned patches. The canyon is managed by the U.S. Forest Service as part of the Austin Ranger District, Humbolt-Toiyabe National Forest, and has been subject to a range of anthropogenic disturbances including cattle grazing, salvage logging, ATV traffic and a now inactive mine. Although these disturbances are found throughout the canyon, they are more frequent near the canyon mouth. Annual precipitation is highly variable but averages approximately 12 inches, mostly distributed as winter snowfall. Winter temperatures range from the upper 30s and the low 40s during the day to the teens at night. Summer temperatures average in the high 80s during the day to the upper 40s and low 50s at night. (USDA Forest Service website, <http://www.fs.fed.us/r4/htnf/districts/austin.shtml> , accessed May 2006)

Pre-burn vegetation was predominately pinyon-juniper woodland as determined from aerial photos, with small pockets of sagebrush grassland at the lower elevations, and mountain mahogany on northeast facing slopes. Soils are primarily lithic, deep arborolls-haplargrids-torriotherits and slopes are classified as rugged (Soil Survey Staff, NRCS 2007). Geology consists of metamorphic or igneous units with predominantly silicate composition (Turner and Bawic 1996).

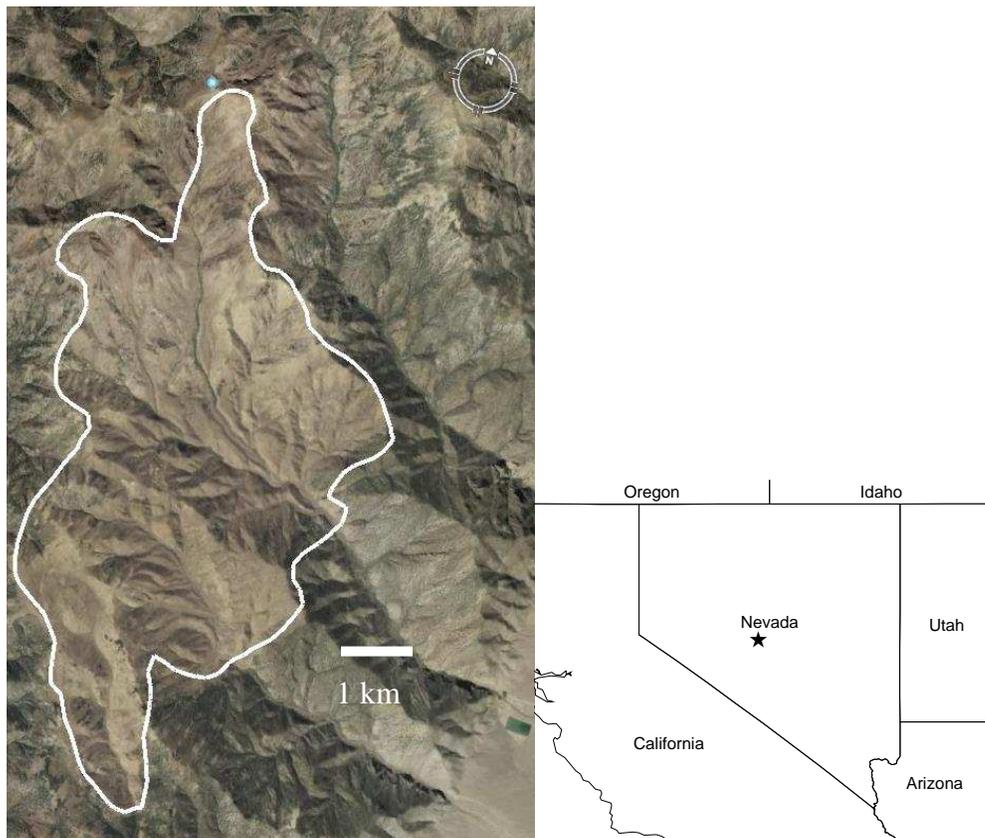


Figure 1. Wall Canyon burn, outlined The burn area was 2800 ha.

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Chapter 1: Landscape scale succession in post-fire pinyon-juniper woodlands: interaction of biotic and abiotic influences

Abstract

Prescribed fire is increasingly used in the Great Basin to counter the expansion of pinyon-juniper woodlands. Plant species establishment following fire is complex as fire often results in a heterogeneous landscape, with patches differing in environmental stresses and propagule availability. This study examines the influences on plant species occurrence following a six year old wildland burn in Wall Canyon of the Toiyabe Range of the central Great Basin. I present a conceptual model demonstrating the role of abiotic and biotic influences on the establishment and regrowth of understory plant species. Abiotic influences include topographic position and soil characteristics. Biotic influences are described by the level of tree dominance before the fire, and the distribution and abundance of unburned patches following fire. Abiotic and biotic influences act as filters to species establishment. I use the term establishment filters to indicate the different challenges a plant propagule must overcome before it will result in a reproductively mature individual. First, a propagule has to be present at a given site for the species to establish, whether it is a seed or an active meristem capable of resprouting. Second, environmental conditions must be within the range of tolerance of the species present for the individual to establish and persist.

Results indicate that the strongest abiotic controls on plant species occurrence were solar radiation and pH. Solar radiation was interpreted as a proxy for moisture availability. High soil pH values can be associated with increased burn severity or reduced soil development. Abundances of invasive species, such as *Bromus tectorum*

and *Descurania* species were correlated with high values of solar radiation, and abundances of *Lactuca serriola* and *Salsola tragus* were correlated with high values of pH. Biotic factors of significance were distance from the burn perimeter, proximity to unburned patch edges, and pre-burn canopy cover. Native perennial species such as *Astragalus filipes*, *Koeleria macrantha*, *Penstemon watsonii*, and *Phlox longifolia* were favored by increased proximity to unburned patches. When increases in pre-burn canopy cover were associated with increases in proximity to unburned patches, perennials such as *Arabis sparsiflora*, *Astragalus purshii*, and *Phacelia hastata* were favored. Increases in pre-burn canopy cover without a concomitant increase in proximity to unburned patches favored exotic invasive annual species. Abiotic factors accounted for 11.3% of the total species variance, biotic factors accounted for 7.1%, and an interaction between abiotic and biotic factors accounted for 1.4% of the total species variance. These findings indicate that land managers should focus pre- and post-fire restoration efforts on sites with high pre-burn canopy cover, and post-fire restoration management should also focus on xeric sites at greater distances from unburned patches. It is under these conditions that plant community resilience to fire was lowest, and where invasive annual species showed the highest frequencies.

Introduction

Plant succession following disturbance is complex as it often depends upon two conditions, both of which are difficult to measure after the fact: pre-disturbance vegetation and disturbance severity (Harper 1977, Sousa 1984, Suding et al. 2004, Bates 2006, Sibold et al. 2007). Fire is especially complex as it results in a landscape that is heterogeneous with respect to propagule availability and suitable microsites for

establishment. Additionally, pre-burn vegetation influences fire intensity through the spatial pattern of fuel loading. In the Great Basin, mountain big sagebrush grasslands have been shown to be more resistant than pinyon-juniper woodlands to invasion by exotic species following fire (Floyd et al. 2006, Seefeldt et al. 2007).

The Great Basin is an arid environment of extremes with dry, hot summers and cold winters that slow rates of plant succession. Succession does not progress at the same rate from year to year as precipitation is highly variable (Mack and Pyke 1983). Environmental stresses must fit within the tolerance range of a given species for an individual to establish and survive. Simultaneously, establishment requires that either plants or plant propagules survive the fire or that the location be within the dispersal range of seed sources. In the Wall Canyon burn, I assumed that nearly all woody vegetation was top killed by fire except in unburned patches as skeletons were infrequent in the landscape. As a result, fire severity was defined in terms of soil heating and effects on surviving root crowns and seedbanks.

After fire, plant propagule availability influences initial floristic composition, which determines the rate and possibly the outcome of succession (Egler 1954, Bates 2006, Sibold et al. 2007). Native species must occupy favorable sites first to inhibit the establishment of invasive species (Chambers 2007). Native species can occupy the site when a seed source or surviving meristem is present. In extreme environments, the establishment or regrowth of certain pioneer species is also likely to facilitate subsequent establishment of other, less stress-tolerant species (Watt 1947, Egler 1954), changing the rate and direction of succession where these species occur. This is referred to as the nurse plant phenomenon (Niering et al. 1963, Cody 1993). In post-burn pinyon-juniper

woodlands, the presence of the nurse plant phenomenon is extended to intraspecific relationships. *Pinus monophylla* establishes more successfully under the cover of trees and shrubs than in the interspaces (Chambers 2001). In comparison to interspaces, microsites under trees and shrubs have elevated levels of soil nutrients, organic carbon, and near surface water (Chambers 2001). Interspaces have higher levels of solar insolation, and soil moisture conditions may not be within the drought tolerance range of juvenile *P. monophylla* trees. As *P. monophylla* grows in stature it shades out the shade-intolerant *A. tridentata*, resulting in a “switch” as described by Wilson and Agnew (1992) implying a transition from facilitation to competition where one species promotes its own establishment. In the Great Basin, I expect environmental stresses, competition, and facilitation to influence species establishment. The effects of these influences, which may have been acting before or immediately after a fire, should be apparent for some time after the initial phases of succession.

Pre-fire site history and vegetation structure determine many of the biotic influences on post-fire succession. In addition to the abiotic factors thought to influence species establishment, I examined the influence of pre-burn canopy cover and proximity to unburned patches. As canopies in pinyon-juniper woodlands become more closed, understory species richness and cover become reduced (Huber et al. 1999, Poulsen et al. 1999, Dhaemers 2006) as does understory seed production (Everett and Sharrow 1983). Such understory plant communities are likely to be less resistant to disturbances, such as fire, as competition for resources eliminates native perennial bunchgrasses, forbs, and shrub species that are capable of rapidly resprouting following fire (Breshears 1993). Disturbances also result in pulses of nutrient availability. Without surviving vegetation

present to absorb these increases, disturbed sites favor establishment by annual species (Davis 2000).

Anthropogenic disturbance is also influential as human impacts reduce pre-burn canopy cover through tree harvesting, grazing, and use of recreational vehicles. Additionally, disturbed areas are likely to show altered species composition as certain grass species are favored by selective grazing (Johnson 1956) and physical disturbances favor more ruderal species (Pianka 1970).

Fire is an intrinsically stochastic process that operates at a landscape scale. When examining the abiotic and biotic factors influencing species establishment following fire, it is important to account for the intrinsic properties of fire, as fire behavior itself is influenced by these same factors that influence species establishment. For example, Rothermel's (1972) model for surface fire spread incorporates the interaction of wind, slope, density of fuels, and moisture to predict the rate of fire spread and fireline intensity. As I lacked pre-fire data, my best estimate as to how these factors act on this particular landscape comes from our knowledge of the fire regime. The fire regime of a given area is characterized by the intensity, severity, extent, seasonality and frequency of fire (Whelan 1995). The pinyon-juniper fire regime is characterized by high-severity fires (Baker and Shinneman 2004, Bauer 2006) and mosaics of burned and unburned areas due to variable fuel loading, high fuel moisture, and variable winds (Baker 2006). Although I could not directly account for variation in fire severity throughout the burn, I predicted that by examining succession in post-burn pinyon-juniper woodlands at the landscape scale I would be able to explain a range of plant species responses due to these unobserved processes.

Figure 1 is a conceptual model of the interacting factors driving plant species distributions after fire in pinyon-juniper woodlands. The model's layers represent the time sequence preceding and following fire, with the first layer representing pre-fire conditions. Plant and propagule sources present in the post-burn environment are a product of what survived the fire as seedbank or other propagule sources, and what was present in the pre-burn understory as a result of past disturbances and increasing

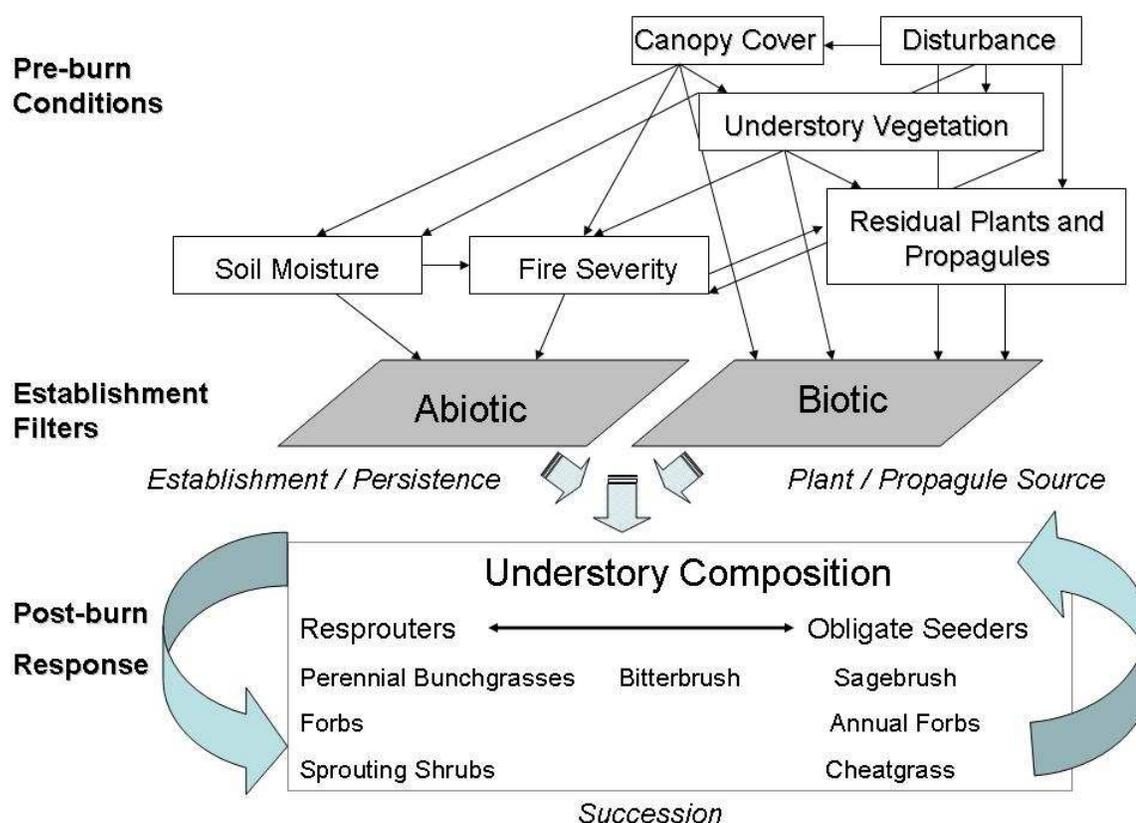


Figure 1. Interacting factors thought to act as filters to plant occurrence after fire

pre-burn tree canopy (leading to the “biotic box” in Figure 1). For successful establishment and persistence, a plant or propagule must be present at a site and environmental conditions must meet species-specific requirements. Abiotic factors considered in this study include location in the watershed, topography, temperature,

proximity to disturbances, soil characteristics, and moisture availability (leading to the “abiotic box” in Figure 1). I use the term “filter” to describe these two categories of variables (abiotic and biotic) affecting plant species establishment and persistence. The interaction of the pre-burn species pool with these two categories of filters results in post-burn understory species composition of varying life history traits.

The relative strength of spatially explicit filters varies at landscape scales. A disturbance event such as a high severity wildfire can alter abiotic filters through effects on the physical environment, and can act as a biotic filter through differential effects on species survival, reproduction, and colonizing ability (White and Jentsch 2004). Biotic and abiotic filters interact with species life history traits, perhaps resulting in a particular, post-fire successional pathway for any given patch with characteristic disturbance severity, physical environment, and proximity to propagules (Figure 1, Table 1). Life history characteristics of a species include its quantity and seasonality of reproduction, dispersal distance, seed viability and ability to recover vegetatively from damaged tissue (Sousa 1980). Therefore, I expected that areas of severe burn, especially as compounded by high pre-burn canopy cover, that were far from available seed sources were likely to be dominated by widely dispersing, seeding species whereas areas of low severity burn were more likely to be dominated by resprouting species. Not all species present after fire are equally represented in the landscape and those that are present, grow at different rates in response to stresses of environment and competition, determining species abundance at a site (Noble and Slatyer 1980, Sousa 1980).

If plant successional pathways are predictable following fire as a function of species life history traits, restoration ecologists can better design disturbance events that

would result in desirable species composition (i.e. native plant communities). Therefore, the over-arching goals of this study were to:

- (1) Assess whether patches of similar microtopography, pre-burn understory composition, and post-burn seed rain are likely to exhibit similar post-burn species composition
- (2) Develop statistical models predicting plant community composition for different patches within a burn
- (3) Develop recommendations for restoration ecologists seeking to use prescribed fire or similar treatment for maintaining native understory composition in pinyon-juniper woodlands

Methods

Data Collection

Study Design

The highest concentration of disturbances was found at the mouth of the canyon. Therefore, I divided the canyon into three equal sections in relation to distance from the canyon mouth to stratify sites by anthropogenic disturbance. Two gradsects within each section were positioned to sample along gradients of elevation and distance from the burn perimeter and that spanned the major drainages of the canyon. I located survey plots along these transects that were > 100-m apart in most cases, although a few plots were closer than 100-m to sufficiently sample unburned patches. A total of 102, 20-m by 50-m (0.1-ha) plots were surveyed (71 within the burn, 16 outside the burn perimeter and 15 in unburned patches). The 50-m baseline of each plot ran perpendicular to the slope to maximize plot homogeneity.

Variables representing both biotic and abiotic factors are listed in Table 1. Solar radiation was calculated for May 15 to correspond with germination and July 15 to correspond with the hottest and most likely lethal temperatures of the year.

Table 1. Environmental variables considered as possible influences on plant establishment Variables marked with an asterisk are those that were found to be relatively uncorrelated with other variables and were included in Canonical Correspondence Analysis. All variables were collected in each sample plot and used in Detrended Correspondence Analysis.

	Abiotic Variables		Biotic Variables
May 15 Solar Radiation*	Solar radiation calculated for May 15.	AveDist to B.Perimeter*	The average distance to the burn perimeter from 8 compass directions.
July 15 Solar Radiation	Solar radiation calculated for July 15.	ED 150	The density of unburned patch edge w/in a 150-m radius of a plot.
Slope*	Field derived measurements of slope steepness (degrees).		
GIS Aspect	GIS derived aspect corrected so that higher values correspond to increased northeastness.	ED 300*	The density of unburned patch edge w/in a 300-m radius of a plot.
Roads	The distance to the nearest road.	Perimeter	The distance to the nearest burn perimeter.
Max Depth*	The maximum soil depth (cm).	UB patch	The distance to the nearest unburned patch.
Min Depth*	The minimum soil depth (cm).	PJCover_A*	The area covered by pre-burn tree canopy in a survey plot.
Average Depth	The average soil depth (cm).		
Northing	The north values provided in universal transverse Mercator.	PJCover_C	No. of tree canopy polygons in a survey plot.
Easting	The east values provided in universal transverse Mercator.		
PerCFrg*	The percent of coarse fragment in surface soils (down to 10 cm) determined by weight.	Relative PJCover	The area of the pre-burn plot covered by tree canopy divided by the specific area of the plot surveyed.
Percent Clay	The average percentage of clay in surface soils (down to 10 cm) assessed by a ribbon test.	UB_A50	The total area of unburned patches w/in a 50-m radius from the surveyed plot.
Plot pH*	The surface soil (down to 10 cm) pH value.	UB_C50	No. of unburned tree polygons in a 50-m radius from a surveyed plot.
Slope Curvature	The curvature of the survey plot: concave, convex, or flat.	UB_A150	The total area of unburned patches w/in a 150-m radius from the surveyed plot.
Slope Position	The position of the survey plot in the landscape: ridge-top, up-slope, mid-slope, low-slope, or valley bottom.	UB_C150	No. of unburned tree polygons in a 150-m radius from a surveyed plot.

Table 1. continuation 1

Abiotic Variables	Biotic Variables	Abiotic Variables	Biotic Variables
TCI*	Topographic convergence index	UB_A300	The total area of unburned patches w/in a 300-m radius from the surveyed plot.
Wall DEM	Elevation derived from a digital elevation model.	UB_C300	No. of unburned tree polygons in a 300-m radius from a surveyed plot.

GIS Derived Data

Abiotic Variables

A number of variables were derived from digital elevation models (DEMs) using ArcGIS 9 software. Survey plot perimeters were recreated in ArcMap from 3 GPS points of the 50-m baseline perpendicular to the slope. The resulting plot polygons were used to sample topographic variables obtained from 30-m DEMs. Topographic variables included elevation, slope aspect, slope steepness, slope position, solar radiation and topographic convergence index. A cosine transformation was used to convert slope aspect to a linear variable ranging from 0 (southwesterly aspects, or drier sites) to 2 (northeasterly aspects, or more mesic sites). Slope, aspect, and latitude were used to estimate solar radiation for May 15 (Kumar et al. 1997) so as to correspond with the germination of most plant species found in the canyon, and for July 15, the hottest temperatures of the year.

Topographic convergence index was calculated as

$$(1) \quad TCI = \ln(\alpha / \tan \beta)$$

where α is the upslope contributing area of water drainage to the point of interest and β the local slope angle. The index generates high values for sites that collect and retain water in runoff events (e.g. depressions), and low values for ridgetop sites or sites with steep slopes.

Biotic and Disturbance Variables

I used distance to the nearest road as a proxy for anthropogenic disturbances such as ATV use, salvage logging, and grazing. Pre-burn canopy cover was sampled for the specific area of each surveyed plot. A polygon layer of pre-burn tree canopy was created using an object oriented classification of 1-m resolution, 1994 (six years prior to the burn), digital orthophotos (DOQs) of the study area, implemented in Ecognition Professional (version 4.0) software after topographic shadows on the photos had been removed with Idrisi (version Kilimanjaro) software by regressing a hillshade map on the brightness values of the DOQ (Greenwood 2006, Weisberg et al. 2007). The object oriented classification used brightness, patch shape, patch area, distance, textural homogeneity, and local neighborhood relationships to segment images into homogeneous patches, delineating those that represent tree polygons (Weisberg et al. 2007). The total area covered by tree polygons in each plot was divided by the area of each plot to derive the pre-burn canopy cover specific to each plot.

