-Final Report-
September 28, 2006

Project Title: Optimizing landscape treatments for reducing wildfire risk and improving ecological sustainability of ponderosa pine forests with mixed severity fire regimes
JFSP Project No.: 01-1-3-22
Project Location: Colorado State University, Western Forest Fire Research Center
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Summary:

Ponderosa pine (*Pinus ponderosa* Laws.) forests in the Colorado Front Range comprise a mixed-severity fire regime with true-mountain mahogany (*Cercocarpus montanus* Raf.) as the dominant undergrowth shrub species. The objective of this project is to relate the sprouting behavior of true mountain mahogany to fire severity gradients at both landscape and individual shrub scales following the 2000 Hi Meadow and 2002 Hayman Fires, located near Pine, Colorado. We were successful in meeting this objective as proposed, but circumstances prevented a more comprehensive examination as initially envisioned. Deliverables (identified in the request for no cost-extension) are appended to this final report. The proposed deliverables include a Master's thesis and poster abstract. In addition, two other posters and a metadata summary were completed. Other highlights from this project included:

- Development of a system for rating burn severity in individual shrubs. The Shrub Burn Severity Rating system (SBSR) provided a classification system that could be used for relating post-fire sprouting characteristics to fire severity.
- A finding that moderately burned true mountain-mahogany shrubs exhibited the greatest asexual reproduction activity (sprout number and length).
- Fire severity proved to be the most important abiotic predictor of post-fire sprouting activity in true mountain-mahogany.
- True mountain-mahogany sprouting characteristics varied depending on pre-fire and post-fire treatments. Results from the Hayman Fire showed that the basal sprout number was larger in treated areas (grouped pre- and post-fire treatments) than in untreated areas one year after fire. Conversely, the epicormic sprout number was higher in untreated areas than in treated areas. Moreover, basal sprout lengths were higher in pre-fire treated areas than in post-fire treated areas in the year of fire.

Managers and practitioners need to be aware that burn severity ratings from Burned Area Emergency Recovery (BAER) maps may inaccurately convey localized burn severity in a forest with shrub understory. For example, in Front Range ponderosa pine forests with a true mountain-mahogany understory we found areas that were assigned a low burn severity rating based on BAER criteria yet the shrub understory burned with high

severity. Thus subsequent decisions, i.e., rehabilitation treatment alternatives, based on BAER burn severity maps may need to be adapted to localized site conditions rather than applied uniformly across the landscape.

Originally this project was attached to another JFSP project (same project number, M. Kauffman, P.I.), then separated. After considerable delay (approx 1.5 yr), funding was routed eventually through DOI-BLM, although the parent project proceeded without delay. Thus, feedback to the original linked project as originally proposed proved limited. Additional complications resulted when the graduate student on this project was unable to complete the Ph.D. preliminary examination successfully. As a consequence, an anticipated manuscript (thesis publication) was not written.

Deliverables Crosswalk Table

Proposed	Delivered	Status
Poster abstract	Liang, L.M. and P.N. Omi. 2006. Treatment effects on true mountain-mahogany post-fire sprouting in Colorado Front Range ponderosa pine forests. Abstract submitted to 3rd International Fire Ecology and Management Congress.	Completed and accepted May 06
M.S. thesis	Liang, L.M. 2005. True mountain-mahogany sprouting following fires in ponderosa pine forests along the Colorado Front Range. M.S. thesis, Colorado State University.	Completed and defended, Summer 05
Metadata summary of plot locations	Liang, L.M. True Mountain-Mahogany Sprouting Database Metadata, including 1. Post-fire sprouting vs. fire behavior; 2. Treatment effects; 3. Sprouts related to pine seedlings	Completed Feb 06
Poster	Liang, L.M. and P.N. Omi. 2004. The role of true mountain mahogany sprouts related to ponderosa pine seedlings in sustaining mixed-severity fire regimes. Poster presented at conference on Mixed Severity Fire Regimes: Ecology and Management. Association for Fire Ecology, Nov. 17-19, 2004, Spokane, WA.	Completed and delivered Nov 04
Poster	Liang, L.M. 2003. True mountain mahogany sprouting behavior following fire. 5th Symp. on Fire and Forest Meteorology and 2nd Internat. Wildland Fire Ecology and Fire Management Congress, Orlando, FL. November, 2003.	Completed and delivered Nov 03

THESIS

TRUE MOUNTAIN-MAHOGANY SPROUTING FOLLOWING FIRES IN PONDEROSA PINE FORESTS ALONG THE COLORADO FRONT RANGE

Submitted by

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In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

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ABSTRACT OF THESIS

TRUE MOUNTAIN-MAHOGANY SPROUTING FOLLOWING FIRES IN PONDEROSA PINE FORESTS ALONG THE COLORADO FRONT RANGE

Ponderosa pine (*Pinus ponderosa* Laws.) forests in the Colorado Front Range comprised a mixed-severity fire regime with true mountain-mahogany (*Cercocarpus montanus* Raf.) as the dominant undergrowth shrub species. We related the sprouting behavior of true mountain-mahogany to fire severity gradients at both landscape and shrub scales following the 2000 Hi Meadow and 2002 Hayman Fires.

A Shrub Burn Severity Rating (SBSR) was introduced as a burn severity classification for individual shrubs. True mountain-mahogany reproduced primarily by sprouting with various sprouting behaviors throughout different fire severities in the early recovery stage following fire. Moderately burned true mountain-mahogany exhibited the greatest asexual reproduction activity (sprout number and length). In ponderosa pine forests in the Colorado Front Range, true mountain-mahogany root reserves did not contribute significant effects on sprouting. The sprouting responses also varied due to pre-fire fuel treatments and post-fire seeding activities. Fire severity seemed to be the most important abiotic predictor of true mountain-mahogany sprouting behavior after fire.

Ponderosa pine seedlings were only found in low fire severity areas four years after the Hi Meadow Fire. Results of this study provided evidence of ponderosa pine seedlings growing faster in the area closer to sprouted true mountain-mahogany than those located farther away. Ponderosa pine seedling recruitment concomitant with true mountain-mahogany sprouting following fire was not yet fully answered by this study.

Post-fire sprouting behavior of true mountain-mahogany suggested that they were well adapted to fire of various intensities. I expected shrubs in a mixed-severity fire regime to be better adapted to fire of various intensities than in high- or low- severity fire regimes.

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INTRODUCTION

Fire is a natural disturbance linked to the dynamics of ecosystems. Plants have opportunities for natural regeneration following fires, and each species may respond differently. The categories of plant responses to fire can be classified as fire ephemerals, obligate seeders, and sprouters (Bell et al. 1984). Some species which survive and recover quickly after fires have the characteristics of easily dispersed tiny seeds, spreading rhizomes, or rapid sprouting ability (Kauffman 1991, de Rouw 1993, Goto et al. 1996). Sprouting has been reported in many studies as an important strategy and key mechanism maintaining survival and persistence of many perennial shrubs following fire or heat stress (Matlack et al. 1993, Olson and Platt 1995, Bellingham and Sparrow 2000, Bond and Midgley 2001, Cirne and Scarano 2001). Shrub species which have the ability to sprout generally have greater chances of surviving under heat stress than the species that do not sprout (Huddle and Pallardy 1996). Studies show that sprouters are more successful than seeders in maintaining abundance between fires (Menges and Kohfeldt 1995, Menges and Hawkes 1998). Knowledge of sprouting behavior is important for understanding of vegetation dynamics, extinction risks, or woody plant management, but this is still poorly described and documented in many biomes (Bond and Midgley 2003).

The terminology used to represent new shoots, which originate from plant parts above or below the ground surface following disturbance, is inconsistent in the literature and still not well defined and clarified. Synonyms include sprout, sprouter, resprout, and resprouter. In this study, "sprout" is used to represent the new shoots originating from the root crown (basal sprout, BS) or aboveground (epicormic sprout, ES) parts of the shrub, and "sprouting" is used to describe the development of sprouts, after National Wildfire Coordinating Group (1994), Hodgkinson (1998), Brown and Smith (2000), and U.S. Department of Agriculture (2001).

This thesis investigates true mountain-mahogany (*Cercocarpus montanus* Raf.) post-fire sprouting behavior, root crown bud number and viability, post-fire root reserves, sprouting affected by pre-fire treatments and post-fire rehabilitation, and spatial distributions of true mountain-mahogany and ponderosa pine (*Pinus ponderosa* var. *scopulorum*) in Colorado Front Range ponderosa pine forests. First I discuss terminology used and state the hypotheses that informed my investigation. Next I introduce the study area and methods used, including data analyses. Results from field and laboratory experiments are discussed next, followed by discussion of results and general conclusions.

HYPOTHESES

Post-fire Sprouting Behavior

Fire regime descriptors, including seasonality, fire frequency, and fire intensity influence the sprouting behavior of shrubs (Moreno and Oechel 1991, Glitzenstein et al. 1995). Sprout vigor of oak species (*Quercus coccifera*), defined by sprout density and growth, are significantly different between fire seasons (Malanson and Trabaud 1988). Young (1973) and Young and Bailey (1975) found significantly greater sprout production for true mountain-mahogany after dormant season fires compared to growing season fires.

True mountain-mahogany is usually temporarily damaged by fire (Ralphs et al. 1975), and since seedling establishment is sporadic and poor (Pase and Lindenmuth 1971, Stanton 1974), sprouting becomes the major response for plant recovery. Only three studies have examined true mountain-mahogany growth morphology following disturbances. Turley et al. (1999) reported true mountain-mahogany annual twig growth ratios are unaffected by the levels of deer and elk winter browsing, whereas growth of shrubs at the unbrowsed site declined. The morphology of grazed true mountain-mahogany becomes shorter and wider (Stutz 1990), and the shrub becomes stagnant and decadent if no browsing occurs over time (Waugh 1990).

The hypothesis tests for true mountain-mahogany sprouting behavior following fire are:

H_{O1}. The number and length of basal and epicormic sprouts of true mountain-mahogany plants does not vary by fire severity class at the landscape scale.

H_{O2}. The number and length of basal and epicormic sprouts of true mountain-mahogany plants does not vary by fire severity class at the individual shrub scale.

Root Crown Bud Test

The number and growth of sprouts is supported by the resources stored in sprouting organs, and the larger sprouting organs increase bud number initiated after the disturbance (Bowen and Pate 1993). Pelaez et al. (1997) indicated that when many buds are killed by fire, the post-fire regrowth of plants is limited. Buds can be categorized as "viable", which includes metabolically active and dormant buds, and "dead", i.e., killed during the fire. Sprouts are generated from the metabolically active buds, and the dormant buds have sprouting potential but do not sprout. The location of dormant buds differs in various plants, including epicormic, root collar, rhizome, stolon, root crown, caudex, bulb, and corm (Brown and Smith 2000). When a shrub species is top-killed by fire, sprouting occurs from the dormant buds located on underground organs (Kauffman and Martin 1990).

Intensive fire kills aboveground parts of true mountain-mahogany, but it sprouts rapidly and abundantly from the root crown following fire (Pase and Lindenmuth 1971, Bradley et al. 1991). The metabolically active buds located in the true mountain-mahogany root crown and old stems may be an important indicator for sprouting ability in different fire severity levels. Since stems of true mountain-mahogany are usually damaged or killed by fire, the sprouting ability from root crown tends to be the most important source for true mountain-mahogany regeneration following fire. No previous studies have examined true mountain-mahogany root crowns. In this study, the buds and basal sprouts at true mountain-mahogany root crowns were examined anatomically for the first time.

The hypotheses of bud number and bud viability on true mountain-mahogany root crown following fire are:

H_{O3}. The number of buds in true mountain-mahogany root crowns does not vary by root crown size.

H_{O4}. The ratio of viable bud number to total root crown bud number in true mountain-mahogany root crowns does not vary by fire severity.

H_{O5}. The ratio of sprout number to viable bud number (S/VB) in true mountain-mahogany root crown does not vary by fire severity.

Post-fire Root Reserves

Manufactured by plants, carbohydrates provide energy for metabolism and structural compounds for growth (Trlica 1977, Sakai et al. 1997, Verdaguer and Ojeda 2002), and successful sprouting may depend on resources stored by plants prior to disturbances (Bellingham and Sparrow 2000, Bond and Midgley 2001). Bowen and Pate (1993) concluded that starch stored in roots prior to fire is strategically related to shoot recovery, and more than 50% of the starches are consumed in the initial recovery phase. Pre-fire storage of starch is a primary limitation of a plant's capacity to produce sprouts, and no sprout is produced after all the starches are eliminated (Bowen and Pate 1993). Sprouting ability is enhanced by increasing the levels of stored carbohydrate (Bowen and Pate 1993, Kabeya et al. 2003).

In true mountain-mahogany, carbohydrate reserves in the root crown provide the energy and materials for sprouting after fire. The damage of true mountain-mahogany under different fire severity levels and seasons may affect the ability of true mountain-mahogany to sprout from the root crown. Root crown carbohydrates have the maximum accumulation at the end of the growing season which is the beginning of the dormant season, and the carbohydrates are decomposing during leaf unfolding at the beginning of growing season. Starch reserves fall to low levels in the initial recovery stages, and reserved starches begin to increase only when the plant biomass attains the same or greater than the pre-fire biomass (Bowen and Pate 1993).