Burn severity throughout Wall Canyon was classified using pre- and post-burn Landsat TM imagery from June 2, July 20, and October 8, 2000, respectively, to calculate differenced Normalized Burn Ratio (dNBR) values (J. Bauer, unpublished data, Figure 2). NBR classifies burned area using a ratio of short-wave infrared bands, Band 4 (0.76 – 0.90-um) and Band 7 (2.08 – 2.35-um) in the equation (Cocke 2005):

$$\text{NBR (x)} = (\text{Band 4} - \text{Band 7}) / (\text{Band 4} + \text{Band 7})$$

The difference in NBR was used to create a classification of burned and unburned areas. The unburned patch layer was ground-truthed at 94 sample locations within the burn perimeter (Table 2). Twenty of 23 (87 %) unburned patches surveyed were accurately

classified, although the boundaries of most patches required adjustments. All 71 of the attempted survey plots within the burn were in fact burned. A layer of field-corrected unburned patches and the burn perimeter was used to estimate the influence of these patches and the outside burn area as seed sources in the post-burn landscape. Area covered by unburned patches was calculated at 50-m, 150-m, and 300-m circular distance neighborhoods from each surveyed plot. The distance to the closest unburned patch and this distance to the closest burn perimeter were calculated. Due to the steep topography of the canyon and the complexity of the burn perimeter, an average distance to the burn perimeter was calculated from eight compass directions. Surveyed plots that are close to the burn perimeter in more than one direction are likely to show more effect of unburned seed source than a plot that may be close to the burn perimeter in a single direction. Unburned patches show varying degrees of edge complexity or edge density. Edge density was calculated for circular neighborhoods with radii of 150-m and 300-m from each surveyed plot.

Table 2. Contingency table comparing predictions of burned and unburned patches from an image classification to field observations

	Observed Burned	Observed Unburned	Row Totals
Predicted Burned	71	0	71
Predicted Unburned	3	20	23
Column Total	74	20	94

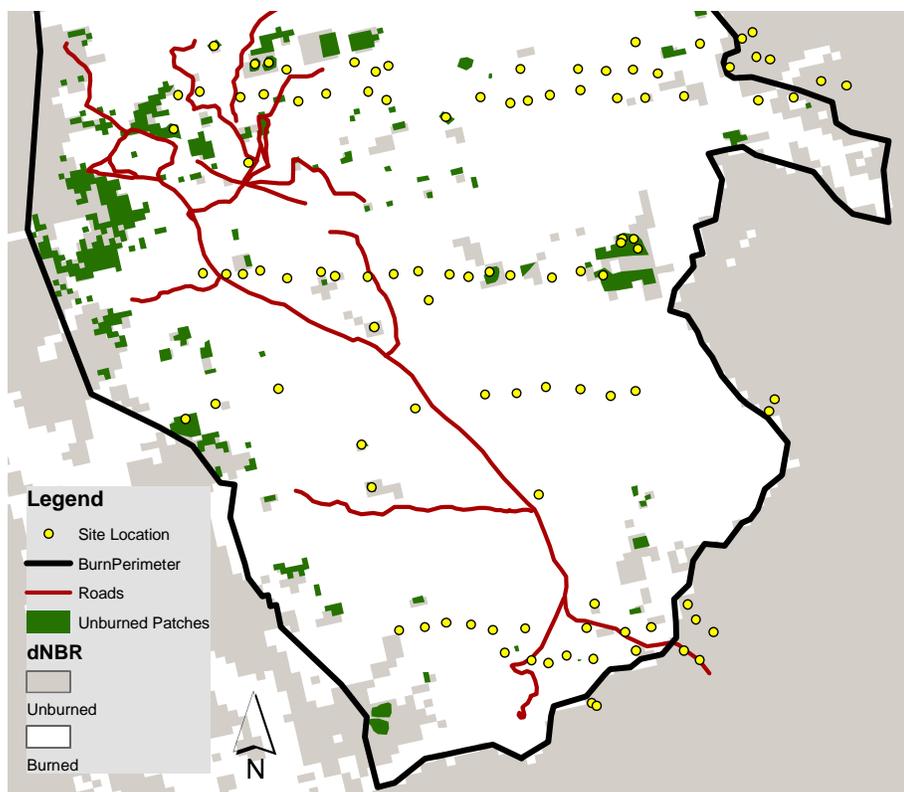


Figure 2. Map of dNBR burn area in Wall Canyon

Field and Literature Derived Data

Abiotic and Biotic Factors and Responses

Life history traits for all species were compiled from a literature review. Aerial cover of all herbaceous and graminoid species was ocularly estimated from 25, 0.5-m² quadrats within a 20-m by 50-m plot (Figure 3). Additional estimates included total plant cover by species and cover of litter, bare ground, gravel, and rock. Gravel was defined as any rock fragment greater than 1 cm and less than 7.5-cm in length. Rock included any fragments that were greater than 7.5-cm in length. Within these quadrats, slope curvature (concave, convex, or flat) and microsite (under tree, under shrub, or interspace) were also recorded. Quadrat positions were randomly selected prior to data collection at 2, 4, 16,

20, 22, 24, 26, and 34 meters along the 50-m transect length, with an additional quadrat at 5 m being surveyed along only the first transect to give a total of 25 quadrats (Figure 3).

Three 50-m belt transects were used to survey shrub and perennial grass species rooted within the transects (Figure 3). Belt transects were 2-m wide for shrubs and 0.2-m wide for perennial grasses. For shrubs, height and lengths of major and minor axes of the canopy were measured regardless of whether the canopy extended beyond the transect. Age class and evidence of resprouting were recorded. Age classes were defined as: seedling (no evidence of flowering, ≤ 15 -cm high), juvenile (no evidence of flowering), adult (evidence of flowering), adult mature ($>50\%$ dead) and dead. Evidence of resprouting was noted if there was char at the base of the plant or a caudex that was clearly too large to have developed in the 6 years following the fire. If more than 100 individual shrubs were encountered within the first two transects, the third transect at 10 m was skipped. Counts of perennial grasses species were tallied within each 0.2-m by 50-m belt transect within each surveyed shrub transect.

Abiotic Factors

Abiotic data collected from each plot included slope steepness, slope curvature (concave, convex or flat), slope position (ridgetop, upslope, midslope, lowslope or valley bottom) and distance to the nearest unburned patch or burn perimeter obtained using a Bushnell Yardage Pro 1000, 1-m precision, rangefinder (Table 1). Elevation at plot origin was recorded using a GeoExplorer XT global positioning system (GPS) with submeter precision. Soil depth was measured by hammering a metal rod into the earth until a change in resistance was felt. The rod was then removed and the depth to the

point of resistance was recorded. Soil depth was recorded as the average of three readings from each of 10, 0.5-m² quadrats (Harner and Harper 1976). These averages were used to calculate maximum and minimum soil depth for each 20-m by 50-m plot. Soil samples were collected from the same 10, 0.5-m² quadrats and subsequently analyzed for texture, pH and percent coarse fragment. Texture was assessed using a ribbon test following the classification of Thien (1979). Soil pH was measured with a Corning pH meter 320 using roughly 10 grams of soil and 19-mL of DI water and 1-mL CaCl₂. Nitrate and ammonium concentrations were measured with KCl extracts.

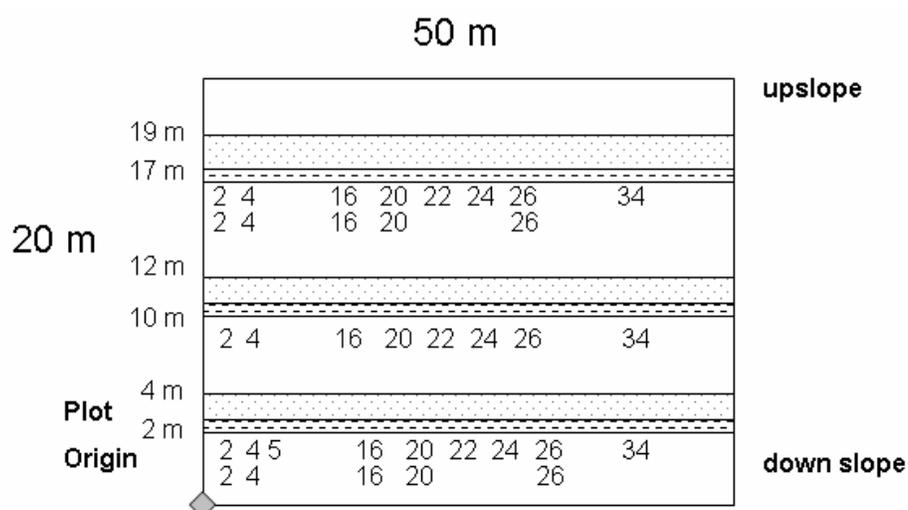


Figure 3. Layout of each 20-m by 50-m macroplot Aerial cover was estimated in 0.5-m² quadrats designated by the rows numbered 2-34. Soils data were gathered from the quadrats designated by the rows numbered 2-26. Perennial grasses were surveyed in 0.2-m by 50-m belt transects represented by dashed belts. Shrubs were surveyed in 2-m by 50-m belt transects represented by dotted belts.

Data Analysis:

Environmental gradients describing species distribution were identified with ordination analyses. All ordination analyses were conducted using PC-Ord software

(McCune and Mefford 1999). Relative Euclidean distance measures determined that no sites were outliers. Principal Components Analysis (PCA) was used to assess the structure of the dataset, based on the correlation matrix of variables (McCune and Grace 2002). For correlated variables, those that explained the most variance as determined by an independent Canonical Correspondence Analysis (CCA) were subsequently used in data analysis.

Cluster analysis was used to identify groups of consistently co-occurring species and the Hotelling's T-squared test was used to test whether these groups were significantly different, using pairwise comparisons. Using a hierarchical agglomerative approach, this cluster analysis sought the smallest element in a dissimilarity matrix and grouped species so that the smallest amount of information was lost. The distance measure used was a proportional coefficient, Sorenson's Index, with a flexible β at 0.20. An indicator species analysis identified the species most characteristic of each group, having the narrowest apparent niche or the most sensitive tolerance to environmental stresses, which aided in the interpretability of species groups. Simultaneous confidence intervals of differences in site group means determined which measured abiotic and biotic variables best distinguished species groups.

Both Detrended Correspondence Analysis (DCA) and Nonmetric Multidimensional Scaling (NMS) were used to infer the driving environmental gradients underlying plant community composition. Both techniques were used to test that the same gradients were identified by each approach.

Detrended correspondence analysis uses reciprocal averaging to show species frequency in ordination space. Species that were more likely to occur in proximity to one

another occur closer together in ordination space. NMS ordinations were also conducted to ensure that results between the two methods converged. Iterative NMS analyses were implemented to select the number of dimensions that reduced the most stress in the final ordination. This is important because as more dimensions are added to NMS, the solutions of the other dimensions change. Too many dimensions can spread important variation over all of the axes making it more difficult to interpret. The Sorensen (Bray-Curtis) index was used as the distance measure of ecological similarity. The number of dimensions was selected to reduce and stabilize the stress or departure in monotonicity of the ordination as indicated by the standard deviation of stress over the last 10-15 iterations. Monte Carlo tests were used to determine the statistical significance of dimensions in the NMS solution.

Canonical correspondence analysis (CCA), a direct ordination method, was used to maximize species-environment relationships. CCA works well both in situations with intercorrelated environmental variables, and in situations in which not all of the factors determining species composition are known (Palmer 1993). The relative contributions of factors driving species distributions were determined with partial CCAs and variance partitioning (Borcard et al. 1992, Cushman and Wallin 2002). Variables often share a common structuring due to an underlying gradient that affects more than one measured variable. Variance partitioning accounts for this overlap in structuring and allows for the calculation of unexplained variance. Unexplained variance is calculated with variance partitioning as total inertia minus the variance explained by the abiotic variables, plus the variance explained by the biotic variables given the effect of the abiotic variables. As I expected to see a different group of species establishing in the understory vegetation with

high pre-burn canopy cover and low proximity to unburned patches, I wanted to separate the effects of these variables from the others. Partial CCAs allowed me to see the individual effect of each factor and groupings of factors into abiotic and biotic categories. Axis scores were centered and standardized to unit variance and axes were scaled to optimize species scores. CCAs calculated linear combinations of variables from multiple linear least squares regressions of weighted averages of site scores. Monte Carlo tests (n=100 simulations) were used to test the null hypothesis that there was no relationship between species occurrences and the variables measured for each axis. Monte Carlo randomizations test the likelihood of achieving an eigenvalue equal to or greater than the stated value, given the number of simulations.

Results

Life History Traits

Life history trait information was compiled for all species found more than twice in the survey plots throughout Wall Canyon (Table 3). Categories of interest included U.S. nativity, fire tolerance, seed production, dispersal distance, seed viability, fire stimulated flowering or vegetative growth, scarification, fire resistance, shade tolerance, and drought tolerance. Fire tolerance refers to the ability of some life stage of the species to survive and re-establish after fire. Fire resistance denotes a physical characteristic of the plant that will resist fire damage.

Table 3. Life history attributes of all plant species found at Wall Canyon more than twice, classified by functional type
Species

Annual Graminoid	Family	U.S. Nativity	Fire Tolerance	Seed Production	Dispersal Distance	Fire Stimulated Flowers / Shoots	Scarification	Fire Resistance	Shade Tolerance	Drought Tolerance
<i>Bromus tectorum</i> * ¹	Poaceae	Non-native	High	High	Low	Both	No	No	Intolerant	Low
<u>Perennial Graminoid</u>										
<i>Achnatherum hymenoides</i> *	Poaceae	Native	High	Moderate	Moderate	?	?	No	Intolerant	High
<i>Achnatherum nevadense</i> ^G	Poaceae	Native	High	Moderate	Moderate	?	?	No	Intolerant	High
<i>Achnatherum thurberianum</i> *	Poaceae	Native	High	Moderate	Low	?	?	No	Intolerant	High
<i>Elymus elymoides</i> * ^{C1}	Poaceae	Native	High	Moderate	Low	Flowers	?	No	Intolerant	Moderate
<i>Festuca idahoensis</i> *	Poaceae	Native	Moderate	High	Low	?	?	No	Intermediate	Low
								No	Intolerant	High
<i>Hesperostipa comata</i> * ^C	Poaceae	Native	Moderate	?	Moderate	Shoots	?			
<i>Koeleria macrantha</i> *	Poaceae	Native	High	Low	Low	?	?	No	Intolerant	High
<i>Poa nervosa</i> *	Poaceae	Native	High	Moderate	Low	?	?	No	Intolerant	High
<i>Poa secunda scabrella</i> *	Poaceae	Native	Moderate	Low	Low	?	?	No	Intermediate	High
<i>Pseudoroegneria spicata</i> * ^C	Poaceae	Native	High	?	Low	?	?	No	Intermediate	High
<u>Annual Forb</u>										
<i>Argemone corymbosa</i> ^{CP}	Papaveraceae	Native	High ?	?	?	?	?	No	Intolerant	High
<i>Chenopodium desiccatum</i> ^e	Chenopodiaceae	Native	?	?	?	?	?	No	Intolerant	?
<i>Chenopodium leptophyllum</i> ^e	Chenopodiaceae	Native	?	?	?	?	?	No	Intolerant	?
<i>Chorizanthe watsonii</i> ^C	Polygonaceae	Native	?	?	?	?	?	No	Intolerant	High
<i>Claytonia parviflora</i> ^G	Portulacaceae	Native	Moderate	Low	?	Flowers	?	No	Tolerant	None
<i>Claytonia perfoliata</i> *	Portulacaceae	Native	Moderate	Low	?	Flowers	?	No	Tolerant	None
<i>Collinsia parviflora</i> *	Scrophulariaceae	Native	Low	Moderate	Low	?	?	No	Tolerant	None
<i>Cryptantha torreyana</i> *	Boraginaceae	Native	?	?	?	?	?	No	Intolerant ?	?
<i>Descurainia sophia</i> *	Brassicaceae	Non-native	High	?	?	Flowers	?	No	Intolerant	High
<i>Eriastrum wilcoxii</i> ^{GC}	Polemoniaceae	Native	High	?	?	Flowers	?	No	Intolerant	?
<i>Eriogonum baileyi</i> ^c	Polygonaceae	Native	High	?	?	?	?	No	?	?
<i>Galium bifolium</i> ^C	Rubiaceae	Native	?	?	?	?	?	No	Intermediate	Low

Table 3. continuation 1

Species	Family	U.S. Nativity	Fire Tolerance	Seed Production	Dispersal Distance	Fire Stimulated	Scarification	Fire Resistance	Shade Tolerance	Drought Tolerance
<i>Gayophytum ramosissimum</i> *	Onagraceae			?			?		?	
<i>Gilia inconspicua</i> var. <i>inconspicua</i> ^C	Polemoniaceae	Native	?	?	?	?	?	No	Intermediate	?
<i>Gnaphalium palustre</i> ^{CJ}	Asteraceae	Native	?	?	High	?	?	No	Intermediate	Low
<i>Lappula redowskii</i> ^J	Boraginaceae	Native	High	?	?	?	?	No	Intolerant	High
<i>Mentzelia albicaulis</i> ^C	Loasaceae	Native	?	?	?	?	?	No	Intolerant	High
<i>Nicotiana attenuata</i> ^C	Solanaceae	Native	High	?	?	?	?	No	Intolerant	High
<i>Phlox gracilis</i> ^{CJ}	Polemoniaceae	Native	?	?	?	?	?	No	Intermediate ?	Intermediate
<i>Polygonum ramosissimum</i> ^{CJ}	Polygonaceae	Native	High	?	High	?	?	No	Intolerant	?
<i>Salsola tragus</i> ^{CE}	Chenopodiaceae	Non-native	High	High	High	?	?	No	Intolerant	High
Perennial Forb										
<i>Antennaria dimorpha</i> *	Asteraceae	Native	High	Moderate	Low	?	?	Yes	Intermediate	High
<i>Arabis holboellii</i> var. <i>retrofracta</i> ^J	Brassicaceae	Native	?	High	?	?	?	No	Intermediate	High
<i>Arabis sparsiflora</i> ^{CG}	Brassicaceae	Native	?	?	?	?	?	No	Intermediate	High
<i>Astragalus filipes</i> * ¹	Fabaceae	Native	Moderate	Low	Low	Shoots	?	No	Intolerant	High
<i>Astragalus purshii</i> * ¹	Fabaceae	Native	Moderate	High	Low	?	?	No	Intolerant	High
<i>Chaenactis douglasii</i> *	Asteraceae	Native	Low	Moderate	High	?	?	No	Intermediate	Moderate
<i>Corydalis aurea</i> *	Fumariaceae	Native	High	?	?	?	?	No	Intolerant	High
<i>Crepis acuminata</i> *	Asteraceae	Native	Low	Moderate	?	?	?	No	Intermediate	High
<i>Epilobium ciliatum</i> ^J	Onagraceae	Native	?	?	High	?	?	No	Intermediate	Low
<i>Eriogonum microthecum</i> ^{F1}	Polygonaceae	Native	Moderate	Moderate	Moderate	Shoots	No ?	No	Intolerant	High
<i>Eriogonum umbellatum</i> * ^{F1}	Polygonaceae	Native	Low	Moderate	Low	Shoots	No ?	No	Intolerant	High
<i>Lactuca serriola</i> ^C	Asteraceae	Non-native	?	High	High	No	?	No	Intolerant	High
<i>Lesquerella kingii</i> ^C	Brassicaceae	Native	Low	?	?	?	?	?	?	?
<i>Lupinus argenteus</i> var. <i>heteranthus</i> ^{CJF}	Fabaceae	Native	High	High	?	Flowers, Seeds	Yes	No	Intolerant	Intermediate
<i>Machaeranthera canescens</i> ^{CJ}	Asteraceae	Native	?	?	High	No	?	No	Intolerant	High
<i>Penstemon eatonii</i> *	Scrophulariaceae	Native	Moderate	High	Moderate	?	?	No	Intermediate	Moderate

Table 3. continuation 2

Species		U.S.	Fire	Seed	Dispersal	Fire		Fire	Shade	Drought
<u>Perennial Forb</u>	Family	Nativity	Tolerance	Production	Distance	Stimulated	Scarification	Resistance	Tolerance	Tolerance
<i>Penstemon watsonii</i> ^{CG}	Scrophulariaceae	Native	Moderate	Low	?	?	?	No	Intermediate	Low
<i>Phacelia hastata</i> [*]	Scrophulariaceae	Native	Moderate	Moderate	Low	?	?	No	Intermediate	High
<i>Phlox hoodii</i> ^C	Polemoniaceae	Native	High	?	?	Shoots	?	No	Intermediate	High
<i>Phlox longifolia</i> [*]	Polemoniaceae	Native	Moderate	Moderate	?	Shoots	?	No	Intermediate	High
<i>Senecio multilobatus</i> ^C	Asteraceae	Native	?	Moderate	?	?	?	No	Intolerant	Moderate
<i>Sphaeralcea parvifolia</i> ^C	Malvaceae	Native	?	?	?	?	?	No	Intolerant	High
<i>Viola purpurea</i> ^{CG}	Violaceae	Native	?	Low	?	Shoots	?	No	Intermediate	Moderate
<u>Shrub</u>										
<i>Artemisia tridentata</i> ssp. <i>vaseyana</i> ^{*1}	Asteraceae	Native	None	Moderate	Low	?	?	No	Intolerant	High
<i>Chrysothamnus</i> <i>nauseosus</i> ^{CG}	Asteraceae	Native	High	High	High	Flowers and Shoots	?	No	Intolerant	High
<i>Chrysothamnus</i> <i>viscidiflorus</i> ^{*1}	Asteraceae	Native	None	High	High	Flowers and Shoots	?	No	Intolerant	Moderate
<i>Ephedra viridis</i> [*]	Ephedraceae	Native	High	Low	Low	Shoots	?	No	Intermediate	High
<i>Prunus andersonii</i> ^{*1}	Rosaceae	Native	High	Very Low	Very Low	Shoots	?	Yes	Intolerant	High
<i>Purshia tridentata</i> ^{*CF}	Rosaceae	Native	High	Moderate	Low	Flowers and Shoots	Yes	No	Intolerant	High
<i>Ribes aureum</i> ^{*F1}	Grossulariaceae	Native	Moderate	Moderate	Moderate	Shoots	Yes	No	Intermediate	Moderate
<i>Ribes cereum</i> ^{*F}	Grossulariaceae	Native	High	High	Moderate	Shoots	Yes	Yes	Intolerant	High
<i>Symphoricarpos</i> <i>oreophilus</i> ^{*F}	Caprifoliaceae	Native	High	Moderate	Moderate	Shoots	Yes	No	Intermediate	High
<i>Tetradymia canescens</i> ¹	Asteraceae	Native	Moderate	High	Moderate	Shoots	?	Yes	Intolerant	High
<u>Trees</u>										
<i>Juniperus osteosperma</i> [*]	Cupressaceae	Native	Low	High	Low	Shoots	Yes	No	Intolerant	High
<i>Pinus monophylla</i> ^{*C}	Pinaceae	Native	Low	Moderate	Moderate	No	?	No	Intolerant	High

* = USDA, NRCS. 2006, ^C = personal observation or conclusion, if cover was said to increase after fire, fire tolerance was interpreted to be high; ^e = www.eFloras.org, ^G = generalized from congeneric species, ^J = Jepson Manual Higher Plants of California (Hickman 1993), ^F = Seeds of Woody Plants in the United States, ^P = Peterson Field Guide: Pacific States Wildflowers (Niehaus et al. 1976), ¹ = J. Chambers personal communication, Note: rate of spread from the USDA plants webpage was interpreted as dispersal distance

Variable Selection

A principal components analysis was conducted on the environmental variables to reduce the multicollinearity of the data set and aid in variable selection. A broken stick eigenvalue estimate (McCune and Grace 2002) suggested that the first 4 axes explained enough variance to be considered for interpretation (Table 4) and the three variables with the highest correlation coefficients were identified for each axis (Table 5). These variables fell into the broader categories of the influence of unburned patches, aspect, pre-burn canopy cover, and slope (Table 5). Incremental R^2 values for individual CCAs of each variable were used for comparison among factors (Table 7). Performance in DCA ordinations, raw correlations with other variables, and the number of significant axes in CCA ordinations as judged by Monte Carlo randomizations were taken into account when deciding on a final set of variables to be used in these analyses. A correlation matrix has been included in the appendix and all variables with correlations higher than 0.4 were closely examined.

The final set of variables included: solar radiation calculated for May 15th, pH, field measured slope, maximum soil depth, minimum soil depth, percent coarse fragment, topographic convergence index, distance to the burn perimeter averaged over eight compass directions, the area of pre-burn canopy cover in a survey plot, and edge density at 300-m from a survey plot.

Table 4. Variance extracted in PCA of environmental variables

Axis	Eigenvalue	% of Variance	Cum % Variance	Broken-stick Eigenvalue
1	7.258	21.347	21.347	4.118
2	4.479	13.174	34.521	3.118
3	3.486	10.253	44.774	2.618
4	2.550	7.499	52.274	2.285

Table 5. Eigenvalues of the top 3 variables associated with each eigenvector Factors in bold are those that independently showed the highest correlations with the species data in individual CCA analyses. 5_15 sol – solar radiation calculated for May 15th, 7_15 sol – solar radiation calculated for July 15th, Cat_Aspect – aspect divided into categories of north, south, east and west, ED 150 – edge density of unburned patches at 150 m of a surveyed plot, ED 300- edge density of unburned patches at 300 m of a surveyed plot, F_Corr_A – field measured aspect corrected for northeastness, F_Slope – field measured slope, GCorr_A – GIS derived aspect corrected for northeastness, Int_road – distance to the nearest road, PJCov_A – area of pre-burn tree canopy cover in a plot, PJCov_C – number of pre-burn tree polygons in a surveyed plot, R_PJCov – percent cover of pre-burn tree canopy cover in a plot, UB_A300 – area of unburned patches within 300 m of a surveyed plot

Eigenvector 1		Eigenvector 2		Eigenvector 3		Eigenvector 4	
Variable	Correlation	Variable	Correlation	Variable	Correlation	Variable	Correlation
ED 300	-0.3222	GCorr_A	-0.3507	PJCov_A*	-0.3398	F_Slope	0.3681
UB_A300	-0.3170	Cat_Aspect	0.3290	R_PJCov	-0.3376	Int_road	0.3516
ED 150	-0.2997	F_Corr_A	-0.3255	PJCov_C*	-0.3357	7_15sol	-0.3458
						5_15 sol	-0.3252

Variables that were selected for further analysis (Table 1) were compared by plot type. Variable means were comparable between plot types with the exception of slope of unburned patches (Table 6). Other differences between plots would be expected based upon the type of plot. Outside burn perimeter plots were immediately outside the burn area. Overall, these plots were closer to the burn perimeter. Unburned patch plots also had higher densities of unburned patch edges.

Table 6. Statistical summary of environmental variables by plot type The mean and standard deviation of each variable is reported. The sample size of each group is reported under the group.

Plot Type	Slope	Max Soil Depth	Min Soil Depth	Plot pH	Percent Coarse Fragment	May 15 th Solar Radiation	TCI	Average Distance to Burn Perimeter	Pre-burn Canopy Cover	Edge Density at 300 m
Burn 71	38.4 (16.3)	53.3 (19.5)	7.7 (4.6)	7.1 (0.5)	42.5 (10.6)	26418.4 (1996.6)	5.5 (2.8)	2209.5 (372.4)	229.9 (71.5)	17.9 (22.6)
Unburned 16	50.9 (10.4)	51.7 (20.7)	5.1 (3.8)	7.1 (0.7)	44.9 (7.9)	25288.9 (2301.3)	6.8 (4.3)	2258.4 (262.8)	185.0 (53.1)	50.5 (34.3)
Outside Burn 15	39.6 (15.9)	64.3 (17.8)	9.5 (5.0)	6.5 (0.5)	48.2 (11.7)	26534.3 (1521.9)	5.4 (1.4)	256.0 (116.7)	225.9 (48.8)	4.0 (6.37)

Table 7. Increment R² values for environmental variables

The following CCAs were run with 100 randomizations. Variables are ordered by increment R² values. Variables with axes determined to be statistically significant are in bold. * Indicates that the variable was kept in further analyses because it was not correlated with another variable at 0.4 or above, or it explained more variance than another, correlated variable. Edge Density 150 m – density of unburned patch edges within 150 m of a surveyed plot, Edge Density 300 m – density of unburned patch edges within 300 m of a surveyed plot, Perimeter – distance to the nearest burn perimeter, PJCov_A – area of pre-burn canopy cover within a surveyed plot, PJCov_C – number of pre-burn tree polygons within a surveyed plot, Relative PJCover – percent cover of pre-burn tree canopy in a surveyed plot, UB_A50 – area of unburned patches within 50-m of a surveyed plot, UB_A150 – area of unburned patches within 150-m of a surveyed plot, UB_A300 – area of unburned patches within 300-m of a surveyed plot, UB_C50 – count of unburned patches within 50-m of a surveyed plot, UB_C150 – count of unburned patches within 150-m of a surveyed plot, UB_C300 – count of unburned patches within 300-m of a surveyed plot, UB patch – distance to the nearest unburned patch from a surveyed plot, Wall DEM – elevation from a digital elevation model

Variable	Significance from Monte-Carlo randomizations	Increment R ²	Interset Correlations
Average Distance to Burn Perimeter*	0.07	0.07	0.587
May 15 Solar Radiation*	0.01	0.062	-0.628
July 15 Solar Radiation	0.12	0.057	-0.613
Slope*	0.01	0.032	0.788
UB_C300	0.01	0.023	-0.706
UB_C150	0.03	0.018	-0.616
Edge Density 300 m*	0.01	0.016	-0.648
TCI*	0.25	0.013	-0.579
Plot pH*	0.04	0.012	0.630
Edge Density 150 m	0.04	0.01	-0.537
UB_A300	0.06	0.01	-0.610
Easting	0.04	0.01	-0.677
Roads	0.12	0.004	0.627
Perimeter	0.13	0.004	0.641
PJCover_A*	0.01	0.003	0.643
UB_A150	0.11	0.003	-0.516
Wall DEM	0.01	0.003	0.669
GIS Aspect	0.01	0.003	-0.701
Average Soil Depth	0.18	0.003	0.693
UB patch	0.01	0.001	0.582
Percent Coarse	0.21	0.001	-0.612
Fragment*			
Percent Clay	0.50	0.001	-0.594
PJCover_C	0.03	0.001	0.583
UB_A50	0.65	0.001	0.533
Relative PJCover	0.01	0.000	0.664
UB_C50	0.25	0.000	0.557
Maximum Soil Depth*	0.06	0.000	0.650
Minimum Soil Depth*	0.03	0.000	0.606
Northing	0.01	0.000	0.693

Cluster and Indicator Species Analyses

The cluster analysis was most interpretable at a proportion of explained variance of 0.20, resulting in 4 groups (Figure 4). The Pillai Trace statistic indicated that groups were significantly different (0.663, $F = 3.03$ on 18, 192, $p < 0.001$). Hotelling's T-squared statistic indicated that all groups were significantly different from each other at a $\alpha = 0.05$ with the exception of groups 2 and 4 which were different at an α significance level of 0.06. These groups could be described with a few variables whose means were found to be significantly different between specified groups, including solar radiation, soil pH, slope, and proximity to unburned patches (Table 8, 9).

The same four groups were used in an indicator species analysis. The species shown to have the highest fidelity to and abundances within those groups are listed in Table 10. The positions of some species in subsequent ordination analyses were used to interpret groups. Group 1 included more mesic species found on sites with greater minimum soil depths, and influence of unburned patches (Table 8, 9, 10 and Figure 7, 8). Group 2 species showed similar preferences to Group 1 but were found on gentler slopes (Table 8, 9, 10). Group 3 species were more abundant on sites with substantial pre-burn canopy cover and little influence of unburned patches (Table 8, 9, 10 and Figure 12). Group 4 species were generalists on sites with lower TCI values (Table 8, 9, 10 and Figure 7).

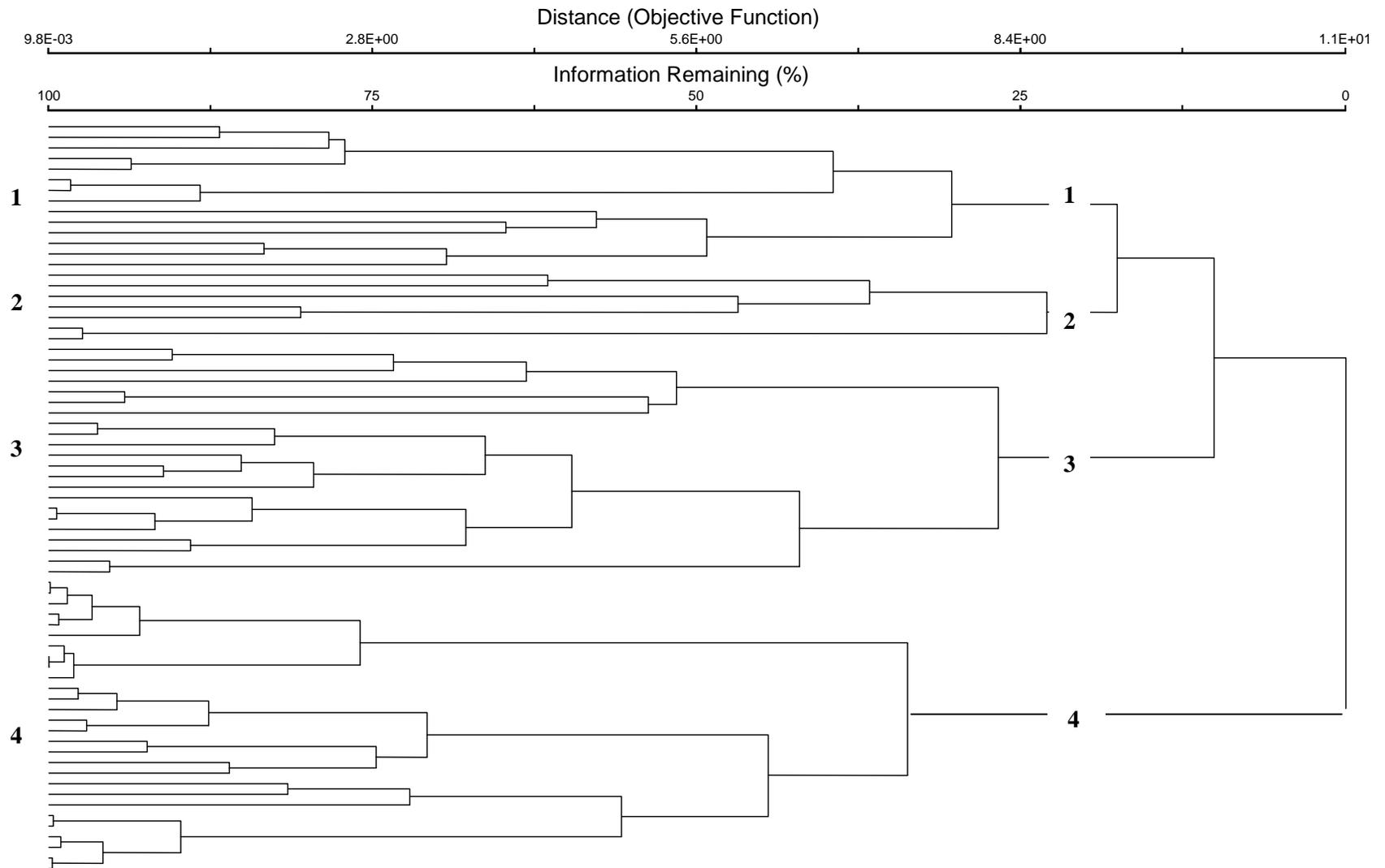


Figure 4. Dendrogram of cluster analysis of all surveyed sites

Table 8. Significant 95% confidence intervals of variables between groups

Groups and Variables	Estimate	Standard Error	Lower Bound	Upper Bound
1-2 Slope	23.80	7.14	4.41	43.20
1-3 Edge Density	23.50	7.31	3.68	43.40
1-4 Solar Radiation	-2210.00	606.00	-3850.00	-563.00
2-3 Plot pH	-0.69	0.22	-1.27	-0.10

Table 9. Statistical summary of environmental variables by cluster analysis groups The mean and standard deviation of each variables is reported. The sample size of each group is reported under the group.

	Slope	Max Soil Depth	Min Soil Depth	Plot pH	Percent Coarse Fragment	May 15 th Solar Radiation	TCI	Average Distance to Burn Perimeter	Pre-burn Canopy Cover	Edge Density at 300 m
Group 1	45.3	54.3	10.3	7.1	41.2	25049.14	5.7	2350.3	244.1	31.4
15	(14.4)	(20.6)	(5.0)	(0.37)	(12.0)	(2288.7)	(2.2)	(267.7)	(57.6)	(26.0)
Group 2	21.9	67.9	9.1	6.6	43.6	27117.9	6.3	2097.2	185.0	12.1
7	(25.8)	(17.0)	(6.7)	(0.3)	(12.7)	(833.0)	(3.9)	(345.7)	(76.3)	(18.1)
Group 3	39.2	47	6.5	7.3	39.3	26349.7	5.9	2309.9	250.3	9.0
22	(13.0)	(17.4)	(3.1)	(0.6)	(7.9)	(2317.3)	(3.0)	(209.0)	(50.1)	(16.5)
Group 4	38.1	54.2	6.9	7.1	45.5	27053.6	4.8	2078.6	217.1	19
27	(14.6)	(19.9)	(4.5)	(0.5)	(10.9)	(1333.6)	(2.5)	(480.3)	(86.2)	(23.0)

Table 10. Species groupings derived from indicator species analysis

1	2	3	4
<i>Lappula redowskii</i> * [^]	Brassicaceae total*	<i>Salsola tragus</i> * [^]	<i>Argemone corymbosa</i> *
<i>Symphoricarpos oreophilus</i> * [^]	<i>Lupinus argentus</i> var. <i>heteranthus</i> * [^]	<i>Lactuca serriola</i> *	<i>Bromus tectorum</i> * [^]
<i>Machaeranthera canescens</i> *	<i>Epilobium ciliatum</i> *	<i>Chrysothamnus nauseosus</i> ^{+^}	<i>Prunus andersonii</i> *
<i>Chaenactis douglasii</i> *	<i>Mentzelia albicaulis</i> *	<i>Chenopodium desiccatum</i> [^]	<i>Purshia tridentata</i> * [^]

Note: * indicates that the species is significant to a p-value of 0.05, and ⁺ a p-value of 0.1 from Monte Carlo randomizations. Species denoted with [^] are shown on the DCA biplot.

Indirect Ordination Analysis: Detrended Correspondence Analysis

All species that occurred in two plots or fewer were omitted from analyses. DCA explained 66.4% of the total variance in species occurrences (Table 11). To understand which variables and species strongly influenced these ordinations, species scores, axes correlations with species abundances and axes correlations with environmental variables were examined. Species highly correlated with Axis 1 (Tables 12, 13) were those species that were either found in drier or wetter environments. Axis 1 represented a soil moisture or productivity gradient (Figure 5). *Descurania sophia*, annual *Chenopodium* species, *Bromus tectorum* and *Lappula redowskii* are annuals which occur on dry sites and avoid drought with short life cycles, while *Penstemon watsonii*, cryptogams, and *Symphoricarpos oreophilus* are perennials found on wetter sites (Table 12, 13). The environmental variable most correlated with this axis was solar radiation, which confirms that species were distributed along this axis in relation to a moisture gradient (Table 14).

Axis 2 was more complicated. The environmental variable most correlated with this axis was pH (Table 14). Species with high scores along axis 2 and that were correlated with lower pH values were *Lupinus argentus* var. *heteranthus*, *Festuca*

idahoensis, and *Achnatherum thurberianum*. *Salsola tragus* had the lowest species score along axis 2 and was correlated with high values of pH and xeric sites with shallow soils (Table 12, 13, 14, Figure 5). Species with moderate scores on this axis were the shrubs that resprout following fire: *Chrysothamnus nauseosus*, *Ephedra viridis*, and *Purshia tridentata* (Figure 5). No variable on axis 3 had an R^2 value equal or greater to 0.2 and so the axis was not interpreted. The results of DCA ordinations were confirmed by converging results with NMS ordinations.

Table 11. DCA Coefficients of determination

Axis	Increment R-squared	Cumulative R-squared
1	0.367	0.367
2	0.187	0.555
3	0.109	0.664

Table 12. DCA extreme species scores for all species occurring more than twice

Species Scores 3 highest
(within 5 units)

Axis 1 Species	Axis 1 Score	Axis 2 Species	Axis 2 Score
		<i>Lupinus argentus</i> var.	
Cryptograms	412	<i>heteranthus</i>	404
<i>Penstemon watsonii</i>	386	<i>Festuca idahoensis</i>	385
<i>Polygonum ramosissimum</i>	355	<i>Achnatherum thurberianum</i>	360
<i>Poa nervosa</i>	351		

Species Scores 3 lowest

Axis 1 Species	Axis 1 Score	Axis 2 Species	Axis 2 Score
<i>Descurainia sophia</i>	-56	<i>Chenopodium desiccatum</i>	-16
<i>Chenopodium desiccatum</i>	-81	<i>Lesquerella kingii</i>	-40
<i>Lesquerella kingii</i>	-91	<i>Salsola tragus</i>	-48

Table 13. DCA species correlations with ordination axes

Axis 1 Species	Axis 1 Score	Axis 2 Species	Axis 2 Score
<i>Bromus tectorum</i>	-0.816	<i>Salsola tragus</i>	-0.806
		<i>Lupinus argentus</i> var.	
<i>Symphoricarpos oreophilus</i>	0.762	<i>heteranthus</i>	0.473
<i>Lappula redowskii</i>	0.645	<i>Tetradymia canescens</i>	0.419

Table 14. DCA environment correlations with ordination axes

Axis 1 Factor	Axis 1 r	Axis 2 Factor	Axis 2 r
May 15 Solar Radiation	-0.465	Plot pH	-0.454
Edge Density 300 m	0.316	Maximum Soil Depth	0.349
Minimum Soil Depth	0.289	Pre-burn Canopy Cover	-0.275

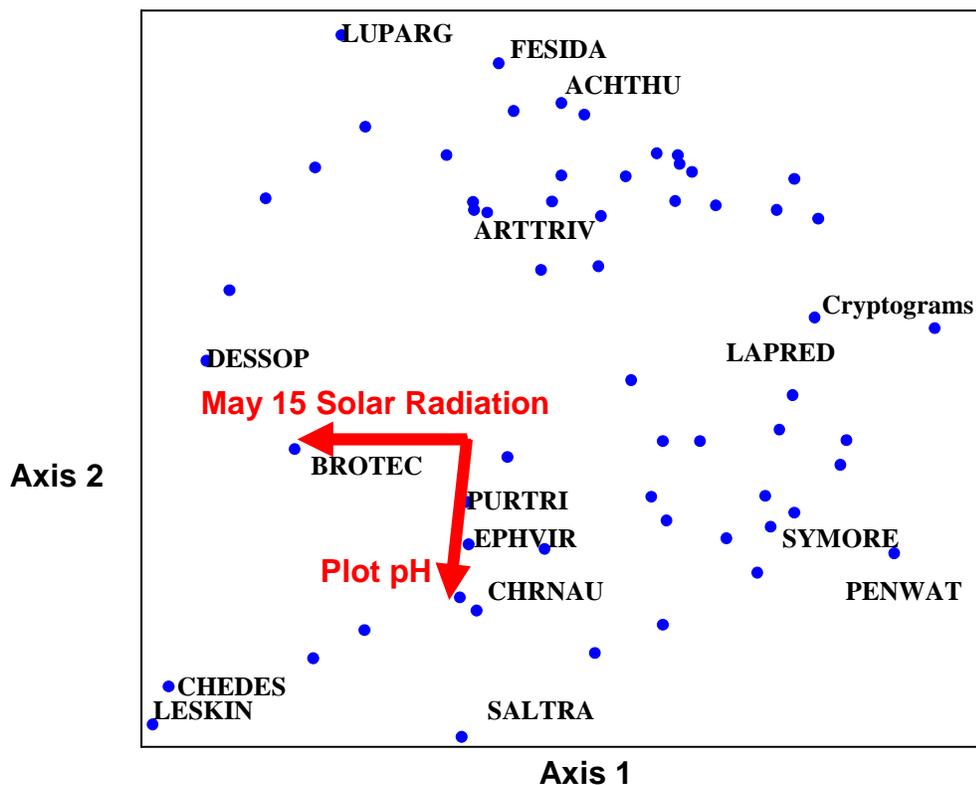


Figure 5. DCA model of species occurring more than twice, axes 1 and 2 The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of correlation with ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ACHTHU- *Achnatherum thurberianum*, ARTTRIV- *Artemisia tridentata* ssp. *vaseyana*, BROTEC- *Bromus tectorum*, CHEDES - *Chenopodium desiccatum*, CHRNAU- *Chrysothamnus nauseosus*, DESSOP- *Descurainia sophia*, EPHVIR – *Ephedra viridis*, FESIDA- *Festuca idahoensis*, LAPRED- *Lappula redowskii*, LESKIN- *Lesquerella kingii*, LUPARG- *Lupinus argenteus* var. *heteranthus*, PENWAT- *Penstemon watsonii*, PURTRI - *Purshia tridentata*, SALTRA- *Salsola tragus*, SYMORE- *Symphoricarpos oreophilus*

Direct Ordination Analysis: Canonical Correspondence Analysis and Variance Partitioning

Canonical Correspondence Analysis included the following environmental variables: field derived slope, solar radiation calculated for May 15th, maximum soil depth, minimum soil depth, plot pH, percent coarse fragment, topographic convergence index, nitrate and ammonium concentrations, average distance to the burn perimeter, the area of pre-burn tree canopy cover on a surveyed plot, and edge density of unburned patches within 300-m of a surveyed plot. CCA ordinations were run for all environmental variables pooled as well as for abiotic and biotic factors separately.