No research has been done with true mountain-mahogany sprouting behavior associated with root crown nutrient storage in various fire severity levels. This study examined the level of total nonstructural carbohydrates (TNC) of true mountain-mahogany root crowns after fire.

The hypotheses are:

$H_{O6.}$ The root reserves of true mountain-mahogany do not vary by fire severity class.

H_{O7}. There is no significant difference between burned and unburned true mountain-mahogany in root reserves one year after fire.

Treatment Effects

Pre-fire fuel treatments and post-fire management activities usually alter stand structure, soil nutrients, microenvironments, and may affect potential fire behavior (Pyne 1984, Graham 2003). In the 2000 Hi Meadow Fire and the 2002 Hayman Fire areas, pre-fire treatments included prescribed burns and thinnings, and the post-fire rehabilitation treatments include seeding and mulching. Prescribed burns and thinnings can change the quality, continuity, and compactness of surface fuels and aerial fuels (Graham 2003). Shrub sprouting behavior may differ as a result of these treatments. Fuel consumption and accumulation is one of the factors that has effects on fire behavior and severity, which might alter sprouting ability. Zedler et al. (1983) reported that high fuel consumption decreases sprouting by killing buds on underground plant organs, such as the rhizome, lignotuber, and root crown. Kauffman and Martin (1990) concluded that moderate fuel consumption has the highest stimulation on shrub sprouting. No previous studies have been conducted in shrub sprouting related to post-fire rehabilitation activities, such as seeding or mulching.

I examined the influences of prescribed burns, thinnings, and seeding in fuel and vegetation alterations and their effects on true mountain-mahogany sprouting behavior. The hypothesis is:

H_{O8}: Pre-fire fuel treatments and post-fire rehabilitation treatments do not influence true mountain-mahogany sprout length and number at the early vegetation recovery stage after fire.

Sprouts Related to Pine Seedlings

Shrubs in the understory of pine forests play an important role in vegetation recovery after disturbances. Shrubs with the ability to sprout rapidly after fire can prevent soil erosion and nutrient losses, and reinstate suitable environmental conditions for both plant and animal community recovery (Espelta et al. 2003). Some true mountain-mahogany stands are in the ecotone between ponderosa pine and true mountain-mahogany shrub communities. In ponderosa pine forests of the Hi Meadow Fire and Hayman Fire, true mountain-mahogany is the dominant understory species. The relationship between true mountain-mahogany as understory and ponderosa pine as overstory canopy is poorly understood as only a few studies have addressed this question.

In the ponderosa pine forest in the Black Hills, South Dakota, true mountain-mahogany may be shaded out by the ponderosa pine canopy at certain successional stages following fires, but it is rarely eliminated from the ponderosa pine community (Hoffman and Alexander 1987). Previous studies of true mountain-mahogany are usually focused on the mountain shrub communities which are dominated by true mountain-mahogany that occur near, but not in, ponderosa pine forest (USDA Forest Service 2001).

In this study, I began an investigation into the role of shrubs, especially true mountain-mahogany, in the ponderosa pine forest. Neeman et al. (1992) stated that pine seedlings which have better mineral nutrition during the first year of growth grow faster and taller. True mountain-mahogany is a nitrogen fixing plant which might create an environment in the surrounding area that favors ponderosa pine seedlings. On the contrary, the inter-specific competition between true mountain-mahogany and ponderosa pine is also an issue. In particular, I was interested in the spatial distribution of sprouted true mountain-mahogany and ponderosa pine at the early stage following fire. The hypotheses are:

H_{O9}: The spatial pattern of true mountain-mahogany sprouts and ponderosa pine seedlings does not vary by fire severity.

H_{O10}: The density and height of ponderosa pine seeding does not change by the distance from sprouted true mountain-mahogany to the seedling.

METHODS

SITE DESCRIPTION

This study was conducted in the South Platte River drainage in the Pike National Forest, Colorado, USA. This drainage furnishes 70% of the water supply for the Denver metropolitan area (Colorado State Forest Service 2000) and is an important watershed in the Pike National Forest. Elevations in the study area range from 2,000m to 4,300m. Granitic and igneous rocks of the Pikes Peak batholith are the most common in Pike National Forest (Moore 1992), and the majority of the soils are of the Sphinx family and Sphinx family complex, defined as sandy-skeletal, mixed, frigid, shallow typic ustorthents. Other soils are classified as rock outcrop-Sphinx complex, mollisols, alfisols, and inceptisols. Strong seasonal differences in temperature and precipitation are present in the Pike National Forest, which is typical of high elevation, continental sites with rapid seasonal and diurnal heating and cooling of land surfaces (Greenland et al. 1985).

The mid-elevation ponderosa pine forests of the Colorado Front Range historically support mixed-severity fire regimes which shape a landscape with a mosaic of tree species and densities in pure or ponderosa pine dominated forests (Ehle and Baker 2003, Schoennagel et al. 2004). Fires occur at variable intervals and burn at variable severity in a mixed-severity fire regime, which contains elements of both the frequent, low-severity and the infrequent, high-severity fire regimes (Agee 1998, Graham 2003).

Fire history studies in the ponderosa pine forests in the Pike National Forest indicate a historical mixed-severity fire regime prior to the Euro-American settlement (Brown et al. 1999, Kaufmann et al. 2000a, Kaufmann et al. 2000b, Huckaby et al. 2001, Kaufmann et al. 2001). Several wildfires have occurred recently in this area, such as the Hi Meadow Fire in 2000 and the Hayman, Schoonover, and Snaking Fires in 2002.

Field sampling and measurements were conducted in summer 2002 and 2003 at Hi Meadow and Hayman burn areas which are located in Pike National Forest, southwest of Denver, Colorado (Figure 1). The Hi Meadow Fire occurred in June 2000, covering 4,500 ha near Bailey. The Hayman Fire occurred in June 2002, burning 55,800 ha around Cheesman Reservoir. Both areas are covered by ponderosa pine forest. The forest vegetation classification of Pike National Forest is warm and very dry *Pinus ponderosa-Cercocarpus montanus* habitat type (Radloff 1983, Alexander 1987), which is usually pure ponderosa pine stands with true mountain-mahogany as the dominant undergrowth shrub species (Figure 2). True mountain-mahogany sprouts abundantly in the area after fire.

Several pre-fire and post-fire treatments were adopted in the Hayman Fire area. Pre-fire activities included prescribed fires, fuel treatments, timber stand improvements, pre-commercial thinnings, commercial thinnings, partial harvests, seed-tree cuts, clear cuts and plantations (Graham 2003). Some areas were involved in both prescribed burn and thinning activities. Post-fire activities were the BAER team land treatments, including ground hydromulching with seed, aerial hydromulching with seed, aerial dry mulching with seed, mechanical scarification with seed, hand scarification with seed, aerial seeding, and noxious weed spot-treatment and biological control (Graham 2003).

Many areas were involved in both thinning and seeding activities, and most mulched areas were also seeded.

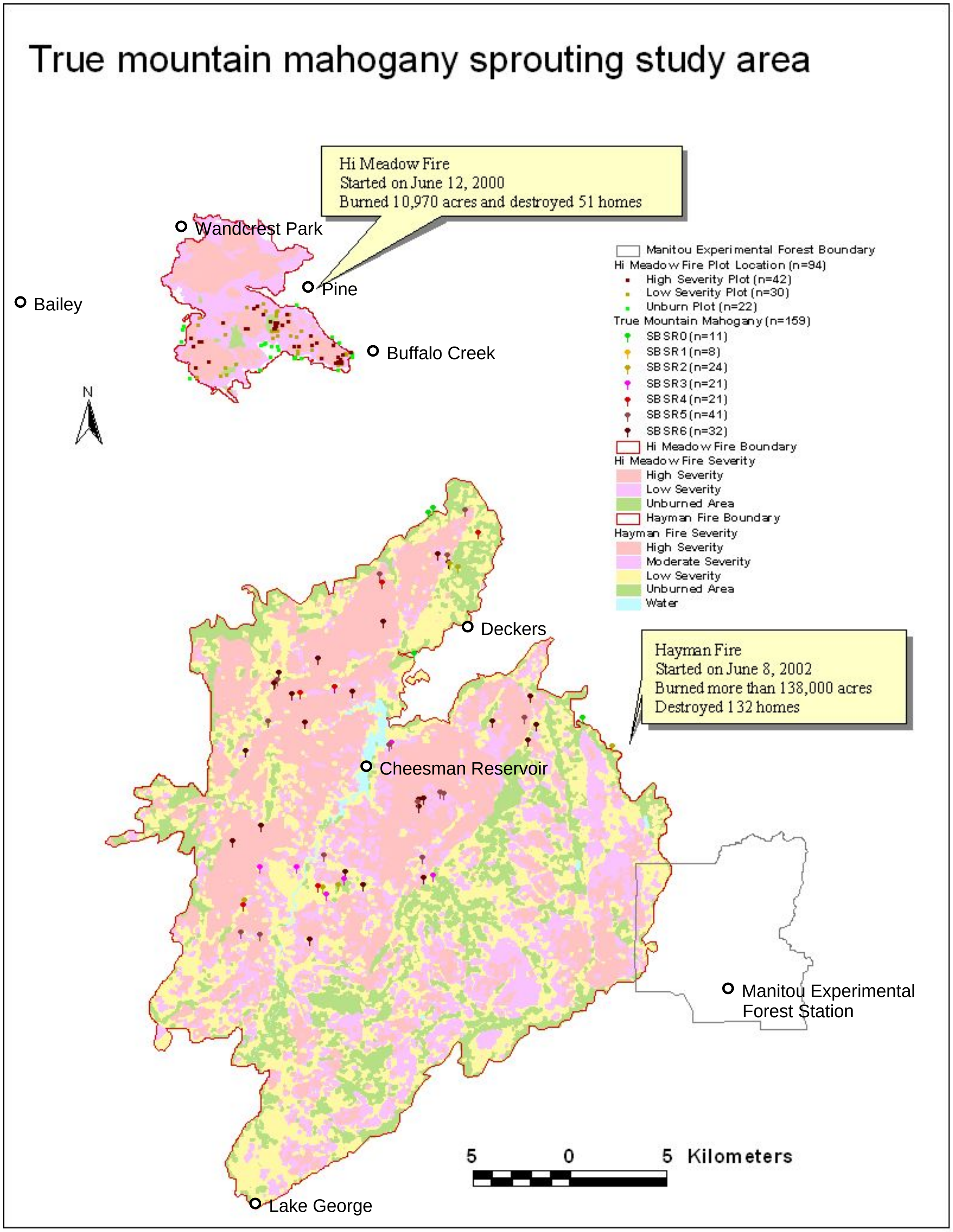

Figure 1. Map of the study area, showing layout, landscape burn severity classifications, and proximity of the Hi Meadow Fire and Hayman Fire, Colorado. Locations of study plots and individual true mountain-mahogany samplings are shown in the Hi Meadow and Hayman burn areas, respectively.

Figure 2. True mountain-mahogany individuals (yellow arrows) dominate the understory in this ponderosa pine forest, one year after the 2002 Hayman burn, Colorado.

PROCEDURES

I used true mountain-mahogany as the focal species for this study. True mountain-mahogany is a fire-sensitive species found throughout much of the ponderosa pine forests in the Colorado Front Range, and it is widely distributed in the central Rocky Mountains at elevations between 1,000m and 3,000m and in the foothills and mountains of Colorado, Utah, and Wyoming (Medin 1960, Greenwood and Brotherson 1978, Davis 1990). It is usually temporarily damaged by fire, responding to consumption and heat injury with basal and epicormic sprouting. Since seedling establishment is sporadic and poor, sprouting becomes the major response for plant recovery (Figure 3). The nitrogen fixation ability in root nodules and ectomycorrhizal facilitation of phosphorus uptake is probably critical for the success of true mountain-mahogany on infertile soils and may also influence the establishment of ponderosa pine seedlings following fire. True mountain-mahogany is also important forage for wildlife and livestock. In this study, I also examined ponderosa pine natural regeneration related to sprouted true mountain-mahogany following fire. Ponderosa pine seedlings are relatively shade intolerant and require canopy-opening disturbance, such as fire, to establish and regenerate (Figure 4).

Figure 3. Typical true mountain-mahogany response (sprouting from the root crown) to low severity burning, four years after the 2000 Hi Meadow Fire, Colorado.

Figure 4. A ponderosa pine seedling germinated in a low severity patch, four years after the 2000 Hi Meadow Fire, Colorado.

Fire Severity Scales

I examined true mountain-mahogany sprouting response following fire in the Colorado Front Range as affected by fire severity on both landscape and individual shrub scales. My examination provided a comparison of coarse- versus fine-scale assessments of fire severity.

Landscape fire severity

Landscape scale fire severity was assessed using Burned Area Emergency Rehabilitation (BAER) fire severity maps, which were based on post-fire Landsat imagery. The fire severity definitions used by BAER are described below (Graham 2003).

1) **Unburned**: no recent evidence of fire.

2) **Low-severity**: fire burned on the surface at low intensity with little or no crown scorched; never or rarely stand-replacing.