Monte Carlo tests implied that all axes were statistically significant in all ordinations (Table 15), although axis 3 was only weakly significant in the partial biotic (biotic | abiotic) CCA ($p = 0.13$). The first axis in the CCA of all environmental variables described a gradient from drier sites with shallow slopes and minimal influence of unburned patch edges to more mesic, steep slopes with more unburned patch edge (Table 16). This interpretation is reinforced by the positions of *B. tectorum*, a relatively drought tolerant, widely dispersing species and *S. oreophilus*, a species generally found on mesic sites that produces few seeds. These species occurred on opposing ends of this gradient (Figure 6, 7). Axis 2 described a gradient from sites with increased coarse fragments that are higher in the watershed (with species such as *Argemone corymbosa*) to sites with decreased coarse fragments that were low in the watershed (with species such as *Nicotiana attenuata*); (Figure 6, 7). Axis 3 delineated sites with deeper soils, low pH values and low nitrate concentrations to sites with shallower soils with high pH values,

and increased nitrate concentrations (Table 16, Figure 7). A group of species occurred on deeper soils with lower pH values: *Senecio multilobatus*, *Lappula redowskii*, *Cryptantha torreyana*, *Ribes aureum*, *Astragalus filipes* and *Arabis sparsiflora*. *S. tragus* occurred on shallower soils with higher pH values and increased nitrate.

Table 15. Monte Carlo Test p-values for CCA eigenvalues The last two categories represent the first variable given the effect of the second variable. e = eigenvalue; p = p-value.

Axis	All Variables		Biotic Variables		Abiotic Variables		Biotic	Abiotic	Abiotic	Biotic
	e	p	e	p	e	p	e	p	e	p
Axis 1	0.295	0.01	0.190	0.01	0.238	0.02	0.145	0.04	0.225	0.02
Axis 2	0.168	0.01	0.097	0.04	0.151	0.03	0.101	0.02	0.142	0.06
Axis 3	0.165	0.01	0.085	0.01	0.143	0.01	0.051	0.13	0.106	0.09

Table 16. Intraset correlations and standardized coefficients of environmental variables for all CCA ordinations Listed factors are the three highest intraset correlations for a given axis and their standardized coefficients. Coef- Coefficient, Intraset- Intraset Correlation, Ave Dist B.P. - ED 300 – Edge Density at 300 m, May 15 Sol Rad – May 15th Solar Radiation, Max Depth – Maximum Soil Depth, Min Depth – Minimum Soil Depth, PerCFrg – Percent Coarse Fragment, PJCover A – Area of Pre-burn Canopy Cover, TCI – Topographic Convergence Index,

a. all environmental variables with correlations greater than 0.4								
Axis 1 Factor	Coef	Intraset	Axis 2 Factor	Coef	Intraset	Axis 3 Factor	Coef	Intraset
Slope	0.601	0.732	TCI	0.133	0.589	Plot pH	0.316	0.577
May 15 Sol Rad	-0.131	-0.480	PerCFrg	-0.239	-0.539	Nitrate	0.388	0.496
ED 300	0.397	0.476	Ave Dist B.P.	0.421	0.462	Min Depth	-0.252	-0.430
b. biotic environmental variables								
Axis 1 Factor	Coef	Intraset	Axis 2 Factor	Coef	Intraset	Axis 3 Factor	Coef	Intraset
ED 300	0.745	0.714	PJCover A	0.754	0.807	Ave Dist B.P.	1.059	0.823
PJCover A	0.675	0.588	ED 300	-0.502	-0.667	ED 300	-0.620	-0.215
Ave Dist B.P.	0.152	0.473	Ave Dist B.P.	-0.179	-0.314	PJCover A	-0.100	0.052
c. abiotic environmental variables								
Axis 1 Factor	Coef	Intraset	Axis 2 Factor	Coef	Intraset	Axis 3 Factor	Coef	Intraset
Slope	0.898	0.893	May 15 Sol Rad	-0.566	-0.666	Nitrate	0.573	0.576
May 15 Sol Rad	-0.048	-0.439	Min Depth	0.357	0.632	PerCFrg	-0.454	-0.526
Max Depth	-0.163	-0.250	Plot pH	-0.258	0.500	Plot pH	0.538	0.447
d. biotic environmental variables given the effect of abiotic								
Axis 1 Factor	Coef	Intraset	Axis 2 Factor	Coef	Intraset	Axis 3 Factor	Coef	Intraset
ED 300	0.858	0.707	PJCover A	0.720	0.808	Ave Dist B.P.	-1.064	-0.956
PJCover A	0.718	0.582	ED 300	-0.582	-0.705	PJCover A	-0.005	-0.094
Ave Dist B.P.	-0.121	0.204	AveDist B.P.	-0.036	-0.210	ED 300	0.312	-0.056
e. abiotic environmental variables given the effect of biotic								
Axis 1 Factor	Coef	Intraset	Axis 2 Factor	Coef	Intraset	Axis 3 Factor	Coef	Intraset
Slope	0.870	0.922	May 15 Sol Rad	-0.551	-0.683	Nitrate	0.757	0.642
PerCFrg	0.158	0.513	Plot pH	-0.387	-0.646	May 15 Sol Rad	-0.381	-0.452
TCI	-0.037	-0.412	Min Depth	0.321	0.635	TCI	0.274	0.366

The interpretation and apparent influence of CCAs of abiotic gradients gave similar results. Slope correlated most strongly with the first axis and May 15 solar radiation with the second axis (Table 16, Figures 8, 9, 10, and 11). On the third axis, plot pH represented the strongest gradient in the CCA of all variables, but in the abiotic and the partial abiotic ordination (abiotic | biotic) it was not as strongly correlated with this axis (Table 16, Figures 7, 9, 11), indicating that the effect of pH was partly explained by measured biotic factors. Once these were taken into account, pH did not appear to influence species distributions as strongly. In all three ordinations, nitrate was strongly correlated with axis three and positively correlated with pH except in the partial CCA of abiotic factors taking biotic influences into account (Table 16).

Results of biotic factors independently, after accounting for other variables, produced comparable ordinations so only the partial biotic ordination (biotic | abiotic) is discussed. Biotic variables separated into three major gradients with all axes being significant as determined from Monte Carlo randomizations (Table 15). The first axis indicated increasing density of unburned edges and higher levels of pre-burn canopy cover (Table 16, Figure 12). The arrangement of species on this axis was interpretable when combined with axis 2, which had higher values for sites with a low influence of unburned patches and greater influence of pre-burn canopy cover. The influence of both unburned patches and pre-burn canopy cover increased along axis 1 in both ordinations of biotic variables. With increasing pre-burn canopy cover, widely dispersing species such as *Lactuca serriola*, *S. tragus*, and *C. nauseous* were more frequent, but when the influence of unburned patches increased, perennial forbs with low to moderate dispersal distances became more frequent, including *Astragalus purshii*, *Phacelia hastata*, *Ribes*

aureum, and *Senecio multilobatus*. The influence of the burn perimeter decreased with the third axis of the partial biotic CCA. Species strongly positively correlated with this axis included *Gilia inconspicua*, *Eriogonum microthecum* and *Cryptantha torreyana*. Although *G. inconspicua* only occurred three times in our sampling, and its seed dispersal distance relationships are unknown, both *E. microthecum* and *C. torreyana* are known to have low dispersal distances (Table 3, Figure 13). *Gnaphalium palustre*, *Crepis acuminata*, and *A. purshii* were strongly negatively associated with this axis.

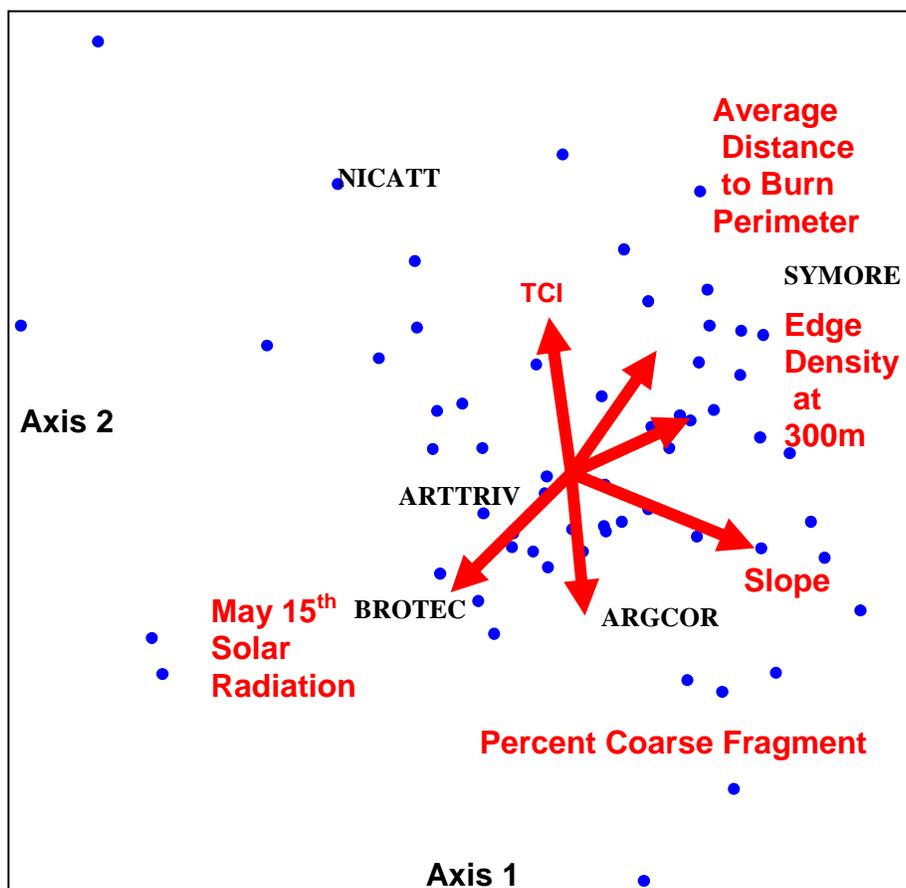


Figure 6. CCA with all abiotic and biotic variables, axes 1 and 2

The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of the variable in structuring the ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ARGCOR – *Argemone corymbosa*, ARTTRIV- *Artemisia tridentata* ssp. *vaseyana*, BROTEC- *Bromus tectorum*, NICATT – *Nicotiana attenuata*, SYMORE- *Symphoricarpos oreophilus*

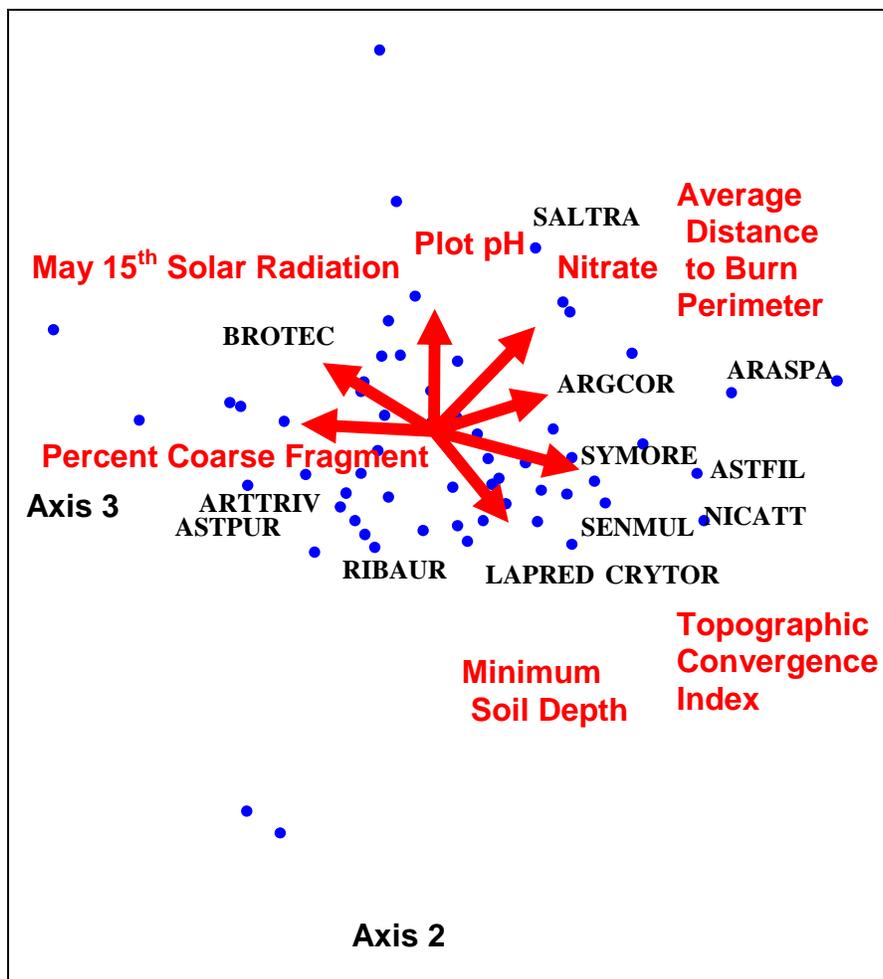


Figure 7. CCA with all abiotic and biotic variables, axes 2 and 3

The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of the variable in structuring the ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ARASPA – *Arabis sparsiflora*, ARGCOR – *Argemone corymbosa*, ARTTRIV – *Artemisia tridentata* ssp. *vaseyana*, ASTFIL – *Astragalus filipes*, ASTPUR – *Astragalus purshii*, BROTEC – *Bromus tectorum*, CRYTOR – *Cryptantha torreyana*, LAPRED – *Lappula redowskii*, NICATT – *Nicotiana attenuata*, RIBAUR – *Ribes aureum*, SALTRA – *Salsola tragus*, SENMUL – *Senecio multilobatus*, SYMORE – *Symphoricarpos oreophilus*

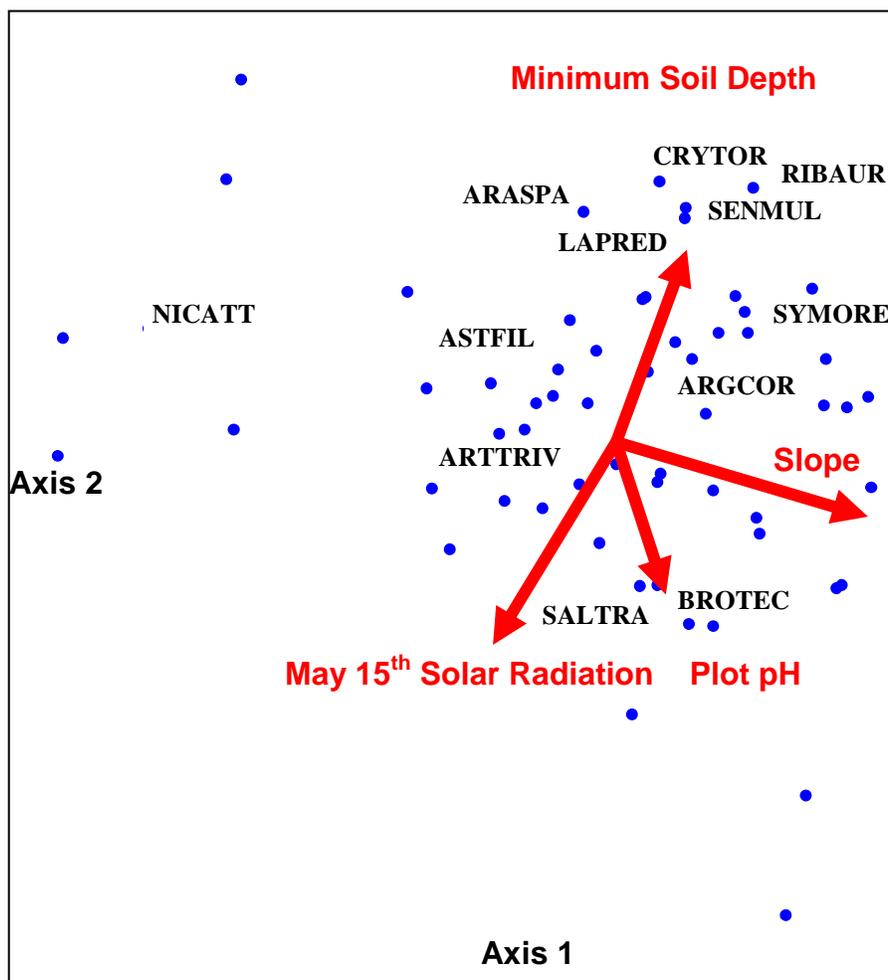


Figure 8. CCA of abiotic variables, axes 1 and 2 The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of the variable in structuring the ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ARASPA – *Arabis sparsiflora*, ARGCOR – *Argemone corymbosa*, ARTTRIV – *Artemisia tridentata* ssp. *vaseyana*, ASTFIL – *Astragalus filipes*, BROTEC – *Bromus tectorum*, CRYTOR – *Cryptantha torreyana*, LAPRED – *Lappula redowskii*, NICATT – *Nicotiana attenuata*, RIBAUR – *Ribes aureum*, SALTRA – *Salsola tragus*, SENMUL – *Senecio multilobatus*, SYMORE – *Symphoricarpos oreophilus*

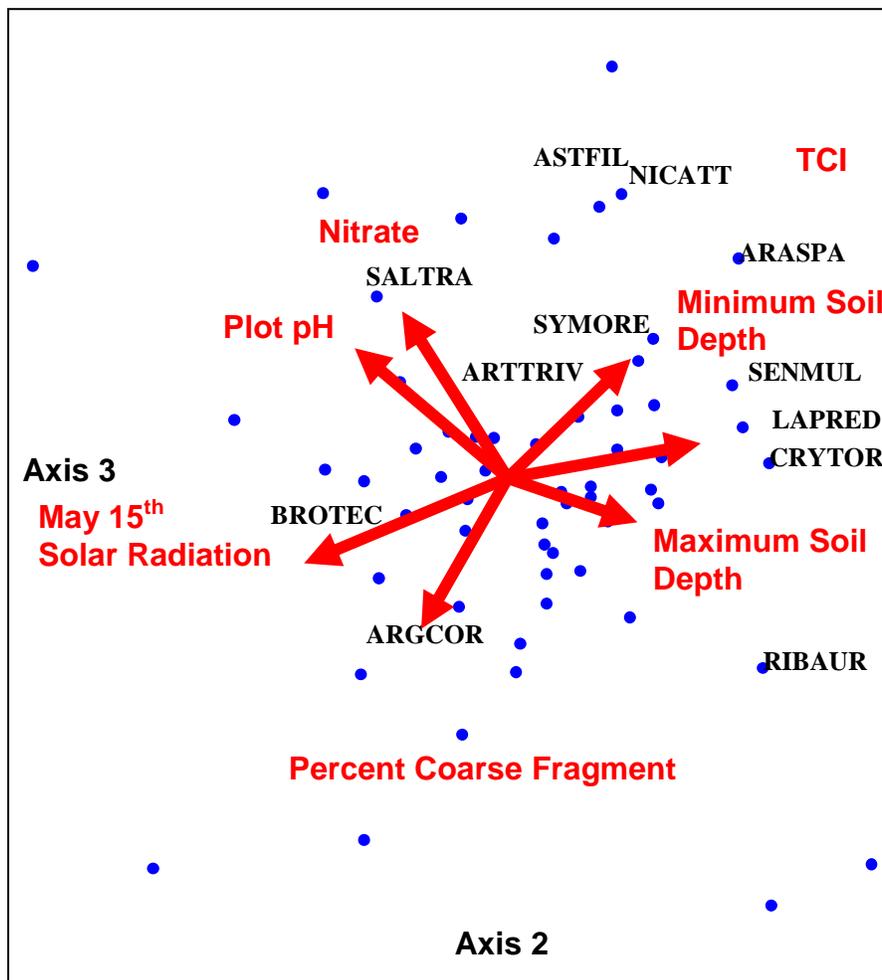


Figure 9. CCA of abiotic variables, axes 2 and 3 The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of the variable in structuring the ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ARASPA – *Arabis sparsiflora*, ARGCOR – *Argemone corymbosa*, ARTTRIV- *Artemisia tridentata* ssp. *vaseyana*, ASTFIL – *Astragalus filipes*, BROTEC- *Bromus tectorum*, CRYTOR – *Cryptantha torreyana*, LAPRED – *Lappula redowskii*, NICATT – *Nicotiana attenuata*, RIBAUR – *Ribes aureum*, SALTRA – *Salsola tragus*, SENMUL – *Senecio multilobatus*, SYMORE- *Symphoricarpos oreophilus*

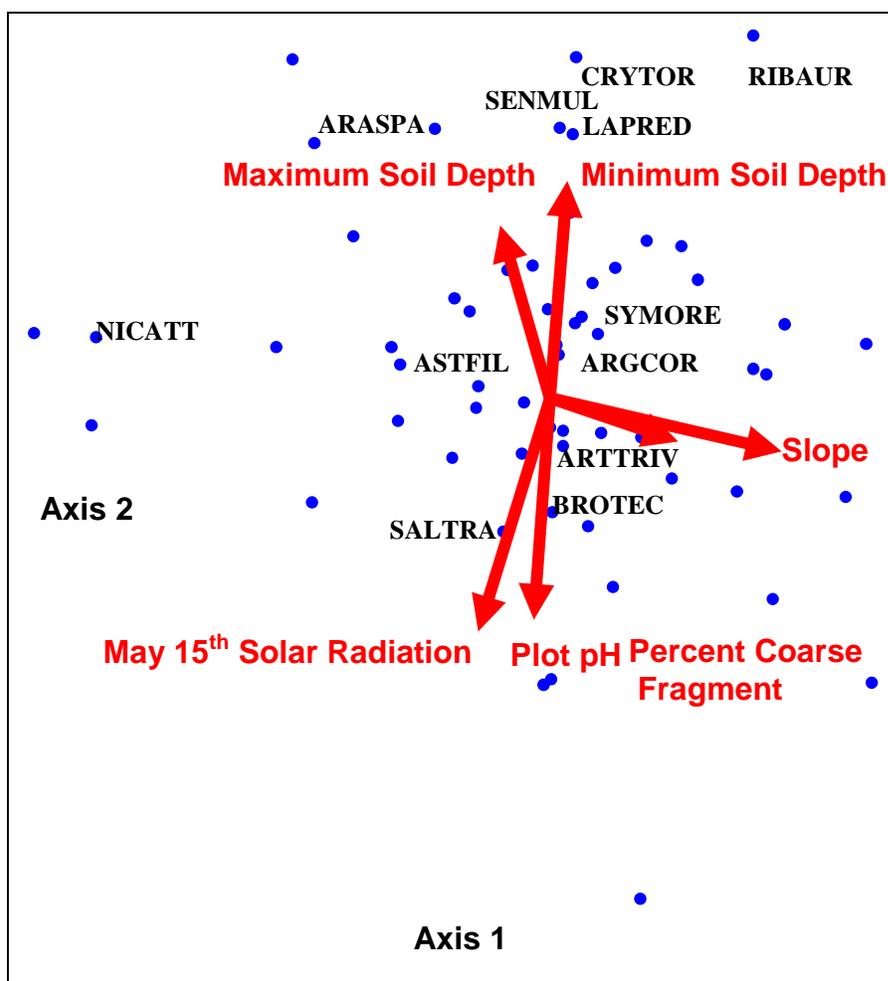


Figure 10. Partial CCA of abiotic variables (given the effect of biotic variables), axes 1 and 2 The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of the variable in structuring the ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ARASPA – *Arabis sparsiflora*, ARGCOR – *Argemone corymbosa*, ARTTRIV- *Artemisia tridentata* ssp. *vaseyana*, ASTFIL – *Astragalus filipes*, BROTEC- *Bromus tectorum*, CRYTOR – *Cryptantha torreyana*, LAPRED – *Lappula redowskii*, NICATT – *Nicotiana attenuata*, RIBAUR – *Ribes aureum*, SALTRA – *Salsola tragus*, SENMUL – *Senecio multilobatus*, SYMORE- *Symphoricarpos oreophilus*

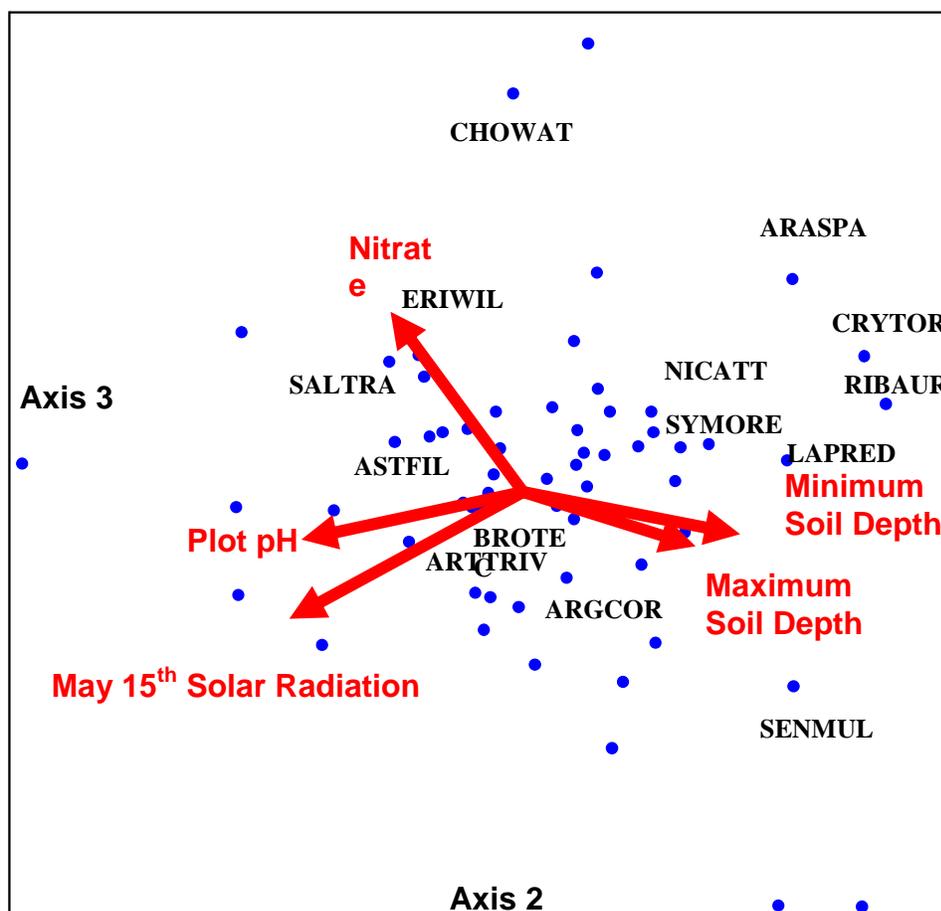


Figure 11. Partial CCA of abiotic variables (given the effect of biotic variables), axes 2 and 3 The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of the variable in structuring the ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ARASPA – *Arabis sparsiflora*, ARGCOR – *Argemone corymbosa*, ARTTRIV- *Artemisia tridentata* ssp. *vaseyana*, ASTFIL – *Astragalus filipes*, BROTEC- *Bromus tectorum*, CHOWAT – *Chorizanthe watsonii*, CRYTOR – *Cryptantha torreyana*, ERIWIL – *Eriastrum wilcoxii*, LAPRED – *Lappula redowskii*, NICATT – *Nicotiana attenuata*, RIBAUR – *Ribes aureum*, SALTRA – *Salsola tragus*, SENMUL – *Senecio multilobatus*, SYMORE- *Symphoricarpos oreophilus*

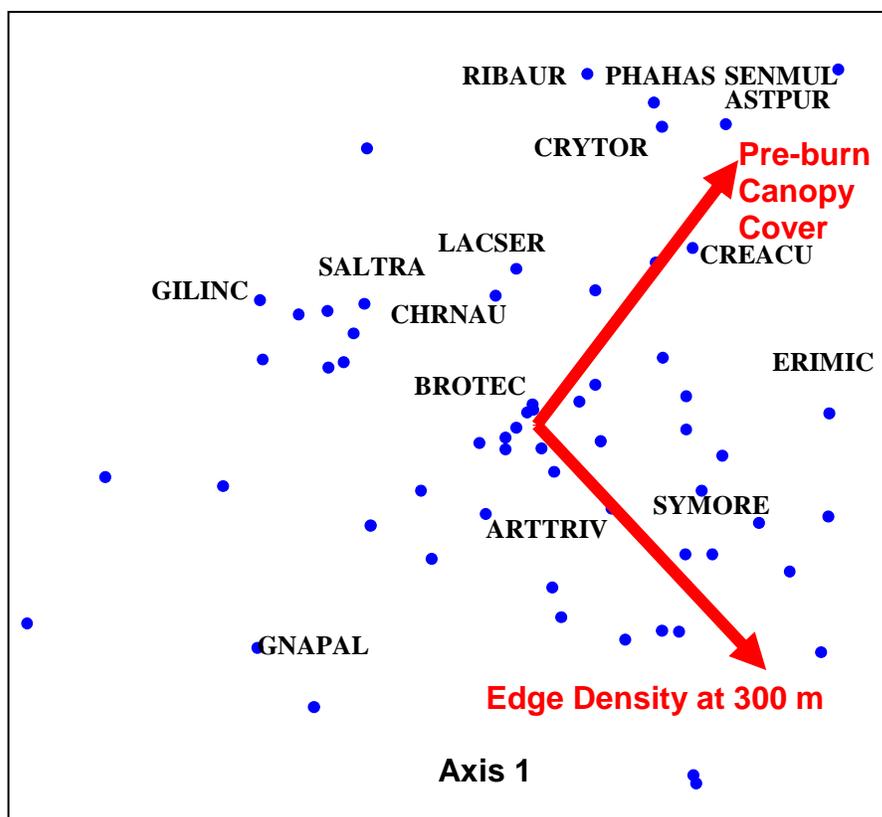


Figure 12. Partial CCA of biotic variables (given the effect of abiotic variables), axes 1 and 2 The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of the variable in structuring the ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ARTTRIV- *Artemisia tridentata* ssp. *vaseyana*, ASTPUR – *Astragalus purshii*, BROTEC- *Bromus tectorum*, CHRNAU – *Chrysothamnus nauseosus*, CREACU – *Crepis acuminata*, CRYTOR – *Cryptantha torreyana*, ERIMIC – *Eriogonum microthecum*, GILINC – *Gilia inconspicua* var. *inconspicua*, GNAPAL – *Gnaphalium palustre*, LACSER – *Lactuca serriola*, PHAHAS – *Phacelia hastata*, RIBAUR – *Ribes aureum*, SALTRA – *Salsola tragus*, SENMUL – *Senecio multilobatus*, SYMORE- *Symphoricarpos oreophilus*

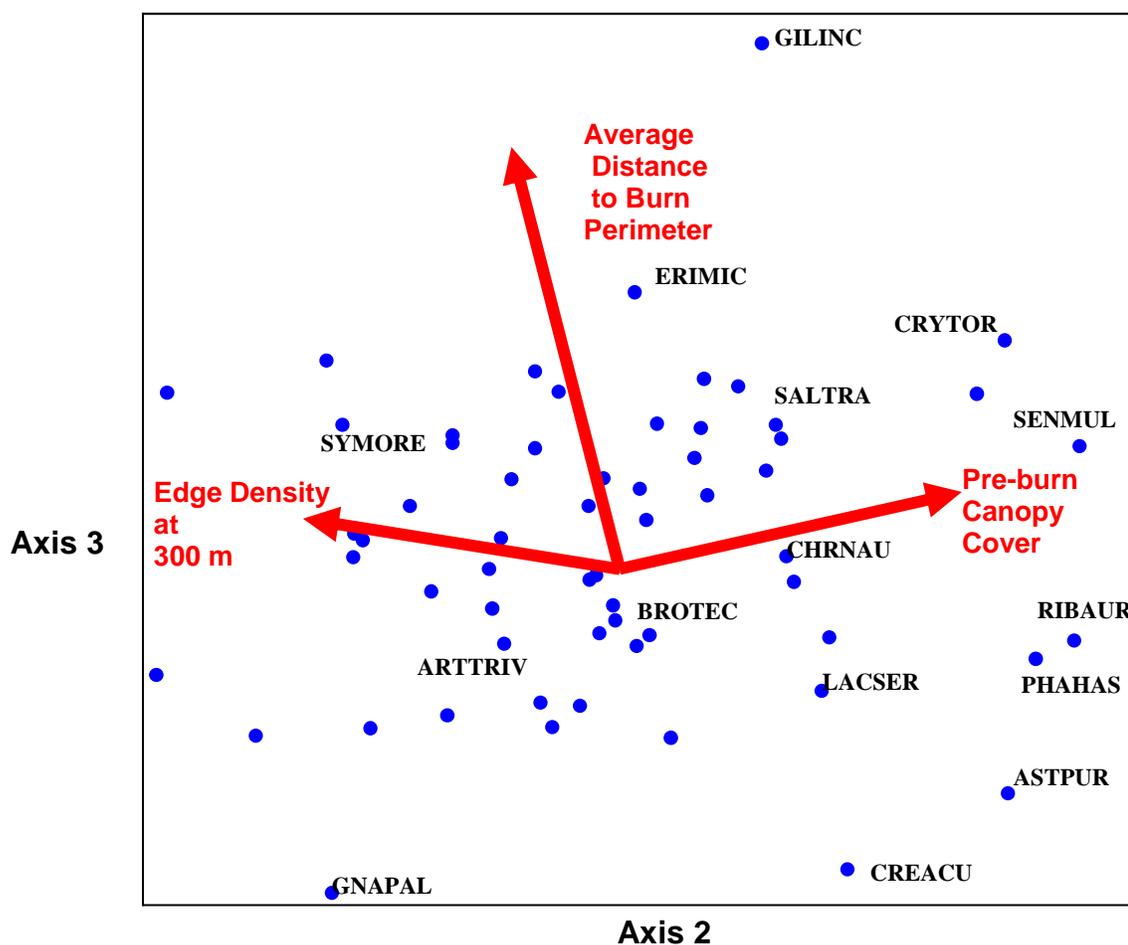


Figure 13. Partial CCA of biotic variables (given the effect of abiotic variables), axes 2 and 3 The full model includes 60 species. Correlations of seven abiotic and three biotic variables with ordination axes were determined, and those variables with $R^2 > 0.2$ are represented as vectors (arrows) on the ordination biplot. Vector length represents the strength of the variable in structuring the ordination axes, and vector direction represents the direction of maximum change of explanatory variables. Species centroids, represented by solid circles, reflect theoretical optima of species distributions in ordination space. The distance between points is proportional to their chi-square distance values. ARTTRIV- *Artemisia tridentata* ssp. *vaseyana*, ASTPUR – *Astragalus purshii*, BROTEC- *Bromus tectorum*, CHRNAU – *Chrysothamnus nauseosus*, CREACU – *Crepis acuminata*, CRYTOR – *Cryptantha torreyana*, ERIMIC – *Eriogonum microthecum*, GILINC – *Gilia inconspicua*, GNAPAL – *Gnaphalium palustre*, LACSER – *Lactuca serriola*, PHAHAS – *Phacelia hastata*, RIBAU – *Ribes aureum*, SALTRA – *Salsola tragus*, SENMUL – *Senecio multilobatus*, SYMORE- *Symphoricarpos oreophilus*

The total variance or “inertia” in CCA analyses including all variables was 4.198. The intersection component of the abiotic and biotic variables was 1.4% ($12.7\% - 11.3\% = 1.4\%$, Table 17). The unexplained variance was 80.3% ($(4.198 - (0.532 + 0.297) = 3.369)$, Table 17). Excluding shared variances, abiotic variables explained 11.3% of the variance and biotic variables explained 7.1%.

Table 17. Eigenvalues of all CCA ordinations used in variance partitioning

Total inertia = 4.198.

Axis	Biotic Variables	Abiotic Variables	Biotic Variables Given the Effect of Abiotic	Abiotic Variables Given the Effect of Biotic
Axis 1	0.190	0.238	0.145	0.225
Axis 2	0.097	0.151	0.101	0.142
Axis 3	0.085	0.143	0.051	0.106
Total	0.372	0.532	0.297	0.473
Percent Variance Explained	8.9%	12.7%	7.1%	11.3%

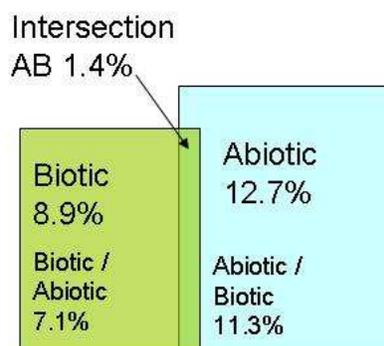


Figure 14. Venn Diagram showing the partitioning of explained variance into abiotic and biotic factors

Discussion

My conceptual model of pre- and post- burn factors influencing understory species composition after fire in pinyon-juniper woodlands included abiotic controls and biotic interactions (Figure 1). In this arid environment, moisture was predicted to strongly influence species' distributions. The results of indirect ordinations (DCA, Tables 12, 13, and 14) showed that moisture (solar radiation) was the primary gradient and pH was secondary in determining species' distributions. Relevant biotic influences take two forms: legacy effects of plant propagules surviving the burn and proximity to seed sources following the burn. Legacy effects are also strongly associated with pre-burn canopy cover. The proximity to seed sources is often due to fire severity, the mosaic pattern of unburned patches, and distance from the burn perimeter. In areas where few plants and propagules survived, unburned patches serving as seed sources were predicted to play a strong role in resulting species composition. This was shown to be the case where pre-burn canopy cover was high (Figure 12). However, where pre-burn canopy cover was high but sites were far from potential seed sources (unburned patches), I observed an increase in the occurrence of widely dispersing or seed banking, and often non-native species (Figure 12). The selection of these variables as underlying gradients in influencing species distributions was reinforced by the classification analyses as species groups divided in response to differences in slope, edge density (influence of unburned patches), solar radiation (moisture), and plot pH.

The interpretation of solar radiation as a proxy for soil moisture was reinforced by the positioning of other measured variables and species occurrences in ordination

analyses. Solar radiation directly opposed increased minimum soil depth and TCI (Figure 6, 7, 8, 9, 10, 11). Species diversity in pinyon-juniper systems had been previously related to moisture in Utah and New Mexico (Harner and Harper 1976). *B. tectorum* is strongly correlated with increased solar radiation (Table 13, 14). Growth of this species decreases with shading (Pierson et al. 1990, Keeley and McGinnis 2007), confirming this result. The species most positively correlated with decreased solar radiation and increased soil moisture, *S. oreophilus* (Table 13, 14) is known to be a mesic species. Mesic sites also favor *Cercocarpus ledifolius* (Schultz et al. 1990), which is typically associated with *S. oreophilus* (per. observation), a common understory species in aspen communities (Bartos and Mueggler 1981). *S. oreophilus* opposes *B. tectorum* on all biplots showing this gradient (Figure 5, 6, 7, 8, 9, 10, 11). These findings help corroborate my prediction that mesic sites favor native perennial species after fire.

As native perennial species often resprout following fire (Table 3), I expected to find fewer native perennial species on xeric sites due to reduced productivity favoring seeding species (Keeley 1981, Clarke et al. 2005, Pausas and Bradstock 2007). Partial abiotic CCA ordinations showed solar radiation (soil moisture) and plot pH to be strongly correlated (Figure 10, 11). The pH gradient may represent differences in fire intensity or soil development. In all cases, whether following a high intensity disturbance or in areas of low soil development and hence low productivity, soil temperatures were either high enough or sustained in duration to kill many resprouting species and seeds in the seed bank (Neary 1999) or the environmental conditions were severe and favored seeding species (Keeley 1981). Severe fires favor seeding species, which can either quickly colonize a site or survive in the seedbank (Lee 2004). After low intensity disturbance,

recolonization is most likely dominated by resprouting species (Sousa 1980, Turner et al. 1997). I therefore expected areas of high pH to be dominated by species that propagate by a large number of widely dispersing seeds, and areas of low pH to be dominated by resprouting species. This was apparent from the DCA ordination analysis (Figure 5, Table 12, 13, 14). Of the three species most strongly correlated with high pH: *Lessingia kingii*, *Salsola tragus*, and *Chenopodium desiccatum*, the last two reproduce solely from seed. These seeding species were also more likely than most to persist in the seedbank following high severity fire. These are pioneer species with low seed weights. Such species are often found in deeper soils (Grandin and Rykin 1998), where burn intensity is lower (Frandsen and Ryan 1986). Species with low dispersal distances that are capable of resprouting following low severity fire: *Lupinus argenteus*, *Festuca idahoensis* and *Achnatherum thurberianum*, (Table 3) (Wright and Klemmedson 1965, Wright et al. 1979, Turner et al. 1997, Goergen and Chambers submitted) were correlated with low pH. If a given area did experience a high severity fire, the post-fire vegetation would be the result of the propagules that reached the area first. Slow spreading species such as *Achnatherum* and *Festuca* species would be the last to reach the site. Wambolt et al. (2001) found *F. idahoensis* slow to recover following fire at most sites. This grass is known to be severely damaged by fire (Wright 1971, Wright 1985). Plant species occurrences separated along a gradient of soil pH in regards to their fire tolerances and seed dispersal distances.

The reduced influence of pH in the partial abiotic CCA (taking the influence of biotic variables into account) supports the idea that pH represents a process that involves both biotic and abiotic components, such as fire severity (Table 16). An increase in fire

severity induced pH values not only affects species establishment in regards to propagule survival, but increased fire severity alters soil chemistry, inhibiting post-fire germination of some species. Increased fire intensity results in increased amounts of ash following fire. More ash increases pH and decreases water potential (Henig-Sever 2001). High pH can affect germination by inhibiting proteolytic enzymes involved in the metabolism of seed storage compounds (Mayer and Poljakoff-Mayber 1989, Henig-Sever et al. 1996). High severity fires can volatilize nutrients, increase the concentration of base cations, increase nutrient loss through erosion, leaching and denitrification, change the rate of mineralization, alter C:N ratios, and denature organic acids (Certini 2005, Neary 1999, Henig-Sever et al. 2001). Although soil pH may represent a number of processes, plant species occurrences, in regards to their life history traits, indicates that soil pH may represent a burn severity gradient.

Although soil pH is known to increase with increasing fire intensity (Certini 2005) increases in pH may be due to a number of other factors. Differences in soil chemistry can change with the plant species present at a site (Garcia-Moya and McKell 1970). Parent material and hydrothermal activity can also influence soil pH. I tested for carbonate in these soils and found carbonate levels to be too low to influence pH. Soils altered hydrothermally show lower pH values and result in a decrease in dry biomass of *A. tridentata* and *B. tectorum* (DeLucia et al. 1989). Such decreases in cover of *A. tridentata* ssp. *vaseyana* and *B. tectorum* was not observed in this study.

Increased pH values may also indicate a lack of soil development (He and Tang 2008). CCAs of abiotic variables showed maximum soil depth opposing pH (Figure 8, 9, 10, 11, and 12). This finding supports the idea that the soil pH gradient represents soil

development, although it does not negate the interpretation of soil pH as a proxy for fire severity. Areas with increased soil depth are likely to have seed banks due to both reduced fire severity and increased soil development.