3) **Moderate fire severity**: forest canopy scorched by an intense surface fire; no leaves and twigs consumed; may be stand-replacing or not.

4) **High fire severity**: crown fire with leaves and small twigs consumed; always stand-replacing.

Fire severity level was verified at each study site. For the purposes of stratification in this study, moderate and high severities in the BAER maps were grouped together.

Shrub Burn Severity Rating (SBSR)

The ponderosa pine forests in the Colorado Front Range comprise a mixed-severity fire regime which usually results from patchy and mosaic burns. Analyses at coarse scales, such as a landscape, may obscure the variability of finer scale burn severity. In this study, I developed a new fine scale burn severity classification named Shrub Burn Severity Rating (SBSR). The SBSR class was derived from individual plant field observations and assigned to individual true mountain-mahogany shrubs selected randomly in the Hayman Fire burn area, using criteria described below.

1) **SBSR0**: no evident burning and no scorch.
2) **SBSR1**: living true mountain-mahogany with green leaves in growing season; almost no stems scorched or charred.
3) **SBSR2**: few stems scorched or charred; less than 50% of stems killed or damaged; base of stems charred.
4) **SBSR3**: most stems scorched or charred; 50% - 100% of stems killed or damaged.
5) **SBSR4**: all stems scorched or charred; all stems killed or damaged.
6) **SBSR5**: all stems scorched and charred; some stems consumed.
7) **SBSR6**: all stems consumed.

Experimental Design and Data Analyses

This thesis was conducted in several parts. Each required different field samplings or plant manipulations.

Post-fire Sprouting Behavior

A completely randomized design (CRD) was employed for sampling of true mountain-mahogany sprouting in the Hi Meadow Fire in summer 2002 and in the Hayman Fire in summer 2003. The Hi Meadow Fire, was sampled at 94 randomly selected Modified-Whittaker plots (Stohlgren et al. 1995) at three fire severity levels (unburned, low, and high). I sampled the Hayman Fire in 122 randomly selected plots at three fire severity levels (unburned, low, and high). The trials were conducted in conjunction with a Joint Fire Science Program project examining relationships among fuels, wildfire severity, exotic plant invasions, and post-fire fuel flammability in grasslands, shrublands, and forests across the western U.S.A. (Omi et al. 2000). A Modified-Whittaker plot (Figure 5) was established at each plot location.

The origins of Modified-Whittaker plots were assigned by random easting and northing coordinates generated by Microsoft® Excel random number function. Directions of 50m were then randomly assigned to cardinal directions. These plots contain ten 0.5 x 2 m^2 subplots, two 2 x 5 m^2 subplots (A and B subplots), arranged systematically inside and along the perimeter of a 20 x 50 m^2 plot (K plot), and one 5 x 20 m^2 center subplot (C subplot).

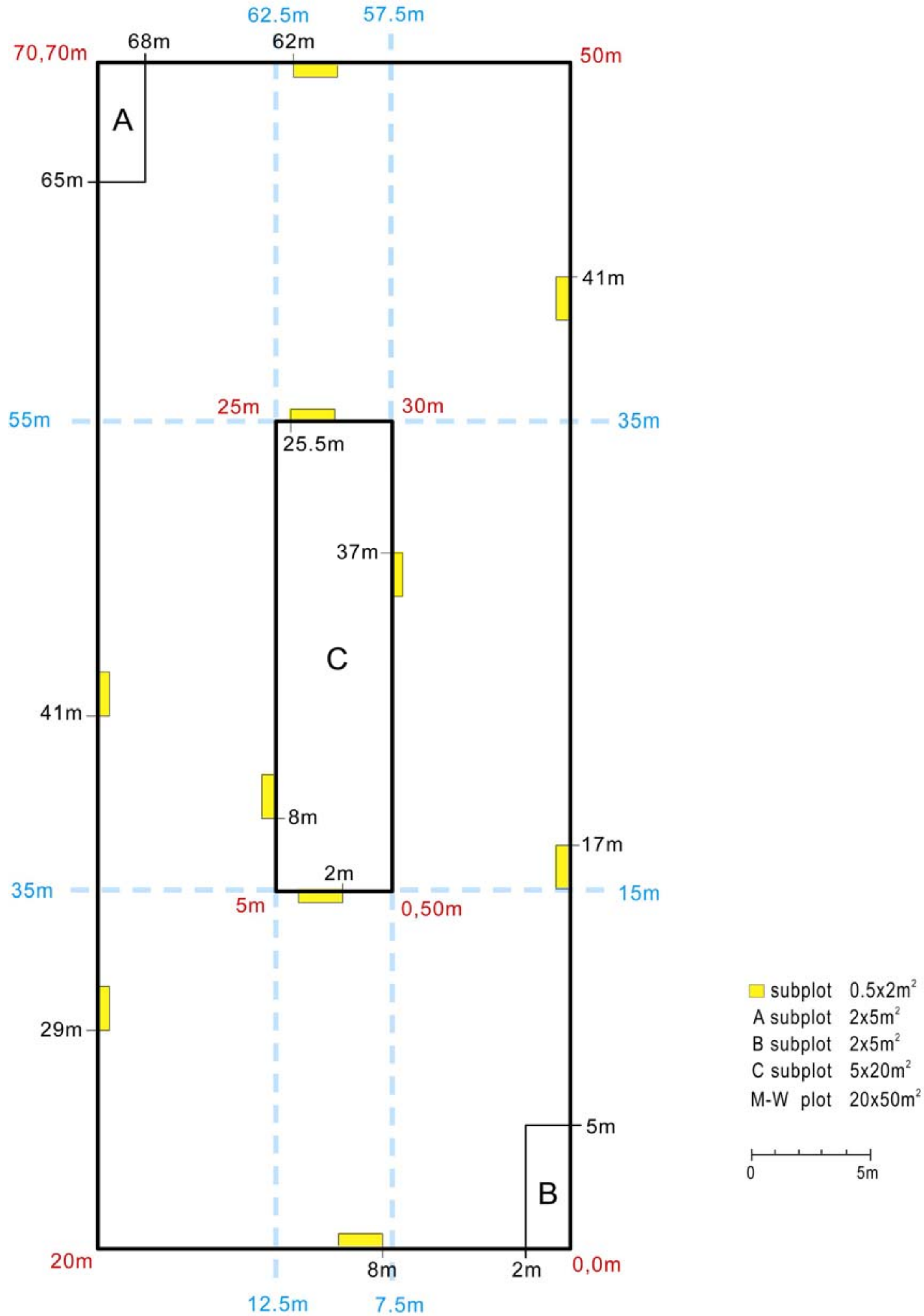

Figure 5. Modified-Whittaker plot (after Stohlgren et al. 1995), showing the subplot locations within the 1,000 m^2 plot.

The true mountain-mahogany sampling method contained three procedures. First, one clump of true mountain-mahogany, which was arising from one root crown, was sampled in each of three randomly selected 0.5 x 2 m^2 subplots. Second, if there were less than three true mountain-mahogany shrubs in these selected subplots, any true mountain-mahogany within subplot C was sampled. Third, if true mountain-mahogany did not occur in 0.5 x 2 m^2 subplots or C plot, subplots A and B, and plot K were inspected. Up to three true mountain-mahogany were sampled in each Modified-Whittaker plot. One hundred and fifty nine true mountain-mahogany were measured in all during 2003 in the Hayman burn.

The SBSR was assigned to each selected shrub to indicate the burn severity for a particular individual shrub. Number of basal sprouts (BSN) and epicormic sprouts (ESN) were obtained for each selected true mountain-mahogany plant. Five sprouts were randomly selected for measurement of length of basal sprout (BSL) and epicormic sprouts (ESL).

An analysis of variance (ANOVA) was used to test the effects of fire severity on length and number of basal and epicormic sprouts in the year of the Hi Meadow and the Hayman Fire, one year after the Hi Meadow and the Hayman Fire, and two years after the Hi Meadow Fire. The ANOVA approach (Ott and Longnecker 2001, Scheiner and Gurevitch 2001) was run with the general linear model procedure (proc glm) in the SAS statistical program for Windows (SAS 9.1, 2003, SAS Institute Inc., Cary, North Carolina) using an alpha level of 0.05. The number and length of basal sprouts and epicormic sprouts were used as dependent variables, and the landscape fire severity (unburn, low, and high) and SBSR (class 0 – 6) were independent variables. Specifically, I addressed the following alternative:

- The number and length of basal and epicormic sprouts of true mountain-mahogany plants does not vary by fire severity class at the landscape scale, but does vary at the shrub scale (SBSR).

Root Crown Bud Test

The 35 root crowns sampled in the Hayman Fire area in the 2003 growing season were examined in the laboratory. After clipping redundant roots and fine roots, the root crowns were washed with tap water to remove remaining soil, and the bark was carefully removed from the root crown. The dissecting microscope was used to observe bud morphology, and buds were cut and stained by a series gradient concentration of triphenyl tetrazolium chloride (TTC) and Evans' blue to determine the viability (Busso et al. 1993). If the bud apex was stained pink or red by TTC, it was considered metabolically active. If the bud was stained dark blue by Evans' blue, it was considered dead. If the bud had no responses to both stains, it was considered dormant.

I investigated the ratio of viable bud number to total root crown bud number and the ratio of sprout number to viable bud number (S/VB ratio). I chose the S/VB ratio to indicate the proportion of viable buds that were metabolically active, thereby representing the sprouting ability for each shrub burn severity class. Specifically, I was interested in testing for the following alternatives:

- Larger root crowns have a greater number of buds.

- True mountain-mahogany has greater ratio of viable bud number to total root crown bud number under low severity (SBSR 1 and 2) than under moderate (SBSR 3 and 4) or high severity (SBSR 5 and 6).
- The S/VB ratio of true mountain-mahogany is higher in moderate severity (SBSR 3 and 4) than the ratio in low severity (SBSR 1 and 2) or in high severity (SBSR 5 and 6) in the first year after fire.
- The S/VB ratio of unburned true mountain-mahogany root crown (SBSR 0) is lower than any other SBSR classes in the first year after fire.

Unfortunately, I did not have significant results for this part of study. First, bud location in true mountain-mahogany root crowns was difficult to determine. Some buds could be found at the initial stage of sprouting in root crowns. However, if the buds had not begun sprouting, they were could not be identified from the surface of peeled root crowns under a dissecting microscope. Second, no buds responded to the stains. After following the procedure to apply the stains onto buds, the stains were ineffective in detecting metabolic activity. Due to the difficulty of determining bud location and ineffectiveness of stains, the hypotheses of root crown buds could not be tested (H_{O3}, H_{O4}, and H_{O5}), and no substantive results can be presented.

An improved technique is needed to further explore the hypotheses presented here. I suggest alternative methods, such as plant paraffin section, could be practiced in future research of true mountain-mahogany root crown bud analysis. Root samples could be embedded in paraffin and serial sectioned transversely or longitudinally on a rotary microtome (Johansen 1940). A similar plant microtechnique was used to inspect the origin of root buds and root sprouts in *Sassafras albidum* (*Lauraceae*) by Bosela and Ewers (1997).

Post-fire Root Reserves

To examine the effects of fire severity on nutrient reserves in the true mountain-mahogany root crowns, as well as effects on sprouting ability and nutrient reserves, 70 true mountain-mahogany root crowns were obtained in June and October 2003. Total nonstructural carbohydrates (TNC) were used for a root crown nutrient storage experiment. The lower part of root crowns was sliced into 0.5 cm thick disk using a powered band saw within one week after excavation from the field to prevent carbohydrate loss. All samples were dried at 70 ^{o}C in the oven for 72 hours or until totally dry, and were ground to pass a 20-mesh screen with small-sized Wiley-Thomas mill prior to analysis.

The ground root crown samples were sent to the Nutrient Analysis Laboratory at Colorado State University. The samples were completely hydrolyzed of extracted carbohydrates using a mild 0.2 N sulfuric acid solution to reduce sugars. The deducing power of the neutralized hydrolysate was determined by titration with standardized sodium thiosulfate using a modified Smith protocol (Smith et al. 1964, Association of Official Agricultural Chemists 1965, Smith 1981). Root TNC concentration was determined by the sum of glucose, sucrose, and starch concentrations (Cruz et al. 2003).

An analysis of variance (ANOVA) was used to test the effects of SBSR on root TNC one year after the fire. The ANOVA approach (Ott and Longnecker 2001, Scheiner and Gurevitch 2001) was run with the general linear model procedure (proc glm) in the SAS statistical program for Windows (SAS 9.1, 2003, SAS Institute Inc., Cary, North Carolina) using an alpha level of 0.05. Specifically, I was interested in testing for the following alternatives:

- The root TNC of true mountain-mahogany varies by fire severity class.
- True mountain-mahogany in unburned areas have the highest root TNC one year after fire.