Fire severity is vital to predicting plant successional pathways (Bates 2006, Sibold et al. 2007). The intensity with which a landscape burns varies with pre-burn fuel loads and topography. However, stochastic conditions such as humidity and wind direction add increased variability. Areas of increased fire severity are lower in surviving propagules and suitable microsites for establishment. Unfortunately, I did not have a direct measure of fire severity.

Nitrogen and phosphorus are the first nutrients to be affected along a continuum of increasing fire intensity. Nitrate explained a large amount of the variation along axis 3 (Table 16). Nitrogen levels become elevated immediately following fire. Six years after fire, I found elevated levels of pH and nitrogen in burned as opposed to unburned areas in this study, indicating that pH might be representative of a burn intensity gradient (pH range = 5.98 – 8.25, $T = 2.09$, $df = 100$, $p\text{-value} = 0.04$, NO_3 range = 0.13 -181.1 $\mu\text{g} / \text{g}$, $T = 4.59$, 99 df , $p\text{-value} = <0.001$, and NH_4 range = 2.2 – 27.72 $\mu\text{g} / \text{g}$, $T = -2.27$, 99 df , $p\text{-value} = 0.03$).

Rau et al. (2005) found an increase in extractable NO_3 immediately post fire and through year three. Increased nitrogen levels favor annual species and delay successional pathways (McLendon and Redente 1991). Three shade intolerant annual species were strongly correlated with this axis, *E. wilcoxii*, *C. watsonii*, and *S. tragus* (Table 3, Figure 11). Increasing fire severity is of concern in pinyon-juniper woodlands as increased tree cover means that more ecosystem nutrients are stored in the biomass. With increased

fuels, especially surface fuels as a result of increased litter (Bradstock and Auld 1995), the likelihood that a severe fire will occur and volatilize the nutrients is increased.

Percent coarse fragment had a significant influence on species occurrences, although it did not show as strong an influence as pH or solar radiation. In xeric environments, a surface layer of coarse textured soils or rocky outcrops provide pockets of relatively mesic habitats. Rock layers provide what is analogous to a mulch layer, slowing evaporation (Walter 1985). Patches of high percent coarse fragment provided pockets of relatively mesic habitat embedded within the broader moisture gradients influenced by solar radiation, soil depth and TCI. The abundance of *Argemone corymbosa* was greater on sites with increased percent coarse fragment without necessarily showing a preference for the greater moisture gradient represented by solar radiation (Figure 6, 9).

Although not as strong as abiotic controls, biotic gradients played an important role in plant species distributions, explaining 7.1% of species variance (Figure 14). All three biotic variables: pre-burn canopy cover, influence of unburned patches and distance to the burn perimeter were significant in explaining species distributions. High levels of pre-burn canopy cover (>25% cover, including 1/3 of plots) were associated with annual invasives and perennial forbs in both the biotic and partial biotic CCAs. One particular combination of perennial forbs, one shrub and one annual species consistently grouped throughout the CCA analysis of the biotic variables: *Astragalus purshii*, *Cryptantha torreyana*, *Phacelia hastata*, *Ribes aureum* and *Senecio multilobatus*. These species favored areas of high pre-burn canopy cover and increased proximity to unburned edges (Figure 12). Although these species have a slow rate of seed spread and range in shade

tolerance from intermediate to intolerant, they are coming into areas of high pre-burn canopy cover (Table 3, Figure 12). Areas of high pre-burn canopy cover showed minimal legacy effects of understory species, so that the post-burn environment was likely to be open to colonization from nearby propagule sources. This implied that proximity to unburned patches influences the rate and trajectory of succession in this system. Sites with increased influence of unburned edge should require less restoration after fire as they are less likely to become invaded by non-native species.

The role of distance from the burn perimeter was unclear. *G. palustre*, *C. acuminata*, and *A. purshii* were strongly negatively associated with distance from the burn perimeter. These species span the spectrum of dispersal distances, indicating that distance from the burn perimeter does not play a strong role in determining species distributions, or that the dispersal distance ratings of these species may need refinement.

As some of the discussed variables were difficult to interpret, it follows that there was substantial variance in the species data that was not explained by the CCA analysis. This is typical for community data which often incorporates 10-50% noise (Gausch 1982) and may be due to the heavy disturbance experienced in the canyon: ATV use, salvage logging and grazing. However, the indirect ordination analyses explained a high proportion of the variance: DCA 66.4% and NMS 74.3%. It does not appear that a large number of components were needed to account for variability in the dataset as three axes were used in both the DCA and the NMS. 55.5% and 65.5% of the variance, relatively, was explained by the first two axes in each ordination. My ordination results indicate that solar radiation, pH, slope, proximity to unburned patches, and pre-burn canopy cover were driving factors behind plant species distributions, as species are consistently

organized in relation to one another along these gradients. However, 80% of the species-environment variance remained unexplained by measured abiotic or biotic variables as shown by CCA ordinations and variance partitioning. This indicates the presence of unexplained processes influencing species distributions.

One explanation for the high amount of unexplained variance in the indirect ordinations may be emergent properties. Emergent properties resulting from interspecific interactions are extremely important for plant successional processes, particularly in high-stress environments. Patches of similar microtopography, pre-burn understory composition and post-burn seed rain (as represented by proximity to unburned patches and burn perimeter) exhibited similar post-burn species composition, according to life history traits (Connell and Slatyer 1977, Noble and Slatyer 1980). However, a large number of abiotic and biotic factors were included in this analysis and only 20% of the species-environment variance was explained by these factors. Emergent properties operate over ecological units that are unpredictable from the observation of components of that unit (Salt 1979) so that there are assemblages of species that operate together and affect one another's distribution (Connell and Slatyer 1977). These groups of species do not respond to disturbances individualistically and would not be apparent from direct ordination analyses such as CCA.

As species-environment interactions are dynamic, the factors driving plant species distributions six years after a wildland fire are limited to that temporal window. In another six years, when plant propagules have distributed across the landscape, different factors will likely drive the system towards more shrub and perennial forb establishment (Mata-Gonzalez et al. 2007).

Management Implications

Restoration ecologists seeking to use prescribed fire to encourage understory plant species can take this work in a number of directions. Post-fire understory species composition varies consistently along gradients of slope, solar radiation, and soil pH in pinyon-juniper woodlands. In Wall Canyon, steep slopes favor *Phacelia hastata*, *Koeleria macrantha*, and *Eriogonum umbellatum*. Increases in solar radiation result in higher occurrences of *Bromus tectorum* and *Descurania sophia*. Increases in soil pH result in a higher occurrences of *Salsola tragus* and *Lactuca serriola*. Proximity to unburned patches results in higher occurrences of *Symphoricarpos oreophilus* and *Astragalus purshii*. These plant species are selecting for similar site conditions. Xeric sites with increased pH, high pre-burn canopy cover and decreased proximity to unburned patches favor non-native invasive species and should be considered for reseeding of natives following fire, although the spread of species of concern, such as *Bromus tectorum*, is not prevented with seeding (Floyd et al. 2006).

Plant response is often unpredictable because of unknown seed reserves, plant recolonization potential and post-fire climatic conditions (Everett 1986). Especially in arid systems, post-fire rainfall is influential in governing seedling establishment (Hodgkinson 1991, Chambers 2000, 2001). There are a number of stochastic factors that come into play after the fire has burned. Although land managers should focus post-fire restoration efforts on xeric sites with high pre-burn canopy cover and minimal influence of unburned patches, other sites are likely to need increased restoration efforts as well if the year following the fire is dry. Seedbank species with low viability may be at risk.

Species diversity can be encouraged by maintaining heterogeneity in prescribed burning. Reduced patchiness may reduce the contribution of seed from fire sensitive species (Whisenant 1990, Wilson 1994, Longland and Bateman 2002). In my work, proximity to unburned patches favored several native, non-ruderal species.

Conclusions

My findings show that the responses of plant species in post-burn pinyon-juniper woodlands vary with their life history characteristics, as proposed by Noble and Slatyer (1980). Abiotic and biotic gradients created ecological filters to establishment. A number of conditions must be simultaneously met for species establishment and persistence: species propagules must be present in the local species pool, the site must be within the environmental tolerance of the species, the site cannot be pre-empted by individuals of another species, and the species must be able to successfully compete for resources with neighboring species. Pre-burn conditions are critical for influencing post-fire succession. For plants and propagules to be present at a site, they must have survived the fire. Increases in pre-burn tree canopy cover prior to the fire lead to greater increases in fire severity, through burn intensity and suppression of understory species, and alterations of the physical characteristics of a site, including increased solar radiation.

The life history characteristics of the species considered in these analyses were used to interpret plant community ordinations, but very little is known about some of these species. Ordinations were interpretable based upon what is known of some of the more common and commercially important species in pinyon-juniper woodlands and sagebrush grasslands. Additional research on some of the less ubiquitous or

economically important species would increase our understanding of post-burn establishment in these systems.

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Chapter 2: Influences of Biological Legacy Effects on Cheatgrass Invasion and Sagebrush Recovery Following Fire

Abstract

The native flora of the Great Basin is at risk of invasion by cheatgrass (*Bromus tectorum*) and resulting increases in fire frequency. High fire frequency can eventually lead to local extirpation of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), with cascading effects to sagebrush obligate species. Increased tree density in pinyon-juniper woodlands reduces site resistance to *B. tectorum* invasion following fire. I examined the distribution and cover of *B. tectorum* and *A. tridentata* ssp. *vaseyana* six years after a wildland fire in central Nevada. I hypothesized that sites with less pre-burn tree canopy cover would have greater cover of *A. tridentata* ssp. *vaseyana* and lower *B. tectorum* cover after accounting for environment and proximity to seed sources. I used principal component regression analyses to reveal the factors that collectively define site type preferences for each species, and structural equation models to explore causal and correlational relationships among environment, pre-burn canopy cover, and distance from seed source. *B. tectorum* preferred sites with lower soil pH, less pre-burn tree canopy cover, gentler slopes and higher ammonium concentrations ($R^2_{\text{adj}} = 0.153$). *A. tridentata* ssp. *vaseyana* preferred mesic sites with deeper soils ($R^2_{\text{adj}} = 0.296$). Structural equation models identified significant pathways predicting the cover of *A. tridentata* ssp. *vaseyana*, including the positive effect of soil depth and the negative effect of pre-burn canopy cover. *B. tectorum* cover was primarily influenced by a positive effect of incident solar radiation. These findings indicate that land managers concerned with site conversion to cheatgrass should focus post-burn restoration efforts on xeric sites with

high pre-burn canopy cover, or reduce tree canopy cover before the elimination of understory species. Alternative successional pathways following fire are weakly predicted by site- and landscape-level characteristics that integrate abiotic forcing variables with biotic legacy effects describing pre-fire conditions.

Introduction

In lower montane ecosystems in the Great Basin, at least two alternative successional pathways prevail following stand replacing fire. Succession can follow a sequence of dominating growth habits from annuals and forbs, to perennial bunchgrasses and resprouting shrubs, to sagebrush grassland and mountain shrubs, to pinyon-juniper woodlands. Alternatively, cheatgrass (*Bromus tectorum*) can invade a site and initiate a sequence of fires occurring over shorter time intervals than the maturation of most native species in pinyon-juniper woodlands (i.e. “cheatgrass fire cycle”). The archetypal species of the two pathways are mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana* and *B. tectorum*, respectively. Both are obligate seeders following fire, yet one is a perennial shrub and the other is an invasive annual. Few studies have compared the ecology of obligate-seeding species of such different life histories and growth forms.

Mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana* is an obligate seeding perennial woody species with low fire resistance and short-lived seed. Seed is viable for up to three years under artificial conditions and one year in field conditions (Mueggler 1956). Generally, few mature individuals survive fire (Blaisdell 1949) and there are only two sources of sagebrush propagules following fire: residual seed bank and surviving adults in unburned patches or outside the fire perimeter. Cover of surviving adults

decreases with increasing canopy cover of pinyon-juniper, as *A. tridentata* ssp. *vaseyana* is shade intolerant and unable to successfully compete with pinyon and juniper trees for soil moisture. Distance from unburned seed sources, pre-burn tree canopy cover and displacement by *Bromus tectorum* are factors potentially influencing the recovery of *A. tridentata* ssp. *vaseyana* after fire.

B. tectorum is a highly fecund, Eurasian annual grass species with short-lived seeds, high seed viability, and rapid growth rates. This species can complete two life cycles in years with adequate spring rains (Hulbert 1955, Harris 1967, Mack and Pyke 1983). Germinating with the first autumn precipitation in some years (Hulbert 1955), *B. tectorum* is able to utilize available water before most native plant species (Booth et al. 2003). Even in dry years, most plants survive to produce seed (Mack and Pyke 1983), making *B. tectorum* a permanent member of plant communities following its arrival. This species is less abundant where growing seasons are short and cold (Chambers et al. 2007) resulting in an upper elevational limit of approximately 2200 m (Baldwin et al. 2002). Like many annuals, *B. tectorum* shows a greater occurrence with increased nitrogen (McLendon and Redente 1991) as occurs immediately following fire. Livestock grazing and fire, both of which are common to central Nevada, are preconditions to *B. tectorum* invasion (Young and Evans 1978, Chambers et al. 2007).

Experimental work has shown that *B. tectorum* produces more biomass and seed following fire and removal of perennial competitors (Chambers et al. 2007). With the appropriate seed source and environmental conditions, repeated fire often results in greater establishment and long-term persistence of *B. tectorum* than *A. tridentata* ssp. *vaseyana* (Young and Evans 1989). However, the amount of establishment differs across

spatial and temporal scales. After fire, the establishment of *B. tectorum* is of particular concern as this species outcompetes seedlings of native plants (Melagoza et al. 1990, Booth 2003) and is negatively associated with understory cover and richness of all species (Keeley and McGinnis 2007). Simulation models of plant growth in sagebrush steppe have shown *B. tectorum* to dominate plant communities for 13-15 years following fire, at times being replaced by *A. tridentata* (Mata-Gonzalez et al. 2007). This conflicts with the experimental work of Booth et al. (2003), showing that *A. tridentata* ssp. *wyomingensis* rarely recruits in *B. tectorum*. Six years after wildfire in mountain big sagebrush sites, I expect the cover of annual species to be declining and the establishment of perennials, such as *A. tridentata* ssp. *vaseyana*, to be increasing.

Declining cover of *A. tridentata* ssp. *vaseyana* is of concern to wildlife biologists as this species comprises up to 99% of the winter diet of Pygmy Rabbit, a sagebrush-obligate species of conservation concern (Green and Flinders 1980). The deterioration of sagebrush grasslands is leading to the decline of Sage Grouse (Connelly and Braun 1997, Fisher et al. 1996; Swenson et al. 1987), Horned Larks, Vesper Sparrows, Brewers Sparrows, and Sage Thrashers (Wisdom et al. 2005, Rowland et al. 2006). This decline in cover is correlated with the expansion of pinyon-juniper woodlands (Miller et al. 1999, Miller and Tausch 2001), range improvement measures (Blaisdell 1949) and the introduction of *B. tectorum* (Whisenant 1990, Brooks et al. 2004).

Factors thought to influence the establishment and persistence of *A. tridentata* ssp. *vaseyana*, such as soil moisture, vary across a landscape. The establishment of *A. tridentata* ssp. *vaseyana* vs. *B. tectorum* following fire has not been examined at the landscape level. This observational study quantifies post-fire site conditions that result in

establishment of *A. tridentata* ssp. *vaseyana* vs. *B. tectorum* throughout a heterogeneous burn. I predict that *B. tectorum* will be more prevalent in xeric sites indicated by ridges with south-facing aspects, low topographic convergence index (TCI), and limited plant cover, because native species cover following fire is greater in more mesic sites (Huber et al. 1999, Dhaemers 2006, Reilly et al. 2006), so that there is limited opportunity for cheatgrass invasion (Figure 1).

I also examine how interacting biotic factors and legacy effects influence the establishment of *A. tridentata* ssp. *vaseyana* and *B. tectorum*. Pre-burn canopy cover is predicted to negatively influence the establishment of *A. tridentata* ssp. *vaseyana*, which is shade intolerant and unable to successfully compete with trees for soil moisture. Additionally, the establishment of *A. tridentata* ssp. *vaseyana* is predicted to benefit from increased proximity of unburned patches acting as post-burn propagule sources, since seed dispersal of this species occurs over short distances (≤ 30 -m; Meyer 1994). This set of interacting predictions is presented in a path diagram (Figure 2). The “mesic model” represents the hypothesis that *A. tridentata* ssp. *vaseyana* will have greater cover on mesic sites, given measured abiotic variables. A second model adds the hypothesized negative influence of pre-burn tree canopy cover on *A. tridentata* ssp. *vaseyana* cover. The hypothesized positive influence of unburned patches on *A. tridentata* ssp. *vaseyana* cover is also tested as unburned patches are likely to be propagule sources for *A. tridentata* ssp. *vaseyana* establishment. I then tested the influence of including *B. tectorum* cover in the final model.

The “xeric model” represents the hypothesis that *B. tectorum* cover will be greatest on xeric sites (Figure 3). I further consider pre-burn tree canopy cover, which

facilitates post-burn *B. tectorum* establishment by reducing cover of native perennial resprouting species. I then tested a hypothesized negative influence of unburned patches as propagule sources for less widely dispersing species that would hinder *B. tectorum* establishment (Figure 3).

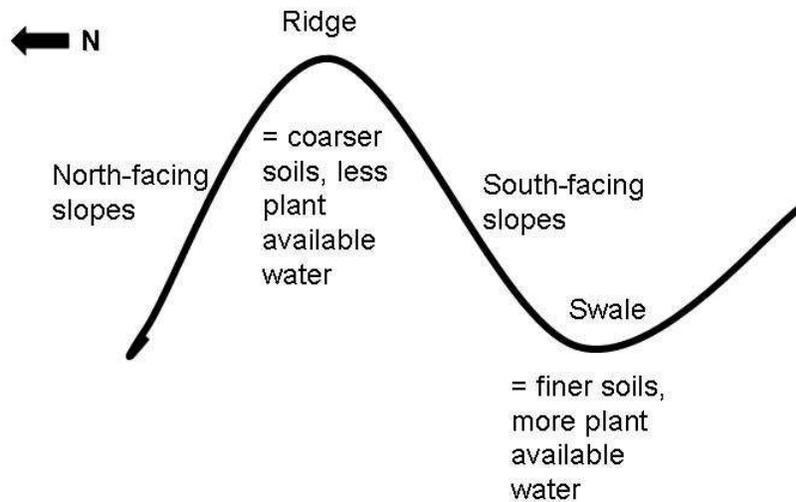


Figure 1. The influence of topography on soil texture and moisture

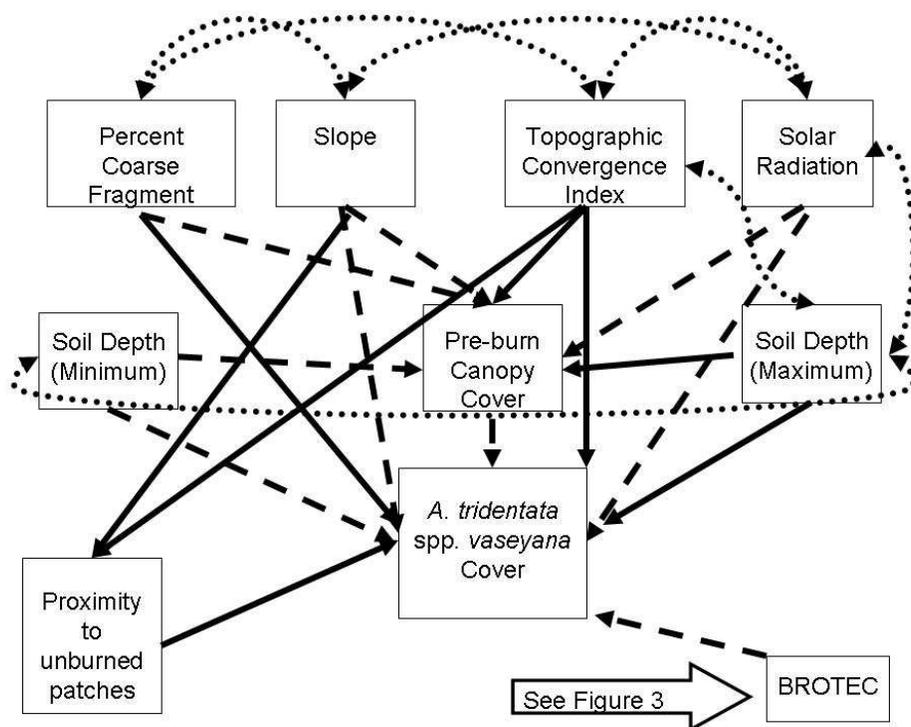


Figure 2. Path diagram of hypothetical model explaining *A. tridentata* ssp. *vaseyana* establishment following fire Correlated abiotic variables are shown with dotted double headed arrows. Negative effects are shown with dashed lines and positive effects are shown with solid lines. BROTEC – *Bromus tectorum* cover (Figure 3)

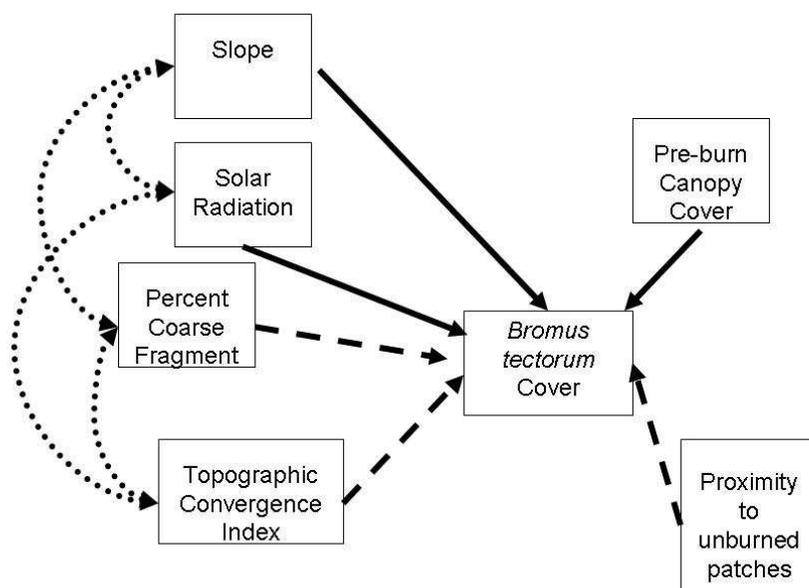


Figure 3. Path diagram of hypothetical model explaining *B. tectorum* establishment following fire Correlated abiotic variables are shown with dotted double headed arrows. Negative effects are shown with dashed lines and positive effects are shown with solid lines.

I examine the distribution of these two species following a six year old wildland fire burn in Wall Canyon of central Nevada's Toiyabe Range, to develop predictive models of species-environment relationships. A structural equation modeling approach is used to explore the indirect and direct influences of pre-fire woodland structure, and proximity to unburned areas for predicting cover and presence of each species. Recommendations are developed for restoration ecologists seeking to use prescribed fire or similar treatments for maintaining *A. tridentata* ssp. *vaseyana* without promoting *B. tectorum* in pinyon-juniper woodlands.

Methods

Data Collection

Study Design

The study area was divided into three equal-area sections in relation to distance from the canyon mouth. Survey plots were randomly stratified by study area section. Two gradsects in each section crossed key environmental gradients of elevation and distance from burn perimeter, and were constrained to be 100 m apart. The burn area was 2800 ha in extent and ranged in elevation from 2145 m to 2455 m. In total, 102, 20-m by 50-m plots were surveyed: 71 within the burn, 16 outside the burn perimeter and 15 in unburned patches.

GIS Derived Data

GIS layers were sampled for plot means of elevation, slope, aspect, estimated solar radiation (for May 15th to correspond with the germination period) (Kumar 1997), pre-burn tree canopy cover and topographic convergence index, after overlaying plot

boundaries reconstructed from GPS points. Tree canopy cover was delineated from panchromatic digital orthophotography (1-m resolution). 1994 DOQs were corrected for topographic shadows with Idrisi (Kilimanjaro 14.02) software (Greenwood 2006) and used to create a polygon layer of tree canopies that existed prior to the fire. The method used brightness, patch shape, patch area, distance, textural homogeneity, and local neighborhood relationships to segment images into homogeneous patches (Weisberg et al. 2007). A class hierarchy was then created to classify these images in an object oriented classification with Ecognition Professional (version 4.0) software. This process delineated tree polygons. The area covered by tree polygons was then sampled by the specific plot area to get pre-burn tree canopy cover. Topographic convergence index was calculated as:

$$(1) \quad TCI = \ln(\alpha / \tan \beta)$$

where α is the upslope contributing area of water drainage to the point of interest and β the local slope angle. High values are assigned to sites that collect and retain water in runoff events (e.g. depressions, low in the watershed), and low values are given to sites with steep slopes that are often high in the watershed.

To develop a layer of unburned patches, normalized burn ratio (NBR), was calculated from Landsat Imagery from June 2, July 20, and October 8, 2000. NBR highlights areas of differing burn severity using a ratio of short-wave infrared bands, Band 4 (0.76 – 0.90-um) and Band 7 (2.08 – 2.35-um) in the equation (Cocke 2005):

$$NBR (x) = (Band 4 - Band 7) / (Band 4 + Band 7)$$

Unburned patches throughout Wall Canyon were identified using differenced NBR (dNBR) values, subtracting the post-fire NBR from the pre-fire. Positive dNBR values

indicate vegetation damage. This classification was groundtruthed at the 94 sample locations within the burn perimeter (see Chapter 1). Twenty of 23 (87 %) unburned patches and 71 of 71 (100%) burned patches were accurately classified. Average distance from survey plots to the burn perimeter was calculated across eight compass directions. The influence of unburned patches was tested in regards to the edge density of unburned patches as increased edge was thought to favor shade intolerant species. Edge density of unburned patches was calculated for a 300-m neighborhood surrounding each surveyed plot.

Field Measurements

Aerial cover, topographic and soils data were collected at each plot. Aerial cover of *B. tectorum* was estimated from 25, 0.5-m² quadrats within a 20-m by 50-m plot (Figure 4). Aerial cover and frequency of *A. tridentata* ssp. *vaseyana* were surveyed along three 2-m by 50-m belt transects. Shrub height and canopy dimensions along major and minor axes were measured for each shrub regardless of whether the canopy extended beyond the transect edge. Belt transects began at 1 m, 10 m, and 17 m along the 20-m side of the plot and ran the 50-m length of the plot. Transects were sampled first at 1 m, then 17 m along the 20-m side of each macroplot in order to incorporate plot heterogeneity. If more than 100 individuals of any shrub species were encountered within these first two transects, the third transect at 10 m was skipped.

Abiotic data were collected from each plot, including topographic position, aspect, slope, slope curvature (concave, convex or flat), and slope position (ridgetop, upslope, midslope, lowslope or valley bottom). The elevation of each plot was recorded using a Trimble GeoExplorer XT with submeter precision. Soil depth was measured by

pounding a 0.5-cm metal rod into the ground until further pounding was resisted by rock (Harner and Harper 1976). Soil depth measurements were recorded as an average of three readings from each of 10, 0.5-m² quadrats. A total of one quart of soil was collected as evenly as possible from the same 10, 0.5-m² quadrats. Soils were analyzed for texture, pH and percent coarse fragment. Soil texture was assessed using a ribbon test according to the classification of Thien (1979). Soil pH was measured with a Corning pH meter 320 using roughly 10 grams of soil and 19-mL of DI water and 1-mL CaCl₂.

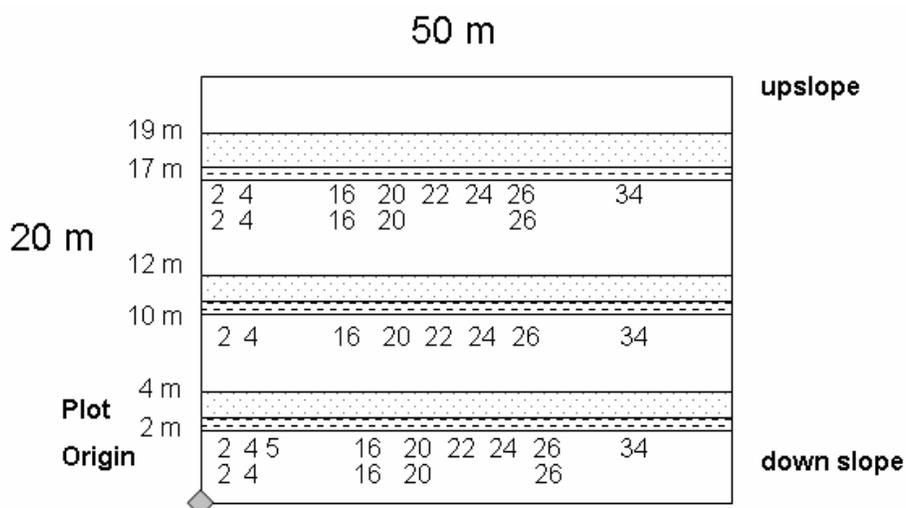


Figure 4. Layout of each 20-m by 50-m macroplot Aerial cover of *B. tectorum* was estimated in 0.5-m² quadrats designated by the rows numbered 2-34. Soils data were gathered from the quadrats designated by the rows numbered 2-26. Cover of *A. tridentata* ssp. *vaseyana* was surveyed in 2-m by 50-m belt transects represented by dotted belts.

Data Analysis

Variables considered for use in statistical analyses were selected from a preliminary analysis of bivariate correlation. All variable pairs with Pearson's correlations between ± 0.4 and ± 1 were re-evaluated and one of each pair was dropped from further analysis. Principal component analyses identified correlated variables that

explained the same underlying environmental gradients. Variables were examined for high values of kurtosis or skewness, and logarithmic or other transformations were applied as necessary to achieve normality and homogeneity of variance of distributions. I used arcsine square-root transformed cover values for both *B. tectorum* and *A. tridentata* ssp. *vaseyana*, as is appropriate for proportional data. The resulting variables are presented in Table 1.

Principal components regression analysis was used to model post-fire *B. tectorum* or *A. tridentata* ssp. *vaseyana* cover according to underlying environmental gradients (Weisberg and Baker 1995). First, principal components analysis was used to create linear combinations of variables that represent underlying environmental gradients hypothesized to influence post-fire successional pathways. A cross products matrix of correlation coefficients was used to ensure that the variables are centered and standardized so that each factor was on equal footing with the others. Second, the resulting principal components were used in linear regressions to predict cover of *B. tectorum* and cover of *A. tridentata* ssp. *vaseyana*. Both forwards and backwards stepwise selection procedures were used to ensure that both methods selected the same models.

Table 1. Environmental variables considered

Abiotic Variables		Biotic Variables	
Solar Radiation	Incident, cloud-free solar radiation estimated for May 15	Average Distance to Burn Perimeter	The average distance to the burn perimeter from 8 compass directions
Slope	Field measured slope steepness (degrees)	Edge Density at 300 m	The density of unburned patch edge within a 300-m radius
Maximum Soil Depth	The maximum soil depth (cm)	Pre-burn PJ Canopy Cover	The area covered by pre-burn tree canopy in a plot
Minimum Soil Depth	The minimum soil depth (cm)		
Percent Coarse Fragment	The percent of coarse fragment in surface soils (down to 10 cm) determined by weight		
Plot pH	The surface soil (down to 10 cm) pH value		
TCI	Topographic convergence index		
Ammonium	Concentration of ammonium in the surface soil (down to 10 cm)		
Nitrate	Concentration of nitrate in the surface soil (down to 10 cm)		

A matrix of Pearson's Correlations among considered variables (Table 5) and cover of *B. tectorum* and *A. tridentata* ssp. *vaseyana* was examined for significant correlations between factors. Structural equation modeling (SEM) further explored these correlations and was used to compare alternative causal models for *B. tectorum* and *A. tridentata* ssp. *vaseyana* cover. This technique permits the testing of complex dependency relationships and partitions direct and indirect effects of explanatory variables such as pre-burn canopy cover. Models are assessed using fit indices, referring to how the hypothesized model corresponds with the observed covariances. Relationships between variables can be unidirectional or direct (shown as a straight,

singe-headed arrow on a path diagram), correlated (shown as a double-headed arrow), or indirect (shown as a single-headed arrow mediated through another variable). To make variables comparable despite disparate units, path coefficients are standardized by dividing each variable by its standard deviation. The size and slope of the coefficient indicates the amount and direction of influence of the predictor variable on the response (Grace and Pugsek 1997). Chi-square values and their probabilities test the fit of the model with the data as does the root mean square error of approximation. If there is not a significant difference between the data and the model, there is agreement between the predicted and observed covariances. Models were compared with the most basic model tested in a nested series using the difference in chi-square statistic (Grace and Keeley 2006). The mesic model was used as the baseline model for *A. tridentata* ssp. *vaseyana* and the xeric model was used for *B. tectorum*. An increase in chi-square of 3.841 for a change in one degree of freedom and an increase in chi-square of 5.991 for a change in two degrees of freedom identifies a significantly better model (Grace 2006). Individual pathways were evaluated with critical ratios and regressions assessing the strength of the hypothesized relationships between variables. A critical ratio is the covariance estimate divided by the standard error. Using a significance level of 0.05, a critical ratio greater than 1.96 indicates that the covariance between variables in the selected pathway is significant.

Results

Principal components regression models included an ecologically interpretable subset of the principal components that proved influential in predicting sagebrush and cheatgrass distributions (Table 2). The best predictive model of *A. tridentata* ssp. *vaseyana* includes four principal components: 2, 5, 7, and 12 (Table 3). The relationship with Principal Component 2 (PC 2) describes greater probability of increased sagebrush cover on sites with deeper soils that are closer to the burn perimeter and further from unburned patches, have lower TCI values (higher in the watershed), and have lower nitrate concentrations. Sagebrush occurrence was also favored by sites with deeper soils that are further from the burn perimeter, are drier, and have greater concentrations of ammonium as shown by principal component 5. Principal component 7 describes sites that are close to unburned patches, are drier, and have lower ammonium and nitrate concentrations. Principal component 12 describes sites with gentler slopes that are moister with lower topographic convergence. Generalizing from these components, *A. tridentata* ssp. *vaseyana* preferred sites with gentle slopes and deeper soils, and within closer proximity to the burn perimeter or to unburned patches (Table 2). The best predictive model of *B. tectorum* (Table 3) describes favorable sites as having gentle slopes, more acidic soils, lower pre-burn canopy cover, and higher ammonium concentrations.

All pathways hypothesized to influence *A. tridentata* ssp. *vaseyana* cover were tested in SEM models and explored in a Pearson's Correlation matrix (Table 5). Percent coarse fragment in surface soils showed a positive correlation with slope and a negative correlation with topographic convergence index (Figure 5, 6). Solar radiation had a

negative correlation with topographic convergence index and slope (Figure 5, 6).

Minimum soil depth had a positive correlation with maximum soil depth and topographic convergence index and a negative correlation with solar radiation (Figure 5, 6). These significant correlations (Table 5) were also significant pathways in SEM models (Figure 5, 6).

Table 2. Principal components and loadings used in regression analysis of *A. tridentata* ssp. *vaseyana* and *B. tectorum* aerial cover PC loadings greater than 0.3 are in bold. Variable abbreviations include AveDist B. Perimeter = average distance to burn perimeter and PerCFrg = percent coarse fragment.

PC2	PC4	PC5	PC7	PC12
EdgeDensity 0.469	Slope 0.460	Max Depth -0.512	Edge Density 0.485	Slope 0.594
AveDist B.Perimeter 0.452	Pre-burn PJ 0.445	Ammonium -0.416	Nitrate -0.444	Solar Radiation 0.515
Nitrate 0.399	Plot pH 0.404	AveDist B.Perimeter -0.389	Ammonium -0.402	TCI 0.467
Max Depth -0.307	Ammonium -0.351	Solar Radiation -0.362	Solar Radiation 0.399	Edge Density -0.195
TCI 0.300	AveDist B.Perimeter 0.291	Min Depth -0.272	Pre-burn PJ -0.250	PerCFrg -0.177
Slope 0.286	TCI -0.276	PerCFrg -0.267	AveDist B.Perimeter 0.248	Max Depth 0.146
Plot pH 0.221	Nitrate -0.208	Slope 0.232	Min Depth -0.238	Ammonium 0.142
Ammonium 0.215	Solar Radiation -0.203	Edge Density -0.169	TCI -0.194	Plot pH -0.137
Pre-burn PJ -0.137	Min Depth 0.172	TCI 0.148	Plot pH -0.134	Nitrate -0.124
Solar Radiation -0.107	Edge Density -0.123 PerCFrg 0.115	Pre-burn PJ -0.136 Plot pH -0.119		Pre-burn PJ 0.120

Table 3. Best stepwise regression predictive model of *A. tridentata* ssp. *vaseyana* cover, $R^2_{adj} = 0.153$

Model parameter	Coefficient	SE	P
Intercept	4.101	1.808	0.027
PC2	-0.007	0.002	0.005
PC5	-0.012	0.007	0.061
PC7	0.013	0.004	0.006
PC12	-0.012	0.004	0.005

Table 4. Best stepwise regression predictive model of *B. tectorum* cover, $R^2_{adj} = 0.296$

Model parameter	Coefficient	SE	P
Intercept	-6.934	2.089	0.0014
PC4	-0.002	0.0005	<0.0001

Table 5. Pearson's Correlations among environmental variables and covers of *B. tectorum* and *A. tridentata* spp. *vaseyana* Significance at a $p \leq 0.1$ is represented by *, $\leq 0.05 = **$, and $\leq 0.001 = ***$.

	Slope	Maximum Soil Depth	Minimum Soil Depth	Percent Coarse Fragment	Pre-burn PJ Cover	May 15 th Solar Radiation	TCI	Edge Density	<i>B.</i> <i>tectorum</i> Cover	<i>A.</i> <i>tridentata</i> ssp. <i>vaseyana</i> Cover
Slope	1									
Maximum Soil Depth	-0.16	1								
Minimum Soil Depth	-0.05	0.39***	1							
Percent Coarse Fragment	0.33**	0.02	-0.12	1						
Pre-burn PJ Cover	-0.07	0.02	0.11	-0.27**	1					
May 15 th Solar Radiation	-0.35**	-0.14	-0.32**	0.08	0.03	1				
TCI	-0.21*	0.01	0.27**	-0.32**	-0.17	-0.32**	1			
Edge Density	0.09	-0.06	0.10	-0.18	-0.12	-0.15	0.34**	1		
<i>B. tectorum</i> Cover	-0.16	-0.08	-0.21*	0.11	-0.07	0.53***	-0.25**	-0.13	1	
<i>A. tridentata</i> ssp. <i>vaseyana</i> Cover	-0.01	0.14	-0.23**	0.11	-0.28*	-0.08	-0.08	-0.01	0.01	1

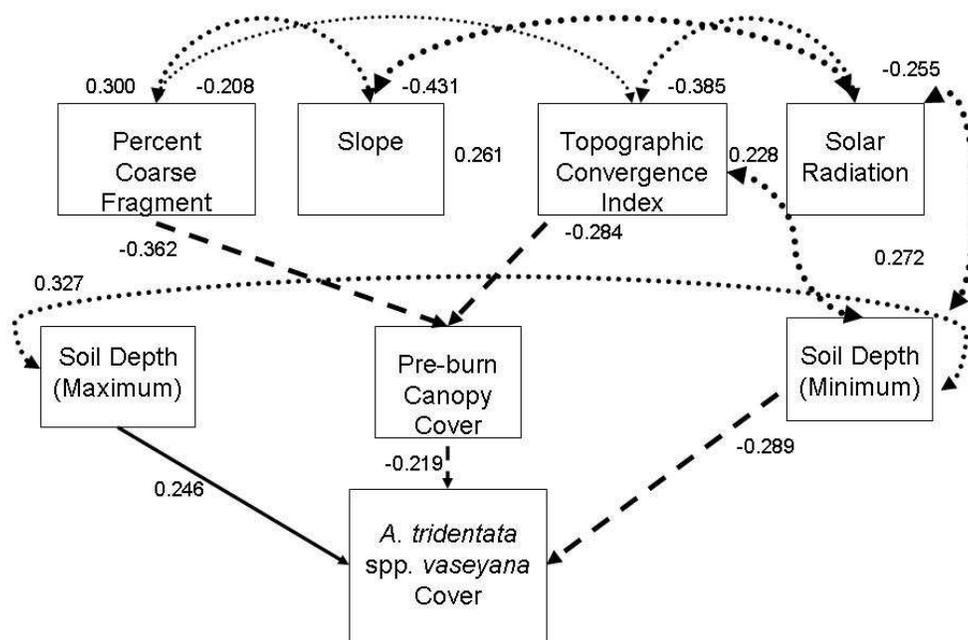


Figure 5. Path diagram of *A. tridentata* spp. *vaseyana* cover with all significant pathways Correlated abiotic variables are shown with dotted double headed arrows. Negative effects are shown with dashed lines and positive effects are shown with solid lines. The relative size each arrow represents the magnitude of the effect.

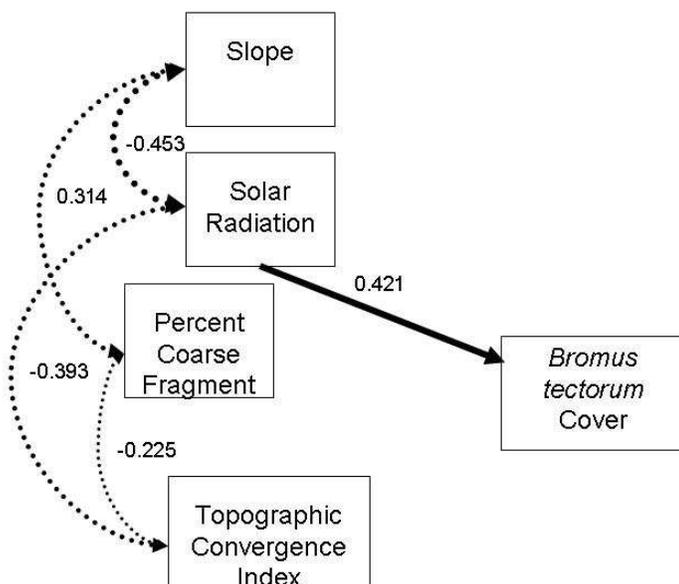


Figure 6. Path diagram of *Bromus tectorum* cover with all significant pathways Correlated abiotic variables are shown with dotted double headed arrows. Negative effects are shown with dashed lines and positive effects are shown with solid lines. The relative size each arrow represents the magnitude of the effect.

Significant models were determined by critical ratios of component pathways. Significant models of *A. tridentata* ssp. *vaseyana* cover consisted of abiotic factors, referred to as the mesic model, and pre-burn canopy cover. In the mesic model, *A. tridentata* ssp. *vaseyana* cover was favored by deeper soils and these pathways (with minimum and maximum soil depths) were kept in the model when testing additional factors (Figure 5, RMSEA = 0.05, $X^2 = 14.474$, $p = 0.271$). Proximity to unburned patches and cover of *B. tectorum* did not have significant effects on *A. tridentata* ssp. *vaseyana* cover. Pre-burn tree canopy cover had a significant direct effect on *A. tridentata* ssp. *vaseyana* cover and mediated the indirect effects of topographic convergence index ($-0.362 \times -0.219 = 0.079$, Figure 5) and percent coarse fragment ($-0.284 \times -0.219 = 0.062$, Figure 5) (RMSEA = < 0.001 , $X^2 = 15.641$, $p = 0.478$). Sites with more percent coarse fragment and greater TCI had less pre-burn canopy cover. These two nested structural equation models of *A. tridentata* ssp. *vaseyana* cover were compared based upon a lower root mean squared error of approximation (RMSEA), and a higher X^2 . The difference in X^2 values between the models did not indicate that the model including pre-burn canopy cover was superior to the mesic model ($\Delta X^2 = 1.167$, $\Delta df = 4$, $p > 0.75$).

Models of *B. tectorum* explored the same biotic influences as were tested in models of *A. tridentata* ssp. *vaseyana* cover, yet the initial model of abiotic factors, the xeric model, was the only model in which all tested pathways were found to be significant. In this model, solar radiation had a positive direct effect on cover (Figure 6).