Treatment Effects

Sampling was performed at 122 randomly selected Modified-Whittaker plots at treated and untreated areas in the Hayman Fire in summer 2003. A total number of 159 true mountain-mahogany were sampled (Table 1). For stratification purposes, the "thin" stratum included areas that were thinned prior to the wildfire. This included timber stand improvements, pre-commercial thinnings, commercial thinnings, partial harvests, and seed-tree cuts. Clear cuts and plantations were not sampled. The "Rx burn" stratum included areas that were prescribed burned prior to the wildfire. In the post-fire treatments, the "seed" stratum included areas that were seeded with grasses, including barley (*Hordeum vulgare*) and triticale (*xTriticosecale rimpaui*), for post-fire erosion control immediately after the wildfire. The "mulch" stratum included areas where straw mulch was applied for erosion control immediately after the wildfire. The number and length of true mountain-mahogany basal sprouts and epicormic sprouts were recorded for individual plants within each plot. Five basal sprouts and five epicormic sprouts from each sampled shrub were randomly selected to measure sprout length. Plots that were subject to both pre- and post-fire treatments were excluded from the study. A total of 102 true mountain-mahogany shrubs were used in the data analysis.

Table 1. True mountain-mahogany plants sampled in pre-fire and post-fire treatment areas in the Hayman Fire, Colorado. Only samples in the none, Rx burn, seed and thin treatments were used in the study.

Treatment	True mountain-mahogany samples	
None	41	
Rx burn	25	
Seed	22	
Thin	13	
Subtotal		102
Mulch	3	
Thin + Rx burn	22	
Seed + Rx burn	3	
Seed + Mulch	14	
Seed + Thin	9	
Seed + Thin + Mulch	3	
Seed + Thin + Rx burn	4	
Subtotal		57
Total		159

An analysis of variance (ANOVA) was used to test the effects of pre- and post-fire treatments on length and number of basal and epicormic sprouts in the year of the fire and one year after the fire. The ANOVA approach (Ott and Longnecker 2001, Scheiner and Gurevitch 2001) was run with the general linear model procedure (proc glm) in the SAS statistical program for Windows (SAS 9.1, 2003, SAS Institute Inc., Cary, North Carolina) using an alpha level of 0.05. Data on true mountain-mahogany were grouped for analyses in three ways: (1) *treated* [Rx burn, thin, and seed grouped together], n=60, and *untreated* [no treatment], n=41, (2) *pre-fire treated* [group Rx burn and thin], n=38, and *post-fire treated* [seed], n=22, and (3) *individual treatment* [Rx burn, thin, or seed, and no treatment], n=102.

Specifically, I was interested in testing for the following alternative hypotheses:

- True mountain-mahogany has taller and larger number of sprouts in untreated areas compared to treated areas (thin, prescribed burn, seed).
- True mountain-mahogany has taller and larger number of sprouts in pre-fire treated areas (thin and prescribed burn) compared to post-fire treated areas (seed).
- True mountain-mahogany sprout number and length varies by pre- and post-fire treatments at the early vegetation recovery stage after fire.

Sprouts Related to Pine Seedlings

Diversity of Sprouted Shrubs

Shrub species with sprouting ability were recorded to investigate understory shrub diversity in the ponderosa pine forest following fire. The data were collected from ten 0.5 x 2 m^2 subplots, two 2 x 5 m^2 subplots (A and B subplots), and one 5 x 20 m^2 center subplot (C plot) at 94 randomly selected Modified-Whittaker plots (Figure 5) at three fire severity levels (unburned, low, and high) in the Hi Meadow Fire in summer 2002.

Spatial Relationship

This part of the study was carried out in three randomly selected 25 x 25 m^2 plots at three fire severity levels (unburned, low, and high) four years after the 2000 Hi Meadow Fire. Around each true mountain-mahogany plant, circumference zones (Figure 6) were identified with diameters of 1m (zone A), 2m (zone B), and 3m (zone C). The zone for each ponderosa pine seedling was recorded along with the distance (from nearest true mountain-mahogany plant) and seedling height. Ponderosa pine with diameter at breast height (DBH) > 2.54 cm was considered a tree and was located in the plot. The position of living ponderosa pine trees and sprouted true mountain-mahogany were located.

The ANOVA approach (Ott and Longnecker 2001, Scheiner and Gurevitch 2001) was run with the general linear model procedure (proc glm) in the SAS statistical program for Windows (SAS 9.1, 2003, SAS Institute Inc., Cary, North Carolina) using an alpha level of 0.05. The density and height of ponderosa pine seedlings were dependent variables, and the circumference zone (distance from centered sprouted true mountain-mahogany) was the independent variable. Specifically, I addressed the following alternatives:

- The spatial pattern of true mountain-mahogany sprouts and ponderosa pine seedlings varies by fire severity.
- Within a homogeneous area, ponderosa pine seedlings grow faster when they are closer to sprouted true mountain-mahogany.

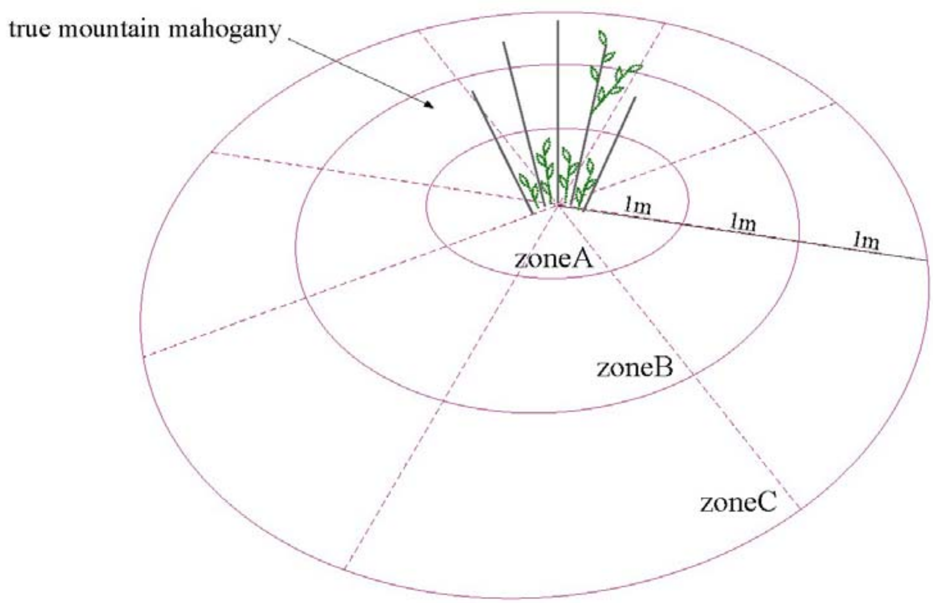

Figure 6. Schematic representation of the three circumference zones around each true mountain-mahogany plant marked in each plot.

Zone A: distance between 0.01m-1.00m from the center true mountain-mahogany.
Zone B: distance between 1.01m-2.00m from the center true mountain-mahogany.
Zone C: distance between 2.01m-3.00m from the center true mountain-mahogany.

RESULTS

Post-fire Sprouting Behavior

I examined sprouting behavior, including sprout length and number, throughout different fire severities in coarse and fine scales in the early recovery stage following the fire. Results from the Hi Meadow Fire and Hayman Fire suggested that true mountain-mahogany was an obligate sprouter with basal sprouts and epicormic sprouts found in low severity areas, only basal sprouts in high severity areas and only epicormic sprouts in unburned areas.

Based on the results from the Hi Meadow Fire, no evidence showed that the sprouting behavior of true mountain-mahogany was significantly different among landscape fire severities, except the number (p=0.0478, Table 2) and the length (p=0.0004, Figure 7) of basal sprouts one year after fire. In the Hayman Fire, landscape fire severity contributed significantly to differences in both basal sprout and epicormic sprout number (p<0.0001, Table 3), and in basal sprout length (p<0.0001, Figure 8) in the first year after fire. Epicormic sprout length was not significantly different by fire severity class in either the year of fire or one year after fire (p=0.8681 and p=0.2296, respectively, Figure 8).

Table 2. Mean number of true mountain-mahogany basal sprouts per root crown in the first two years after the Hi Meadow Fire, Colorado by landscape fire severity scale.

Landscape Fire Severity	Basal sprout the year of fire (*p*=0.2414)	Basal sprout one year after fire (*p*=0.0478)	Basal sprout two years after fire (*p*=0.0536)
High fire severity	0	3.47	14.60
Low fire severity	1.44	11.56	7.56
Unburned	2.67	2.33	3.56

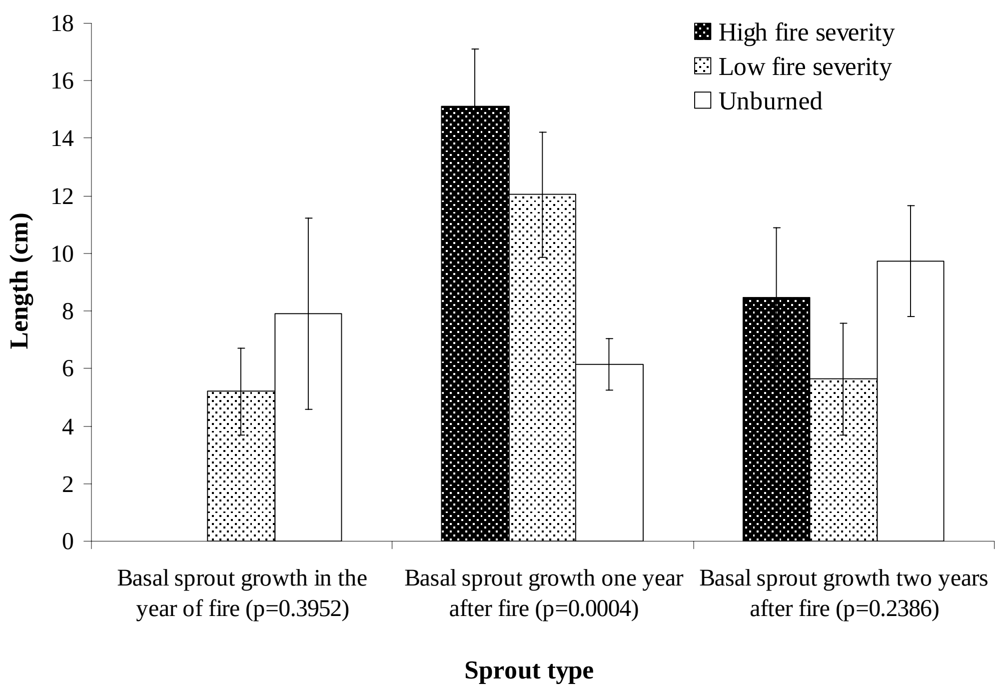

Figure 7. Mean length of true mountain-mahogany basal sprout growth in the first two years after the Hi Meadow Fire, Colorado by landscape fire severity scale. Error bars represent two standard error values. Differences between landscape fire severity (high, low, and unburn) groups are statistically significant at the $p<0.05$ level only in one year after the fire, not in the year or two years after the fire.

Table 3. Mean number of true mountain-mahogany sprouts per root crown one year after the Hayman Fire, Colorado by landscape fire severity scale.

Landscape Fire Severity	Basal sprout the year of fire (*p*<0.0001)	Basal sprout one year after fire (*p*<0.0001)	Epicormic sprout the year of fire (*p*<0.0001)	Epicormic sprout one year after fire (*p*<0.0001)
High fire severity	5.72	15.62	0	0.19
Low fire severity	3.03	8.53	0.08	5.44
Unburned	1.25	1.83	36.92	102.75

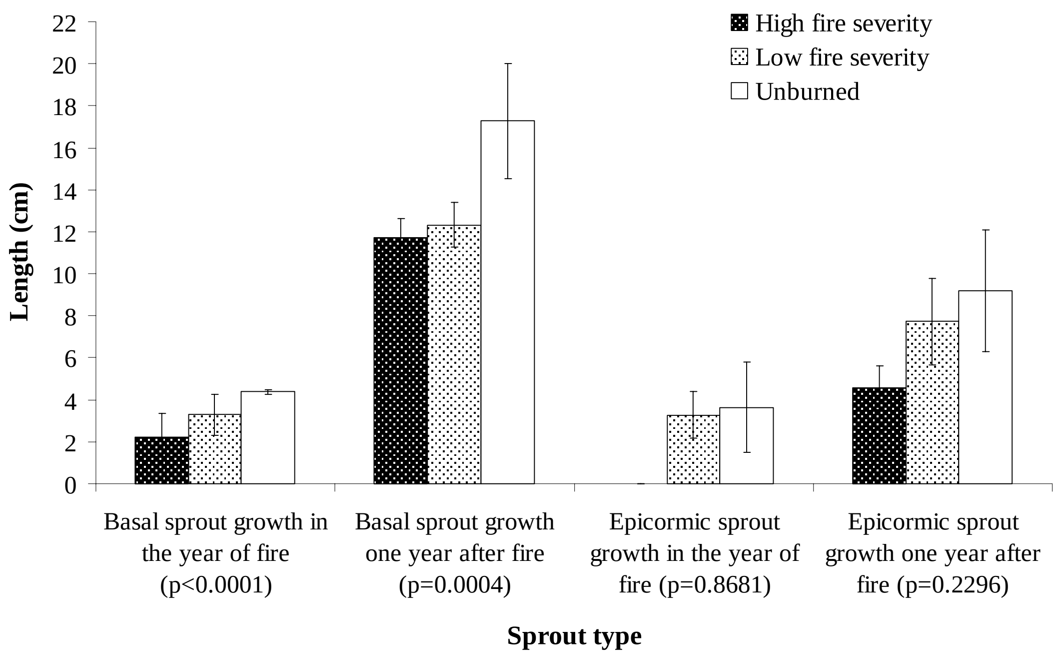

Figure 8. Mean length of true mountain-mahogany basal sprout growth one year after the Hayman Fire, Colorado by landscape fire severity scale. Error bars represent two standard error values. Differences between landscape fire severity (high, low, and unburn) groups are statistically significant at the *p*<0.05 level only in basal sprout length, not in epicormic sprout length after the fire.