Discussion

Although it was predicted that *A. tridentata* ssp. *vaseyana* would be more abundant on mesic sites and *B. tectorum* would be more abundant on xeric sites, results indicated that the site preferences of these species were complex. Results of principal components regressions supported the prediction that *A. tridentata* ssp. *vaseyana* was more likely to be abundant on mesic sites, specifically sites with gentler slopes, deeper soils, and within closer proximity to seed sources (unburned patches or the burn perimeter). However, *B. tectorum* was also more likely to be abundant on gentler slopes with less pre-burn canopy cover. Although *A. tridentata* ssp. *vaseyana* cover was negatively associated with pre-burn tree canopy cover (PCs 7 and 12); the loading of this variable was not greater than 0.3 (Table 2). Interpretations of stepwise regressions of principal components showed a large overlap in factors predicting high covers of both species. However, there was greater cover of *A. tridentata* ssp. *vaseyana* on sites in close proximity to seed sources and greater cover of *B. tectorum* with increased solar radiation.

SEM results confirmed that *A. tridentata* ssp. *vaseyana* cover was greater on mesic sites, with greater soil depths and lower pre-burn tree canopy cover. Pre-burn canopy cover had a significant negative effect on cover of *A. tridentata* ssp. *vaseyana* that was not as apparent from the principal component regression analyses. This may have been due to the significant negative relationships of percent coarse fragment and topographic convergence with pre-burn tree canopy cover. After accounting for the effects of percent coarse fragment and topographic convergence index, pre-burn tree canopy cover had a slightly negative effect on *A. tridentata* ssp. *vaseyana* cover (Figure 5). Neither proximity to unburned patches (seed sources) nor cover of *B. tectorum* had a

direct effect on *A. tridentata* ssp. *vaseyana* cover. Even though the previous winter had been wet and favorable for *A. tridentata* ssp. *vaseyana* establishment, this would have only resulted in an increase in seedling cover, which if present, does not greatly increase the total cover of this species. Most *A. tridentata* ssp. *vaseyana* cover was attributed to mature individuals. Due to deep rooting structures, individuals would not have been in competition for soil moisture with *B. tectorum*.

A relationship of *A. tridentata* ssp. *vaseyana* cover with proximity to unburned patches would have implied that seed sources from outside the burn area contribute to establishment of this species. However, it is not clear to what extent *A. tridentata* ssp. *vaseyana* establishes from a surviving seed bank following fire or if it is dependent on seed sources from outside the burn area. In either case, establishment is unlikely to occur in years of low precipitation (Mueggler 1956). Establishment of *A. tridentata* ssp. *wyomingensis* increases with an increase in seeding rates (Williams et al. 2002), perhaps indicating a positive influence of unburned patches in sagebrush-grasslands. However, studies have shown ambiguous evidence as to the pattern of *A. tridentata* ssp. *vaseyana* establishment. Using paired covered and uncovered plots, Mueggler (1956) showed that seedlings in the center of a burn appeared to be the product of a residual seed bank instead of wind-borne seed. Mueggler (1956) also found more seedlings on less intensely burned areas, further supporting the argument for *A. tridentata* ssp. *vaseyana* regeneration from a seed bank. However, seed from unburned seed sources may also contribute to establishment as he found an increase in seedling density within a few hundred feet of an unburned seed source. Young and Evans (1989) argued that low densities of *A. tridentata* seedlings immediately following fire suggested minimal seed-

banking. However, neither burn severity nor annual precipitation were accounted for in this study. Johnson and Payne (1968) observed regeneration of *A. tridentata* ssp. *vaseyana* following non-fire disturbance (plowing and herbicide) that did not decrease with increasing distance from the disturbance edge, indicating seed-banking. In this study, the influence of proximity to unburned seed source was correlated with increased topographic convergence index (Table 5), showing that the soil seed bank may have been more likely to survive due to reduced fire severity in deeper soils. The hypothesized interaction of topography and soil texture predicts that these productive sites favor *A. tridentata* ssp. *vaseyana*. Although this study did not show a significant relationship between *A. tridentata* ssp. *vaseyana* establishment and proximity to unburned patches, the potential effects of unburned patches to act as post-fire seed sources should not be disregarded. Experimental research is needed to test the influence of proximity to seed sources in unburned patches while controlling for environmental variation.

SEM analyses predicted higher cover of *B. tectorum* on drier sites (higher solar radiation) but differed in principal components regression models which attributed more influence to slope. This may have been due to strong, significant correlations between solar radiation and slope (Table 5). Stepwise regressions indicate that *B. tectorum* prefers sites with gentler slopes, lower pre-burn canopy cover, more acidic soils, higher ammonium concentrations and a slight positive influence of solar radiation.

Proximity to roads and elevation have also been shown to influence the cover of *B. tectorum* (Bradley and Mustard 1996), but these factors were not found to be significant in this study. Distance to nearest road, unburned patches and elevation were all highly correlated (greater than 0.4; Appendix 1). When each of these factors was

tested independently, distance to nearest road and elevation were not significant predictors of *B. tectorum* cover. However, the elevation gradient of 300 m covered in this survey may not have been adequate to show a range in *B. tectorum* cover that could be attributed to elevation. Additionally, elevation is often a proxy for productivity, which was addressed using other variables such as solar radiation. Proximity to unburned patches may explain some portion of the variation that would have been explained by proximity to roads.

SEM models account for many of the correlations between predictors and indicated that *B. tectorum* cover was driven by abiotic factors (namely solar radiation and soil moisture), and not pre-burn conditions. The preference of *B. tectorum* for drier sites is accounted for by the negative influence of established native vegetation (Chambers 2007), which is likely to be most dominant on mesic sites.

Numerous studies have shown that the cover of *B. tectorum* is not predicted only by static factors, but also by site and climatic history. Mack and Pyke (1984) showed that cover of *B. tectorum* is determined by a series of environmental events. Cohorts of differing ages experience different stresses: desiccation, grazing, smut fungus, and winter death, though these were shown to be unrelated to site features (Mack and Pyke 1984). Desiccation and winter death are associated with climate, which varies from year to year. Low levels of *B. tectorum* cover may result from a reduced seed bank in the previous year (Mack and Pyke 1983, Keeley and McGinnis 2007). Without the inclusion of pre-fire seed bank in structural equation models, Keeley and McGinnis (2007) found that positive effects of abiotic conditions were more apparent. In a wet year, this highly fecund species exerts propagule pressure on surrounding communities, increasing the

likelihood of establishment and invasion following disturbance (Bradford and Lauenroth 2006). These findings should be interpreted in light of factors affecting cover, after a moderately wet year, at a site with steep terrain that has historically and currently been subjected to anthropogenic disturbances. A similar study conducted in a dry year is likely to have yielded different results.

These findings highlight the importance of the pre-disturbance legacy effects, particularly for *A. tridentata* ssp. *vaseyana* cover, which is reduced with increasing pre-burn tree canopy cover according to SEM models. Biological legacies facilitate post-disturbance succession, contributing to resilience of native plant communities and resistance to invasion. The contribution of legacy effects to native plant communities following fire is closely tied to fire severity (Moreno and Oechel 1991, Frelich and Reich 1999, Lee 2003, Freeman et al. 2007, Sibold et al. 2007). Higher severity fire results in increased cover of bare ground, opening sites to invasion by exotic species in coniferous forests (Freeman et al. 2007). Even though this study lacks a direct measure of fire severity, higher pre-burn canopy cover often leads to higher severity fire due to increased fuel loads. Additionally, sites with high pre-burn canopy cover would have had minimal propagule sources prior to the fire. Pre-fire conditions in pinyon-juniper woodlands, such as time since the last fire, correlate with an increase in canopy cover and a subsequent reduction in the cover and seed production of understory species to low levels (Koniak and Everett 1982, Tausch and Nowak 1999, Poulsen et al. 1999, Miller et al. 2000). Similar reductions in understory cover and seed production have been observed in the forests of the Pacific Northwest (Halpern and Spies 1995, Odion and Sarr 2007). Reduced propagule density decreases the likelihood of species' establishment. If legacy

effects of native communities are low, and seed sources of non-native plant species are within dispersal distance, there is greater probability that post-disturbance vegetation will be dominated by non-native species.

Management Implications

My work showed a significant negative influence of pre-burn tree canopy cover on cover of *A. tridentata* ssp. *vaseyana* after fire. To maintain high resilience of this species to fire disturbance, managers should reduce tree dominance in pinyon-juniper woodlands before canopy cover substantially reduces legacy effects of *A. tridentata* ssp. *vaseyana*, so that managed systems will be resilient to unplanned disturbances. The degree to which unburned seed sources influence establishment of *A. tridentata* ssp. *vaseyana* is still uncertain, although I observed a weak positive relationship between proximity to unburned seed sources and increased cover of *A. tridentata* ssp. *vaseyana*. Land managers should consider preserving unburned patches when conducting prescribed burning. Due to higher fuel moisture conditions, spring burns result in more unburned patches (Knapp and Keeley 2006). Even though native plant species may not be adapted to early season burns, burning at this time of year will promote legacy effects with persistence of unburned patches and reduced burn intensity.

Fire is within the range of tolerance of many native understory species in pinyon-juniper woodlands, and even species with low fire tolerances regenerate after fire (Chapter 1) including *A. tridentata* ssp. *vaseyana* (Mueggler 1956, Young and Evans 1989). However, fire can also promote invasion by *B. tectorum*. Mechanical treatments such as chaining and thinning have been used as an alternative to fire (Loftlin 1999, Stevens 1999). Native annual and perennial herbaceous species have been shown to

regenerate immediately following mechanical treatments (Loftlin 1999) although the long-term effects of these treatments are uncertain. In this study, the only sites where I did not find *B. tectorum* were within unburned patches or outside the burn area.

Although burns in more mesic areas, with deeper soils, and with less pre-burn canopy cover will require less intensive restoration efforts, active restoration in other areas is needed. This appears to be true even at the level of individual patches within a single large burn.

Following fire, *B. tectorum* often creates continuous swaths of fuels, which with the next fire, results in reduced legacy effects as plants have not had enough time to reach reproductive maturity (Whisenant 1990). Obligate seeding species such as *A. tridentata* ssp. *vaseyana* are placed at a disadvantage given the altered fire regime facilitated by *B. tectorum*. Management approaches should balance restoration efforts to inhibit *B. tectorum* and promote *A. tridentata* ssp. *vaseyana* cover. In this case, restoration efforts that foster legacy effects will be more likely to thwart increased dominance by *B. tectorum* and non-native plant species.

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Appendix 1

Table 1. Pearson's Correlations among environmental variables.

	Field Aspect	GIS Aspect	Slope	Max Dpth	Min Dpth	Ave Dpth	PerClay	Plot pH	PerCFrg	R PJ Cover
Field Aspect	1	0.662	-0.015	0.215	0.414	0.206	0.3	-0.248	-0.212	-0.031
GIS Aspect	0.662	1	-0.014	0.26	0.373	0.215	0.201	-0.391	-0.066	-0.085
Slope	-0.015	-0.014	1	-0.156	-0.053	-0.057	-0.162	0.14	0.332	0.087
Max Dpth	0.215	0.26	-0.156	1	0.387	0.663	-0.062	-0.298	0.016	-0.048
Min Dpth	0.414	0.373	-0.053	0.387	1	0.601	0.031	-0.144	-0.118	0.246
Ave Dpth	0.206	0.215	-0.057	0.663	0.601	1	-0.069	-0.148	-0.012	0.201
PerClay	0.3	0.201	-0.162	-0.062	0.031	-0.069	1	-0.232	-0.463	0.171
Plot pH	-0.248	-0.391	0.14	-0.298	-0.144	-0.148	-0.232	1	0.076	0.212
PerCFrg	-0.212	-0.066	0.332	0.016	-0.118	-0.012	-0.463	0.076	1	-0.245
R PJ Cover	-0.031	-0.085	0.087	-0.048	0.246	0.201	0.171	0.212	-0.245	1
No. UB Polygons w/in 50m	0.113	-0.074	0.234	-0.218	-0.044	-0.207	-0.025	0.091	0.066	0.056
UB Area w/in 50m	0.057	-0.032	0.256	-0.17	-0.085	-0.203	0.053	-0.01	0.1	0.048
No. UB Polygons w/in 150m	0.143	0.236	-0.02	-0.074	0.041	-0.198	0.061	-0.077	-0.168	0
UB Area w/in 150m	0.106	0.16	0.146	-0.154	0.047	-0.16	0.083	-0.17	-0.035	0.112
No. UB Polygons w/in 300m	0.282	0.337	0.054	0.034	0.247	0.049	-0.004	0	-0.181	0.072
UB Area w/in 300m	0.142	0.265	0.141	-0.006	0.09	-0.05	0.015	-0.046	-0.174	0.07
AveDist to B.P.	0.041	0.065	0.241	0.023	0.119	0.088	-0.032	0.212	-0.032	0.164
PJCover Area	-0.141	-0.257	-0.073	0.016	0.105	0.207	0.002	0.34	-0.27	0.748
PJCover No. Polygons	-0.216	-0.164	-0.013	0.024	0.103	0.263	0.042	0.161	-0.199	0.475
Dist. to Nearest Road	-0.092	0.035	0.093	0.155	-0.056	0.055	0.114	-0.122	0.037	0.028
Dist. to Nearest B.P.	-0.034	-0.084	0.135	0.048	0.149	0.099	-0.058	0.265	-0.034	0.216
Dist. to Nearest UB Patch	-0.297	-0.296	-0.078	-0.036	-0.071	0.01	-0.001	0.041	0.018	-0.007
Wall DEM	-0.107	-0.107	0.228	-0.276	-0.015	-0.238	-0.148	0.295	-0.092	0.191
July 15 th Solar Radiation	-0.247	-0.432	-0.397	-0.112	-0.275	-0.181	-0.169	0.137	0.053	-0.176
May 15 th Solar Radiation	-0.304	-0.52	-0.349	-0.138	-0.322	-0.207	-0.205	0.193	0.084	-0.176
Easting	-0.053	-0.101	-0.148	0.135	-0.052	0.09	0.107	-0.293	0.049	-0.08
Northing	0.004	0.046	0.194	0.136	0.089	0.098	0.067	0.177	-0.047	0.109
TCI	0.284	0.451	-0.21	0.013	0.265	0.01	0.282	-0.082	-0.323	-0.006
ED300	0.155	0.288	0.094	-0.058	0.009	-0.085	0.001	-0.024	-0.181	0.004
ED150	0.143	0.128	0.134	-0.133	0.012	-0.175	-0.029	-0.116	-0.002	-0.048

Table 1. continuation 1.

	No. UB Polygons w/in 50m	UB Area w/in 50m	No.UB Polygons w/in 150m	UB Area w/in 150m	No. UB Polygons w/in 300m	UB Area w/in 300m	AveDist to B.P	PJCover Area	PJCover No. Polygons	Nearest Road
Field Aspect	0.113	0.057	0.143	0.106	0.282	0.142	0.041	-0.141	-0.216	-0.092
GIS Aspect	-0.074	-0.032	0.236	0.16	0.337	0.265	0.065	-0.257	-0.164	0.035
Slope	0.234	0.256	-0.02	0.146	0.054	0.141	0.241	-0.073	-0.013	0.093
Max Dpth	-0.218	-0.17	-0.074	-0.154	0.034	-0.006	0.023	0.016	0.024	0.155
Min Dpth	-0.044	-0.085	0.041	0.047	0.247	0.09	0.119	0.105	0.103	-0.056
Ave Dpth	-0.207	-0.203	-0.198	-0.16	0.049	-0.05	0.088	0.207	0.263	0.055
PerClay	-0.025	0.053	0.061	0.083	-0.004	0.015	-0.032	0.002	0.042	0.114
Plot pH	0.091	-0.01	-0.077	-0.17	0	-0.046	0.212	0.34	0.161	-0.122
PerCFrg	0.066	0.1	-0.168	-0.035	-0.181	-0.174	-0.032	-0.27	-0.199	0.037
R PJ Cover	0.056	0.048	0	0.112	0.072	0.07	0.164	0.748	0.475	0.028
No. UB Polygons w/in 50-m	1	0.868	0.327	0.54	0.213	0.273	0.102	-0.019	-0.1	-0.133
Unburned Area within 50-m	0.868	1	0.315	0.688	0.138	0.356	0.219	-0.143	-0.15	-0.149
No. UB Polygons w/in 150m	0.327	0.315	1	0.561	0.702	0.63	0.135	-0.081	-0.1	-0.245
UB Area w/in 150m	0.54	0.688	0.561	1	0.443	0.745	0.275	-0.228	-0.159	-0.111
No. UB Polygons w/in 300m	0.213	0.138	0.702	0.443	1	0.755	0.309	-0.034	-0.111	-0.324
UB Area w/in 300m	0.273	0.356	0.63	0.745	0.755	1	0.358	-0.108	-0.122	-0.144
AveDist to B.P.	0.102	0.219	0.135	0.275	0.309	0.358	1	0.056	0.15	-0.273
PJCover Area	-0.019	-0.143	-0.081	-0.228	-0.034	-0.108	0.056	1	0.661	0.047
PJCover No. Polygons	-0.1	-0.15	-0.1	-0.159	-0.111	-0.122	0.15	0.661	1	0.225
Nearest Road	-0.133	-0.149	-0.245	-0.111	-0.324	-0.144	-0.273	0.047	0.225	1
Nearest B.P.	0.154	0.198	0.138	0.216	0.376	0.286	0.828	0.102	0.034	-0.379
Nearest UB Patch	-0.461	-0.398	-0.563	-0.443	-0.562	-0.421	0.037	0.051	0.215	0.126
Wall DEM	0.283	0.346	0.214	0.365	0.376	0.492	0.565	0.126	0.026	-0.493
July 15 th Solar Radiation	-0.072	-0.158	-0.039	-0.179	-0.053	-0.144	-0.143	0.015	-0.098	-0.233
May 15 th Solar Radiation	-0.063	-0.145	-0.08	-0.212	-0.1	-0.179	-0.116	0.033	-0.1	-0.237
Easting	-0.23	-0.244	-0.302	-0.314	-0.527	-0.478	-0.569	0.04	0.11	0.679
Northing	0.119	0.131	0.116	0.29	0.272	0.417	0.532	0.02	0.132	0.473
TCI	0.051	0.137	0.391	0.29	0.25	0.292	0.145	-0.167	-0.125	-0.134
ED300	0.282	0.322	0.702	0.728	0.803	0.976	0.328	-0.123	-0.148	-0.181
ED150	0.661	0.709	0.634	0.923	0.474	0.716	0.2	-0.223	-0.163	-0.169

Table 1. continuation 2.

	Nearest B. P.	Nearest UB Patch	Wall DEM	July 15 th Solar Radiation	May 15 th Solar Radiation	Easting	Northing	TCI	ED300	ED150
Field Aspect	-0.034	-0.297	-0.107	-0.247	-0.304	-0.053	0.004	0.284	0.155	0.143
GIS Aspect	-0.084	-0.296	-0.107	-0.432	-0.52	-0.101	0.046	0.451	0.288	0.128
Slope	0.135	-0.078	0.228	-0.397	-0.349	-0.148	0.194	-0.21	0.094	0.134
Max Dpth	0.048	-0.036	-0.276	-0.112	-0.138	0.135	0.136	0.013	-0.058	-0.133
Min Dpth	0.149	-0.071	-0.015	-0.275	-0.322	-0.052	0.089	0.265	0.099	0.012
Ave Dpth	0.099	0.01	-0.238	-0.181	-0.207	0.09	0.098	0.01	-0.085	-0.175
PerClay	-0.058	-0.001	-0.148	-0.169	-0.205	0.107	0.067	0.282	0.001	-0.029
Plot pH	0.265	0.041	0.295	0.137	0.193	-0.293	0.177	-0.082	-0.024	-0.116
PerCFrg	-0.034	0.018	-0.092	0.053	0.084	0.049	-0.047	-0.323	-0.181	-0.002
Relative PJ Cover	0.216	-0.007	0.191	-0.176	-0.176	-0.08	0.109	-0.006	0.044	-0.048
No. UB Polygons w/in 50m	0.154	-0.461	0.283	-0.072	-0.063	-0.23	0.119	0.051	0.282	0.661
UB Area w/in 50m	0.198	-0.398	0.346	-0.158	-0.145	-0.244	0.131	0.137	0.322	0.709
No. UB Polygons w/in 150m	0.138	-0.563	0.214	-0.039	-0.08	-0.302	0.116	0.391	0.702	0.634
UB Area w/in 150m	0.216	-0.443	0.365	-0.179	-0.212	-0.314	0.29	0.29	0.728	0.923
No. UB Polygons w/in 300m	0.376	-0.562	0.376	-0.053	-0.1	-0.527	0.272	0.25	0.803	0.474
UB Area w/in 300m	0.286	-0.421	0.492	-0.144	-0.179	-0.478	0.417	0.292	0.976	0.716
AveDist to B.P.	0.828	0.037	0.565	-0.143	-0.116	-0.569	0.532	0.145	0.328	0.2
PJCover Area	0.102	0.051	0.126	0.015	0.033	0.04	0.02	-0.167	-0.123	-0.223
PJCover No. Polygons	0.034	0.215	0.026	-0.098	-0.1	0.11	0.132	-0.125	-0.148	-0.163
Nearest Road	-0.379	0.126	-0.493	-0.223	-0.237	0.679	0.473	-0.134	-0.181	-0.169
Nearest B.P.	1	-0.006	0.534	-0.023	0.009	-0.588	0.484	0.145	0.286	0.158
Nearest UB Patch	-0.006	1	-0.081	-0.009	0.034	0.285	-0.051	-0.029	-0.466	-0.524
Wall DEM	0.534	-0.081	1	0.019	0.051	-0.74	0.103	0.032	0.465	0.354
July 15 th Solar Radiation	-0.023	-0.009	0.019	1	0.987	-0.017	-0.245	-0.292	-0.11	-0.11
May 15 th Solar Radiation	0.009	0.034	0.051	0.987	1	-0.029	-0.242	-0.324	-0.151	-0.136
Easting	-0.588	0.285	-0.74	-0.017	-0.029	1	-0.118	-0.136	-0.519	-0.325
Northing	0.484	-0.051	0.103	-0.245	-0.242	-0.118	1	0.177	0.411	0.221
TCI	0.145	-0.029	0.032	-0.292	-0.324	-0.136	0.177	1	0.34	0.228
ED300	0.286	-0.466	0.465	-0.11	-0.151	-0.519	0.411	0.34	1	0.717
ED150	-0.169	0.158	-0.524	-0.11	-0.136	-0.325	0.221	0.228	0.717	1