The Hi Meadow Fire and the Hayman Fire both occurred in June, which were in the growing season in Colorado, and true mountain-mahogany started to sprout within two weeks after the fires. Basal sprouts occurred in the unburned and low severity area in the Hi Meadow Fire, while no sprouts occurred in the high severity area (Table 2). But in the Hayman Fire, more basal sprouts occurred in the high severity area than in unburned or low severity areas in the year of the fire and in one year after the fire (Table 3). No epicormic sprouts grew in the burned area, either in high or low severity areas, in the year of the Hayman Fire. Epicormic sprouts started to grow in the burned area one year after fire, and there were more epicormic sprouts in low severity area than in high severity area.

Landscape fire severity did not contribute to differences in basal sprout length in the year of and two years after the Hi Meadow Fire, but the basal sprout length was significantly different among fire severities in the first year after the Hi Meadow Fire (Figure 7) and in the year of and one year after the Hayman Fire (Figure 8). True mountain-mahogany had tallest basal sprouts in the unburned area, and the basal sprouts were taller in low severity areas than in the high severity areas after the Hayman Fire. No evidence showed that the length of epicormic sprouts varied by fire severity class.

Although fire severity apparently contributed to significant differences in sprouting behavior of true mountain-mahogany, the burn severity of individual shrubs might be more consequential and crucial than landscape fire severity. Fire usually burns patchily in the understory, and sometimes true mountain-mahogany with high SBSR were found in low landscape fire severity areas (Figure 9). Based on the data from the Hayman Fire burn area, the SBSR at the individual plant scale was more capable of explaining the sprouting behavior of true mountain-mahogany than fire severity classifications at the landscape scale.

Figure 9. High shrub burn severity true mountain-mahogany within low fire severity ponderosa pine forest in the Hayman burn, Colorado. The picture shows the mosaic burn severity which is not recognized using landscape scale fire severity assessments.

Post-fire sprouting behavior of true mountain-mahogany varied across SBSR classes (Figure 10). True mountain-mahogany with SBSR 0 had many axillary leaves, few epicormic sprouts, and no basal sprouts (Table 4). True mountain-mahogany with SBSR 1 and SBSR 2 had few axillary leaves, and SBSR 3, 4, 5, and 6 had no axillary leaves. Epicormic sprouts only grew in true mountain-mahogany with SBSR 0, 1, and 2, and grew in abundance in the least severely burned true mountain-mahogany (Figure 11). Basal sprouting in true mountain-mahogany was the most significant response to fire, especially in higher SBSR classes ($p<0.0001$). In SBSR 3, basal sprouts did not grow abundantly in the first couple months after the fire; however, true mountain-mahogany with higher burn severities grew basal sprouts right after the fire and continuously generated new basal sprouts in the following growing season (Figure 11). Figure 13 illustrates the general morphology of true mountain-mahogany in each SBSR class.

In the Hayman Fire, SBSR contributed significantly to differences in the basal sprout length in the year of fire and one year after fire ($p<0.0001$, Figure 12), but the epicormic sprout length was not significant in SBSR class in both years ($p=0.2653$ and $p=0.2793$, respectively, Figure 12). True mountain-mahogany basal sprouts had greatest number in SBSR 4 and SBSR 5 (Figure 11), and had longest length in the moderate burned shrubs after fire (Figure 12). In the first couple months after fire, true mountain-mahogany had taller basal sprouts in moderately burned shrubs than in shrubs burned with lower or higher severity (Figure 12). The tallest basal sprouts occurred in SBSR 3 (Figure 12) whereas the fewest basal sprouts occurred in this category (Figure 11). This indicated that in SBSR 3 true mountain-mahogany shrubs generated less basal sprouts but had faster growth rates at the early recovery phase following fire. Conversely, one year after the fire, the basal sprouts in SBSR 3 were the shortest among basal sprouts in all SBSR categories (Figure 12).

Table 4. True mountain-mahogany sprouting behavior in each Shrub Burn Severity Rating class in the Hayman burn. No = 0, Few = 1~5, Many = >5.

Sprouting	Shrub Burn Severity Rating						
	0	1	2	3	4	5	6
Axillary leaves	Many	Few	Few	No	No	No	No
Epicormic sprouts	Few[1]	Many[1]	Few[1]	No	No	No	No
Basal sprouts	No	Few[1]	Many[1]	Many[1]	Many[1]	Many[1, 2]	Many[1, 2]

[1] Sprout growth began one year after fire (year 2003)
[2] Sprout growth began in the year fire occurred (year 2002)

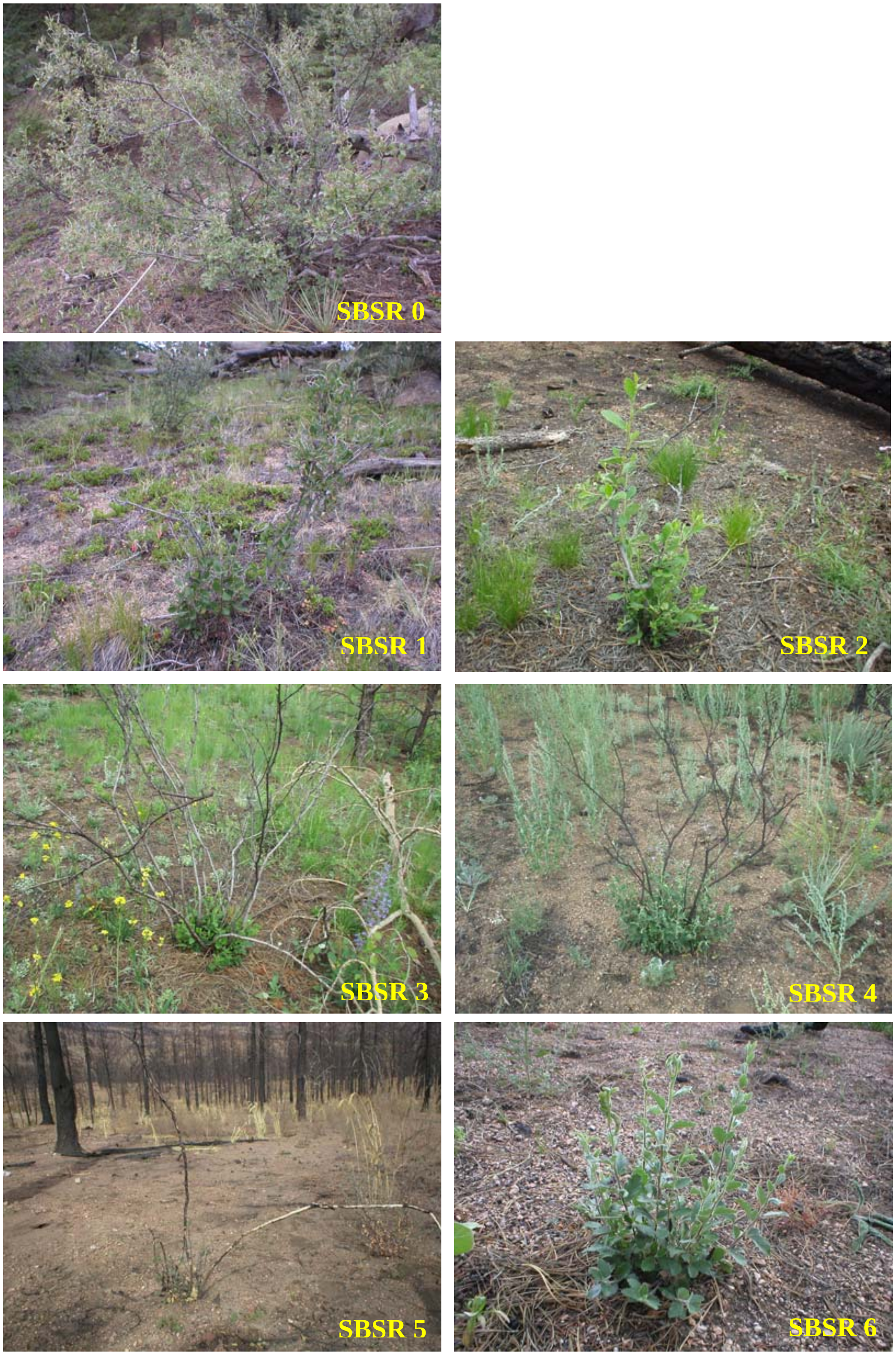

Figure 10. Pictures of true mountain-mahogany at each Shrub Burn Severity Rating (SBSR) class. Pictures were taken in July 2003, one year after the Hayman burn.

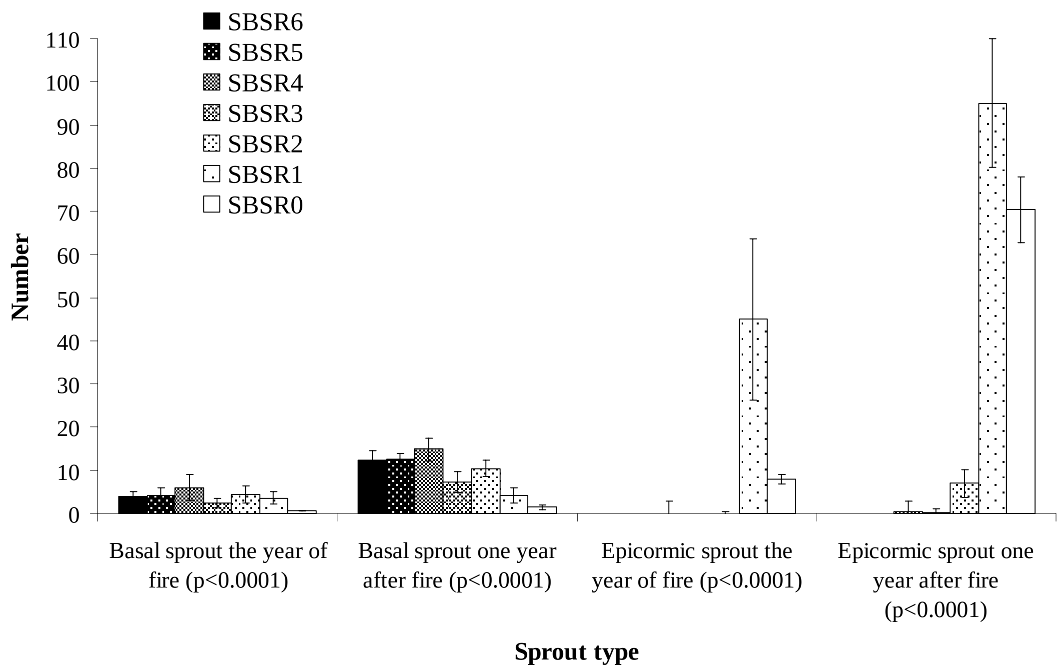

Figure 11. Mean number of true mountain-mahogany sprouts per root crown one year after the Hayman Fire, Colorado by Shrub Burn Severity Rating (SBSR) scale. Error bars represent two standard error values. Differences between SBSR groups are statistically significant at the $p<0.05$ level in both basal and epicormic sprouts after the fire.

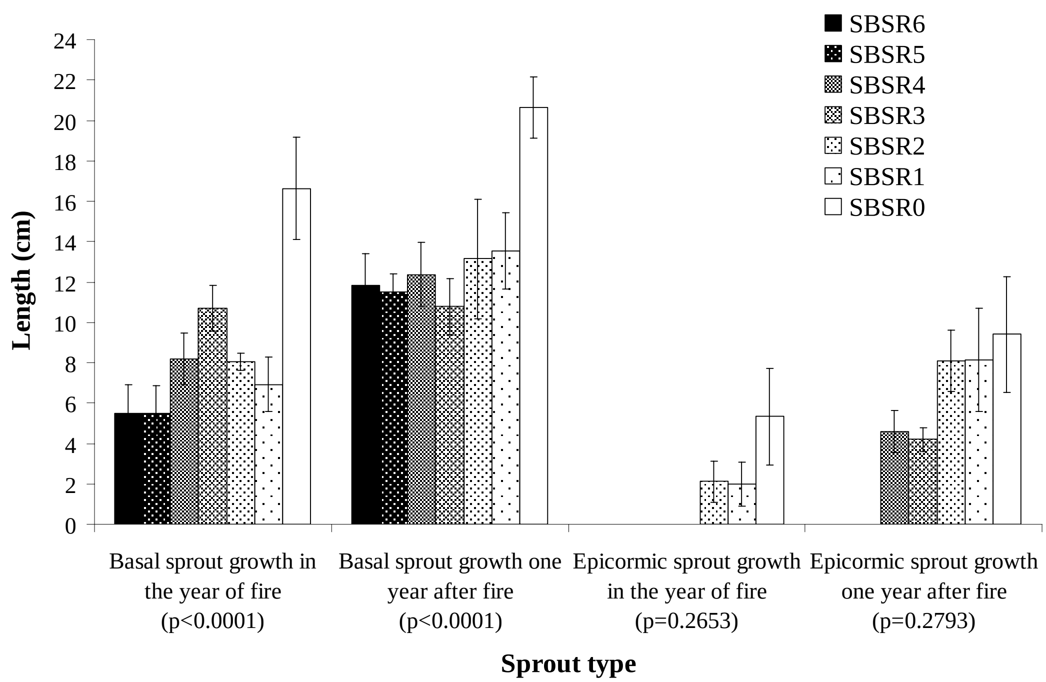

Figure 12. Mean length of true mountain-mahogany sprout growth one year after the Hayman Fire, Colorado by Shrub Burn Severity Rating (SBSR) scale. Error bars represent two standard error values. Differences between SBSR groups are statistically significant at the $p<0.05$ level in basal sprout length after the fire.

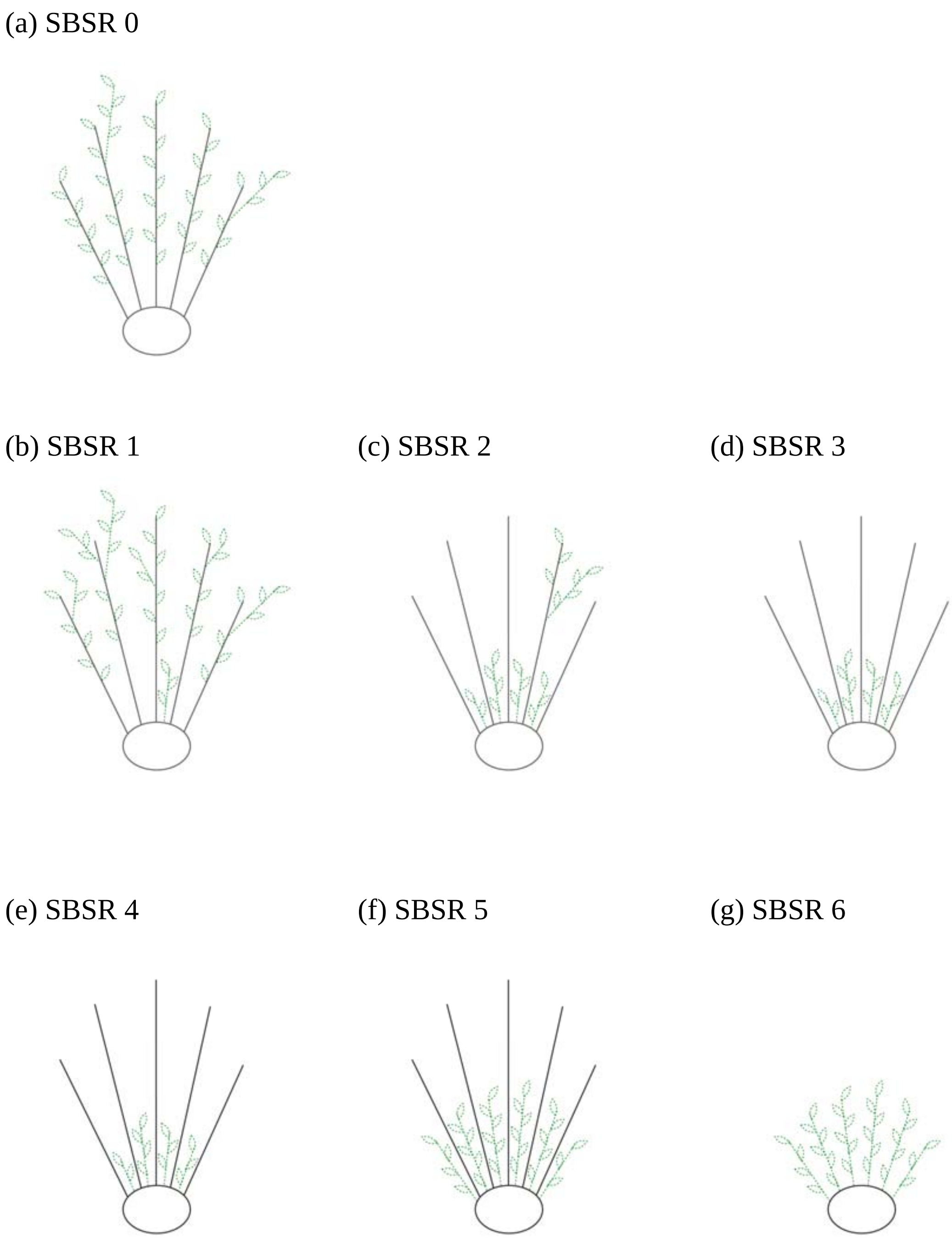

Figure 13. True mountain-mahogany sprouting morphology in each Shrub Burn Severity Rating (SBSR) class. Gray lines represent true mountain-mahogany stems, greens represent leaves and sprouts one year after fire, and the oval represents a root crown.

Post-fire Root Reserves

The total nonstructural carbohydrate (TNC) was not significant in different SBSR burned shrubs (Figure 14, p=0.8740), and it was also not significant (p=0.3349) in landscape fire severity (unburn, low, and high severity). The alternative hypothesis about root reserves varying by fire severity was not confirmed in the Hayman Fire area. However, the TNC was significantly different between burned and unburned true mountain-mahogany root crowns (p=0.0003). True mountain-mahogany in unburned areas had the highest root TNC one year after fire (Figure 14), confirming the alternate hypothesis.

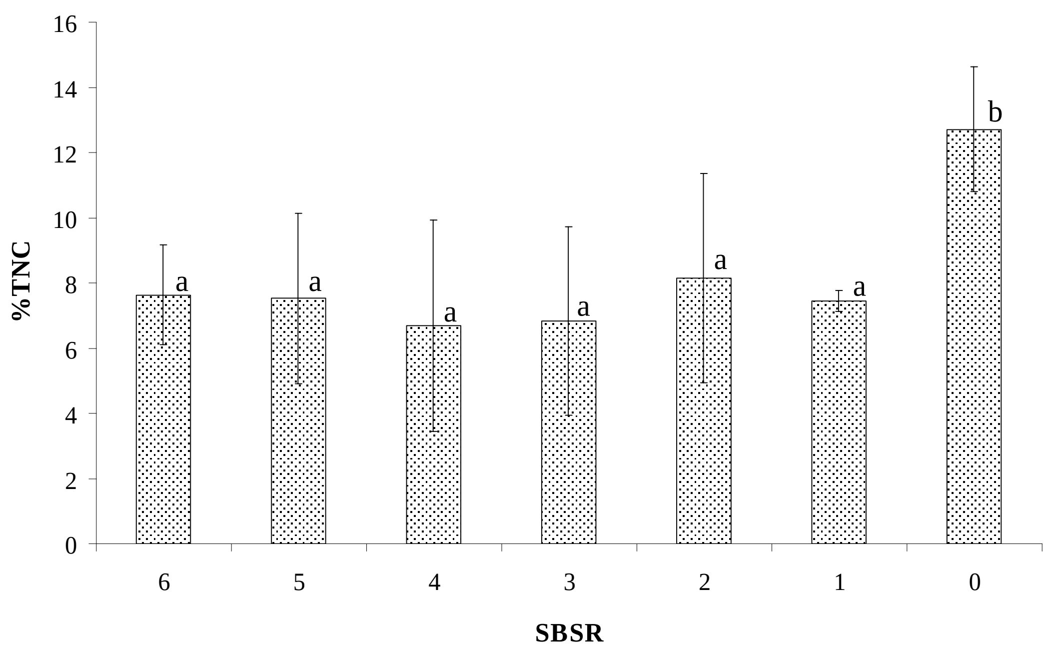

Figure 14. True mountain-mahogany percent root total nonstructural carbohydrates (%TNC) one year after 2002 Hayman burn, Colorado. Error bars represent two standard error values. Different letters next to the columns represent a significant difference between SBSR at the $p<0.05$ level.

Treatment Effects

In the Hayman Fire, 159 true mountain-mahogany were sampled in the treated and untreated areas, but since many areas were involved in more than one treatment, only 102 samples which were in the single treated areas were analyzed here (Table 1). I grouped true mountain-mahogany into three ways: (1) treated and untreated, (2) pre-fire treated and post-fire treated, and (3) individual treatment.

Treated vs. Untreated Areas

The treated group included true mountain-mahogany samples measured in the prescribed burn, thin, and seeded areas. The untreated group included the samples measured in no treatment areas. There were significant differences between treated and untreated sample areas in basal and epicormic sprout number one year after fire and epicormic sprout number the year of fire (Table 5), but no differences in basal sprout number in the year of fire. Basal sprout length was not significantly different between treated and untreated areas, except one year after fire (p=0.0012) when the basal sprouts were longer in untreated areas than in treated areas (Table 5 and 6). True mountain-mahogany had greater number of epicormic sprouts in untreated areas than in treated areas at both years. However, basal sprout number was smaller in untreated areas than in treated areas one year after fire (Table 6). The results of the treated versus untreated analysis confirmed the alternative hypothesis, that true mountain-mahogany has taller and larger number of sprouts in untreated areas than treated areas, in epicormic sprout number at both years and basal sprout length one year after the Hayman Fire. This alternative hypothesis was not confirmed by basal sprout number in both years, basal sprout length in the year of fire, or epicormic sprout length in both years following the fire.

Table 5. ANOVA results of the true mountain-mahogany sprout length and number pre root crown of different treatment groups in the 2002 Hayman Fire, Colorado. Treated group includes Rx burn, thinning, and seeding. Pre-fire treated group includes Rx burn and thinning, and post-fire treated group includes seeding. The *p*-values less than 0.05 indicate significant effects.

	Sprout	Treated versus Untreated				Pre-fire versus Post-fire treated			
		F	*d.f.*	*p*-value	N	*F*	*d.f.*	*p*-value	N
Number	Basal sprout the year of fire	0.00	1	0.9726	500	0.47	1	0.4942	290
	Basal sprout one year after fire	13.17	1	0.0003	500	1.28	1	0.2594	290
	Epicormic sprout the year of fire	10.57	1	0.0012	501	8.56	1	0.0037	291
	Epicormic sprout one year after fire	50.66	1	<0.0001	501	13.49	1	0.0003	291
Length	Basal sprout growth in the year of fire	0.09	1	0.7635	204	7.61	1	0.0068	116
	Basal sprout growth one year after fire	10.60	1	0.0012	458	1.62	1	0.2045	278
	Epicormic sprout growth in the year of fire	0.03	1	0.8656	19	.	0	.	4
	Epicormic sprout growth one year after fire	0.02	1	0.8889	85	.	0	.	10

Table 6. Mean of true mountain-mahogany sprout length and number per root crown of different treatment groups in the 2002 Hayman Fire, Colorado. Treated group includes Rx burn, thinning, and seeding. Pre-fire treated group includes Rx burn and thinning, and post-fire treated group includes seeding. Symbols represent the level of significance for differences between treatments: ***, $p<0.0001$; **, $p<0.01$; *, $p<0.05$; n.s., not significant. The table indicates if the alternative hypotheses were confirmed (v) or not (x).

	Sprout	Treated versus Untreated				Pre-fire versus Post-fire treated			
		Treated	Untreated		H_{A1}	Pre-fire treated	Post-fire treated		H_{A2}
Number	Basal sprout the year of fire	3.48	3.50	n.s.	x	3.33	3.73	n.s.	x
	Basal sprout one year after fire	11.41	7.60	**	x	12.03	10.41	n.s.	x
	Epicormic sprout the year of fire	0.09	10.55	**	v	0.00	0.23	**	x
	Epicormic sprout one year after fire	0.69	30.81	***	v	0.00	1.82	**	x
Length (cm)	Basal sprout growth in the year of fire	7.26	7.56	n.s.	x	8.79	5.03	**	v
	Basal sprout growth one year after fire	10.99	13.25	**	v	10.59	11.63	n.s.	x
	Epicormic sprout growth in the year of fire	4.14	3.63	n.s.	x	.	4.14	.	.
	Epicormic sprout growth one year after fire	8.50	8.20	n.s.	x	.	8.51	.	.

H_{A1}: True mountain-mahogany has taller and larger number of sprouts in untreated areas compared to treated areas
H_{A2}: True mountain-mahogany has taller and larger number of sprouts in pre-fire treated areas compared to post-fire treated areas

Pre-fire vs. Post-fire Treatment Areas

The pre-fire treated group included true mountain-mahogany samples in the prescribed burn and thin areas, and post-fire treated group consisted of samples from the seeded areas. Results from the Hayman burn indicated that pre-fire treated and post-fire treated groups did not contribute significant difference to basal sprout number at both years (Table 5), but did contribute to epicormic sprout number at both years. Moreover, basal sprouts were higher in pre-fire treated areas than in post-fire treated areas (Table 6). The results of the pre-fire treated versus post-fire treated analysis confirmed the alternative hypothesis, that true mountain-mahogany has taller and larger number of sprouts in pre-fire treated areas compared to post-fire treated areas, only in basal sprout length in the year of the Hayman Fire. This alternative hypothesis was not confirmed by sprout number or by epicormic sprout length.

Individual Treatment

This stratum included Rx burn, thin, seed, and no treatment. Results showed sprout number was significantly different between treatments, except basal sprouts in the year of fire (p=0.1002, Figure 15). Epicormic sprout numbers were affected by the treatments which, interestingly, did not influence the epicormic sprout length (Figure 16). Results also showed significant differences in basal sprout length in both years. The alternative hypothesis, that true mountain-mahogany sprout length and number varied by treatments at the early vegetation recovery stage after fire, was confirmed by sprout number and basal sprout length.

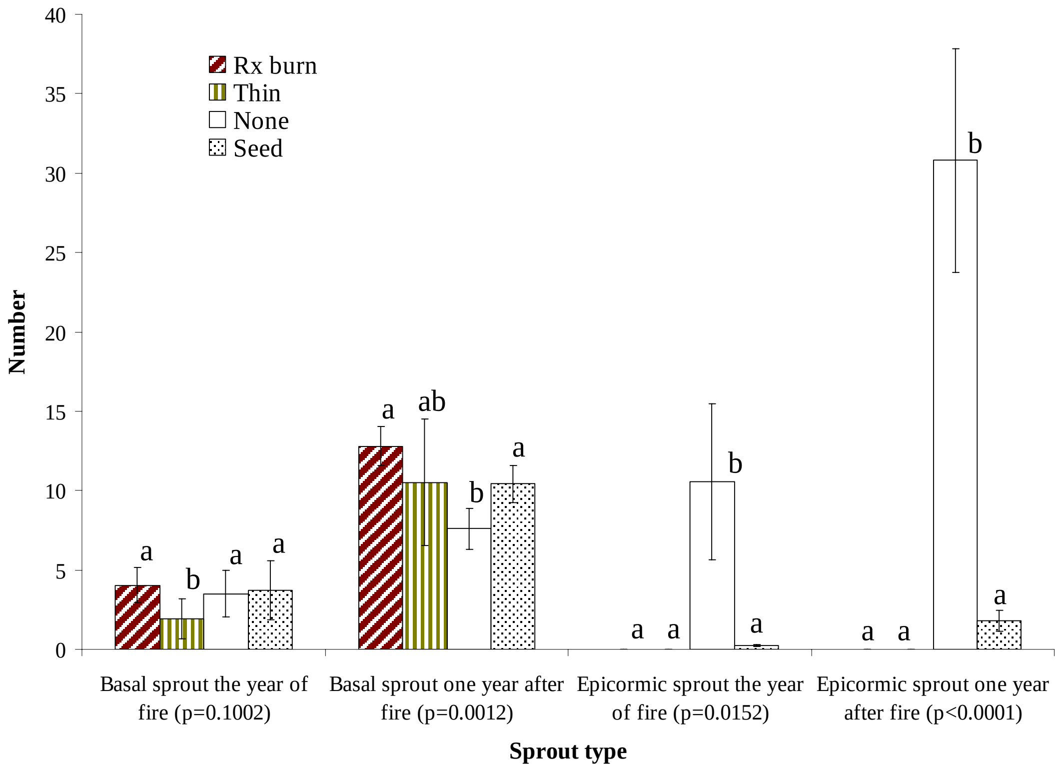

Figure 15. Mean number of true mountain-mahogany sprouts per root crown in pre-fire and post-fire treatments in the Hayman Fire, Colorado. Error bars represent two standard error values. Different letters next to the columns represent a significant difference at the $p<0.05$ level within each group.

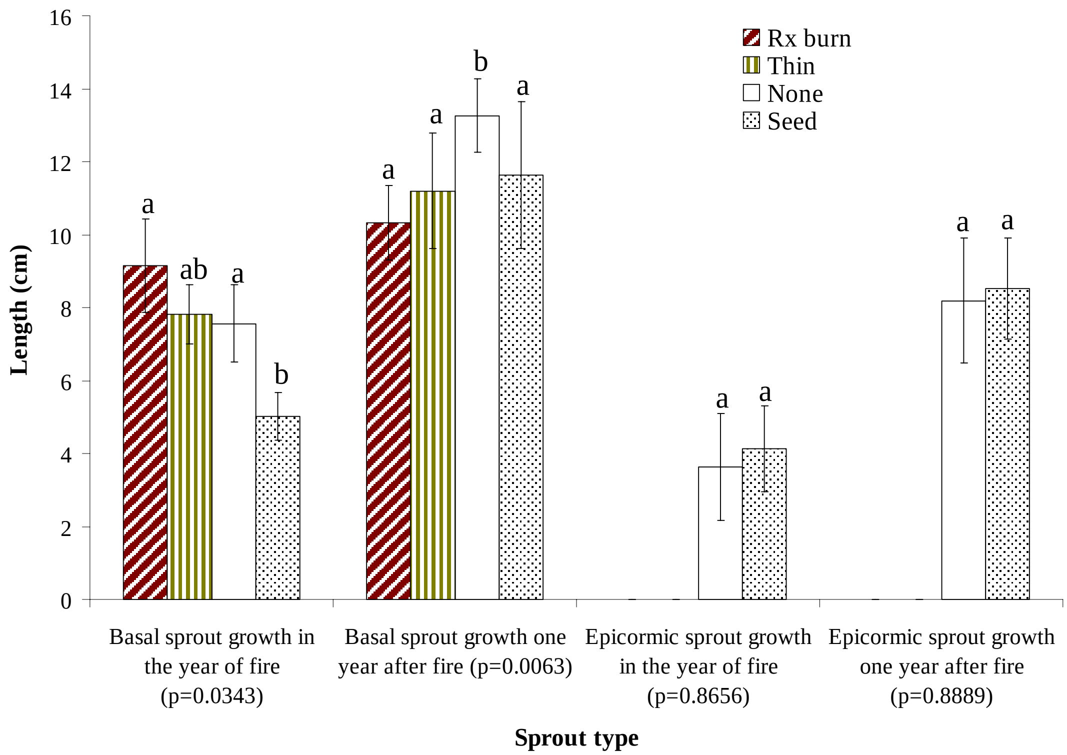

Figure 16. Mean length of true mountain-mahogany sprouts in pre-fire and post-fire treatments in the Hayman Fire, Colorado. Error bars represent two standard error values. Different letters next to the columns represent a significant difference at the $p<0.05$ level within each group.

Sprouts Related to Pine Seedlings

Based on the data in summer 2002 from the Hi Meadow Fire, twelve shrub species with sprouting ability were recorded in the plots (Table 7). I used Microsoft® Excel to plot the locations of sprouted true mountain-mahogany and ponderosa pine trees in each landscape fire severity class. The spatial distribution of ponderosa pine trees and sprouted true mountain-mahogany are shown in Figures 17-19.

Table 7. Sprouting shrub species in the Hi Meadow Fire, Colorado.

Adoxaceae	
Acer glabrum Torr.	Mountain maple
Anacardiaceae	
Rhus trilobata Nutt.	Skunkbrush
Caprifoliaceae	
Symphoricarpos occidentalis Hook.	Snowberry
Cornaceae	
Cornus stolonifera Michx.	Dogwood
Grossulariaceae	
Ribes cereum Dougl.	Wax Currant
Ribes lacustre (Pers.) Poir	Prickly Currant
Hydrangeaceae	
Jamensia americana T. & G.	Waxflower
Rosaceae	
Cercocarpus montanus Raf.	True Mountain-mahogany
Holodiscus dumosus (Nutt.) Heller	Bush oceanspray
Prunus virginiana L.	Choke Cherry
Rosa acicularis Lindl.	Wild Rose
Rubus idaeus L.	Wild Red Raspberry

The data from four years after Hi Meadow Fire indicated ponderosa pine seedlings were only found in the low fire severity area, but not found in high fire severity or unburned areas. In the high fire severity area, most of the ponderosa pine were killed by fire (Figure 20), and the seed sources from either canopy seed bank or soil seed bank were consumed and eliminated. Here, I focused on ponderosa pine seedling regeneration in the low fire severity area only. Although no significant differences in the density of pine seedlings between the zones were found (Figure 21, p=0.53), our results indicated that ponderosa pine seedlings in circumference zone A (Figure 6), which was closer to true mountain-mahogany, are taller than those in zone C (Figure 22). The differences in the pine seedling height may be caused by the influence of true mountain-mahogany persistence. Shrubs that sprout quickly post-fire can retard soil erosion and nutrient losses, and restore suitable environmental conditions for pine regeneration.

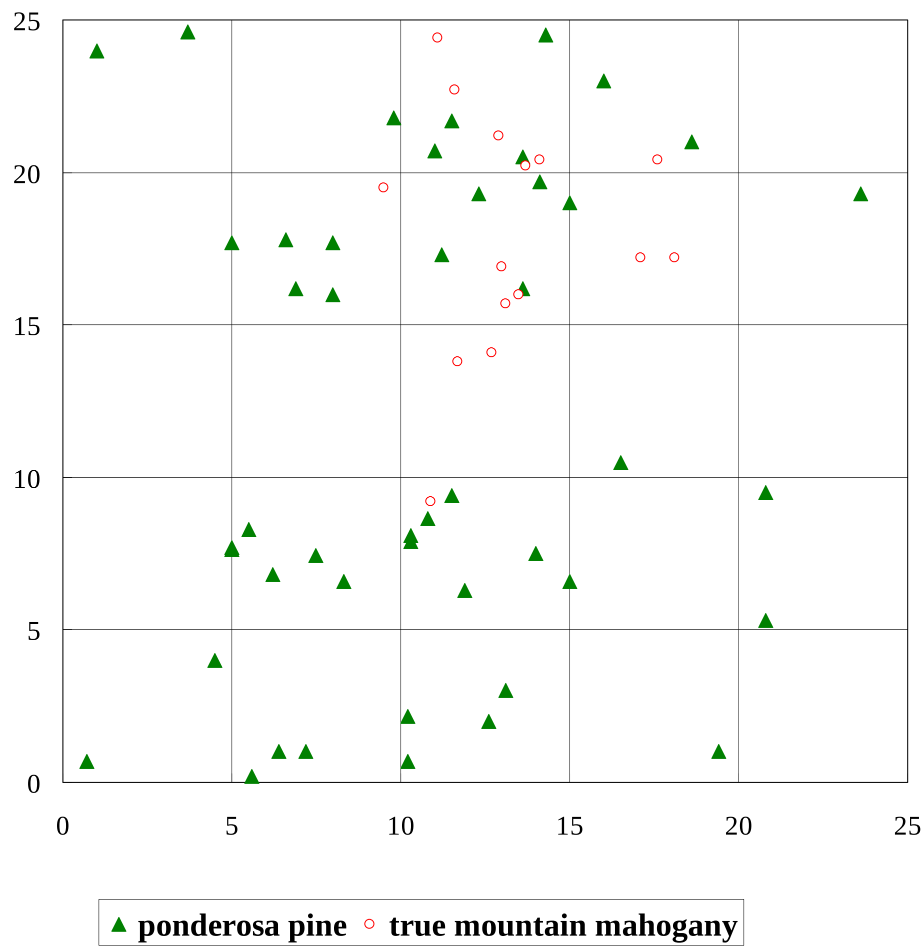

Figure 17. Spatial distribution of ponderosa pine trees and sprouted true mountain-mahogany in the 25 x 25 m^2 high fire severity plot, 2000 Hi Meadow Fire, Colorado. Ponderosa pine seedlings are not found in this plot.

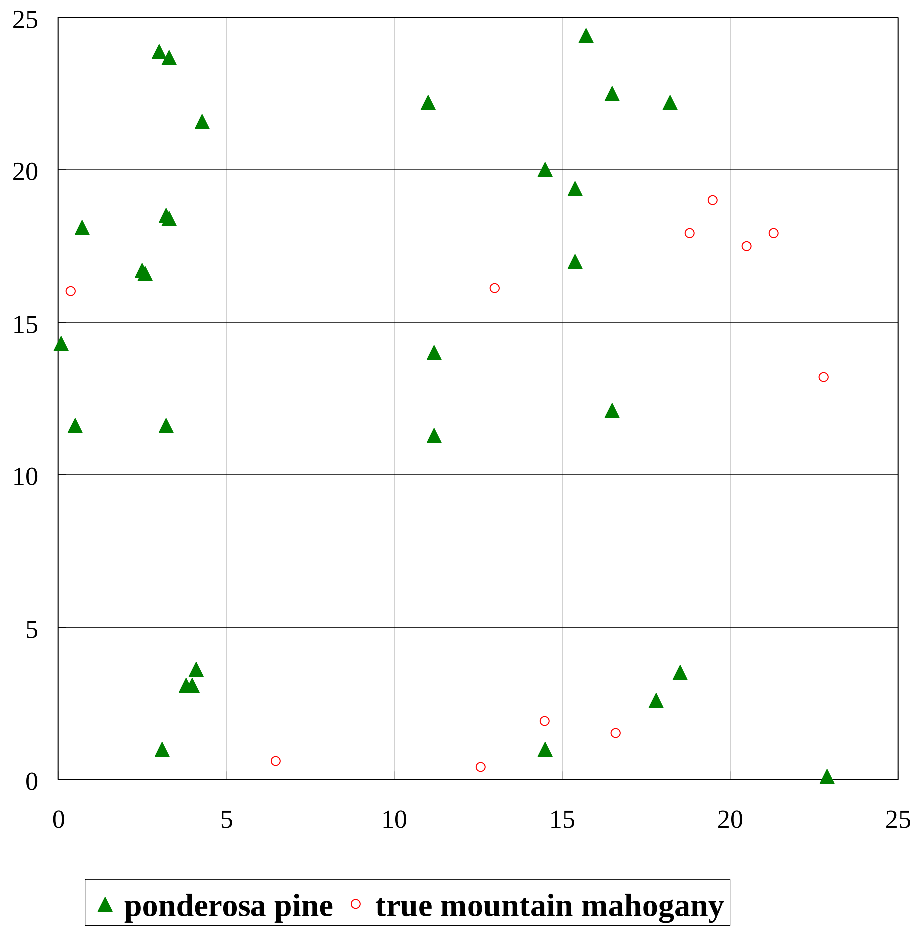

Figure 18. Spatial distribution of ponderosa pine trees and sprouted true mountain-mahogany in the 25 x 25 m^2 low fire severity plot, 2000 Hi Meadow Fire, Colorado. Although ponderosa pine seedlings are found in this plot, the locations of pine seedlings are not shown here.

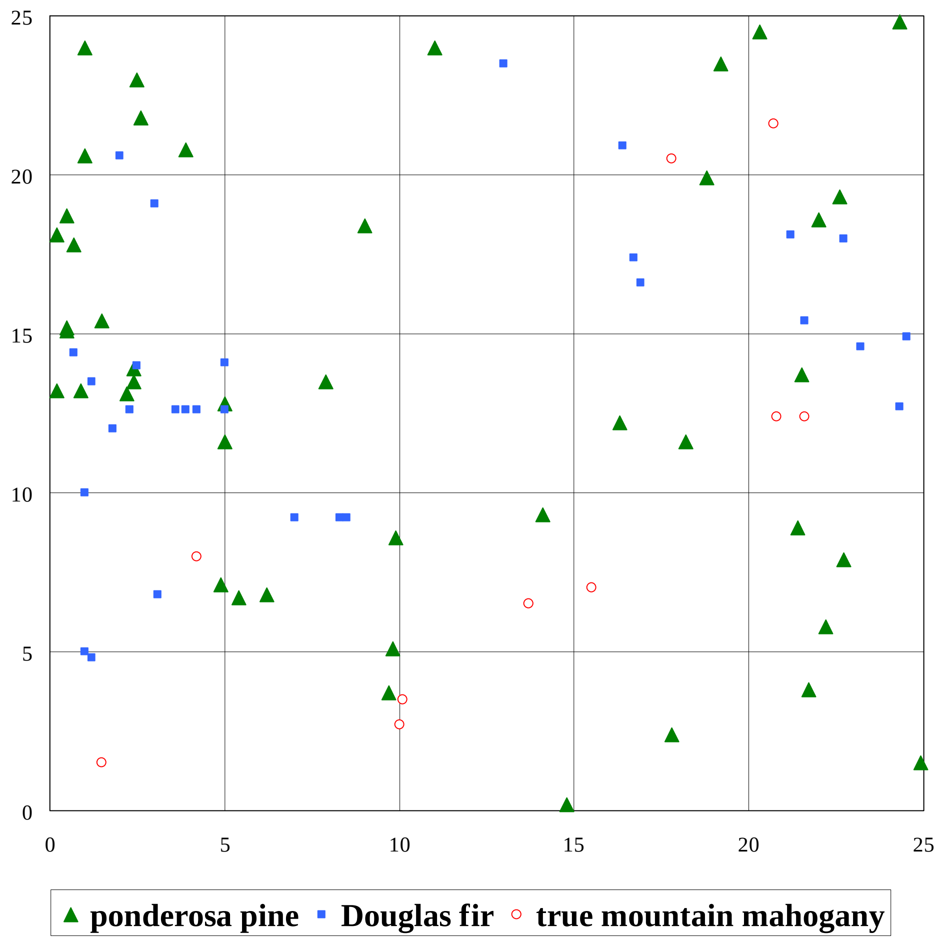

Figure 19. Spatial distribution of ponderosa pine trees, Douglas fir trees, and sprouted true mountain-mahogany in the 25 x 25 m^2 unburn plot, 2000 Hi Meadow Fire, Colorado. Ponderosa pine seedlings are not found in this plot.

Figure 20. The ponderosa pine forest within a high fire severity burned area, four years after the 2000 Hi Meadow Fire, Colorado. Seedling regeneration is low due to absence of seed source.

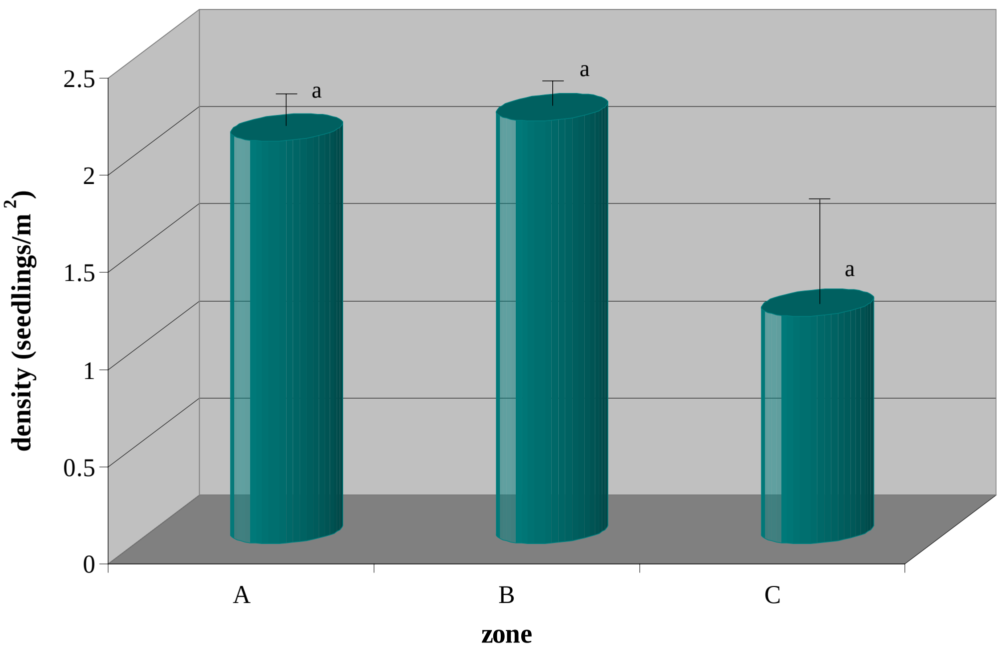

Figure 21. The mean density of ponderosa pine seedlings per square meter in each circumference zone (Figure 6) around true mountain-mahogany plants in the low fire severity burned area within the 2000 Hi Meadow Fire, Colorado. Error bars represent standard error values. No significant difference was found between circumference zones at the $p<0.05$ level.

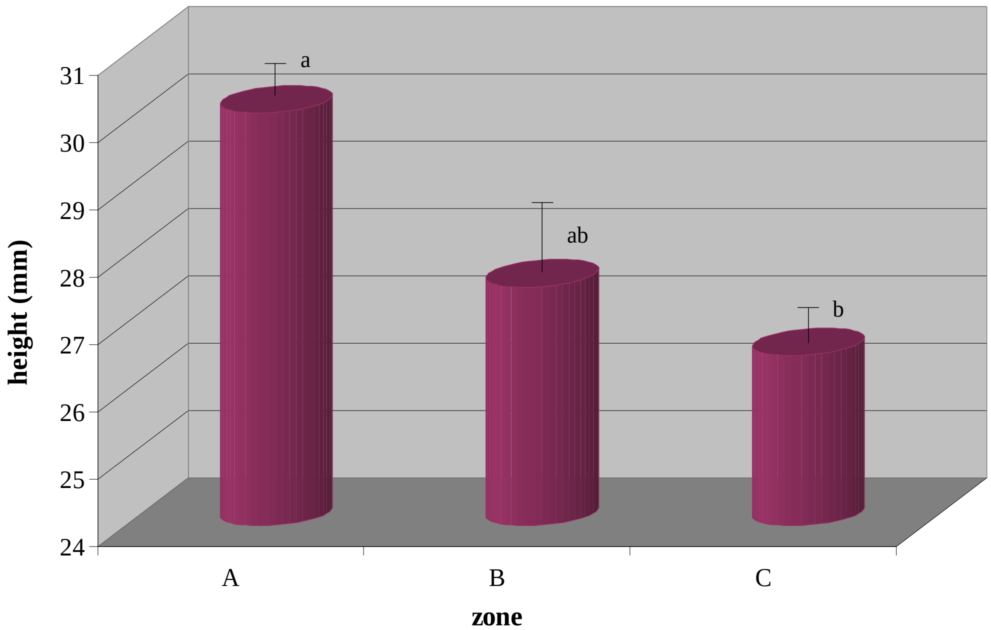

Figure 22. The mean height of ponderosa pine seedlings in each circumference zone (Figure 6) around true mountain-mahogany plants in the low fire severity area within the 2000 Hi Meadow Fire, Colorado. Error bars represent standard error values. Different letters next to the columns represent a significant difference between circumference zones at the $p<0.05$ level.

DISCUSSION

The results of this thesis reveal a complex relationship between shrub sprouting and fire in the ponderosa pine forest. Here I summarize the decisions made with respect to hypotheses tested (Table 8).

Table 8. Summary of decisions for the null hypotheses tested in the true mountain-mahogany sprouting study following fires in ponderosa pine forests along the Colorado Front Range. Results for testing hypotheses Ho_3, Ho_4, and Ho_5 were inconclusive as described in Methods.

Null Hypothesis	**Decision**
H_{O1}. The number and length of basal and epicormic sprouts does not vary by fire severity class at the landscape scale.	Fail to reject * Reject *
H_{O2}. The number and length of basal and epicormic sprouts does not vary by fire severity class at the shrub scale.	Reject
$H_{O6.}$ The root reserves do not vary by fire severity class.	Fail to reject
H_{O7}. No significant difference between burned and unburned root reserves one year after fire.	Reject
H_{O8}: The treatments do not influence sprout length and number at the early vegetation recovery stage after fire.	Reject
H_{O9}: The spatial pattern of true mountain-mahogany sprouts and ponderosa pine seedlings does not vary by fire severity.	-
H_{O10}: The density and height of pine seeding does not change by the distance from sprouted true mountain-mahogany.	Reject

* Results differ by sampling time and fire events. The hypothesis is rejected in the Hayman Fire but is not rejected in the Hi Meadow Fire

\- Insufficient data to test the hypotheses

Failure to reject the first hypothesis (H_{O1}) associated with landscape scale fire severity in the Hi Meadow Fire indicates the potential risk of misleading usage of landscape fire severity maps, especially in a mixed-severity fire regime. A mixed-severity fire regime indicates a number of individual trees burned at mixed severities with some nonlethal and some stand-replacement fires (Arno et al. 2000), and a typical mixed-severity fire usually leaves an erratic, patchy pattern of fuel and stand structures (Brown and Smith 2000). Arno (2000) claimed that historical mixed-severity fire regimes are associated with ponderosa pine growing east and west of the Continental Divide. He also concluded that although the extent and ecological relationships of these mixed-severity ponderosa pine fire regimes are yet to be determined, the most compelling evidence for a large area of mixed-severity fire regime comes from the Front Range of the Rocky Mountains in Colorado and Black Hills of South Dakota.

Mixed-severity fire regimes typically create a mosaic of patchy heterogeneous environments, due to uneven burn patterns. Thus, an appropriate spatial scale for better understanding of post-fire effects and better prediction of fire behavior seems more important in mixed-severity fire regimes. Developing consistent ecologically meaningful information related to secondary fire effects is a challenge for burn severity classification (Jain and Graham 2003). Fire severity maps, which are based on large scale remote sensing data such as post-fire Landsat imagery, are sometimes insufficient to explain finer scale fire effects. A smaller spatial scale of individual plant was introduced in this study.

In the second field season at the Hayman burn, I adopted both a large spatial scale and a small spatial scale of fire severity. The finer scale burn severity classification, Shrub Burn Severity Rating (SBSR), was applied on each true mountain-mahogany in the field measurements. Sprouting behavior of true mountain-mahogany varied by fire severity in the ponderosa pine forest after the Hayman burn, and the results did not conflict at different spatial scales. Both first (H_{O1}) and second hypotheses (H_{O2}) were confirmed in the Hayman burn.

True mountain-mahogany sprouting behavior was axillary leaves, epicormic sprouts, and basal sprouts in response to increments of shrub burn severity. Similar plant sprouting response patterns to a continuum of disturbance severities is also reported by Bellingham and Sparrow (2000) and Bond and Midgley (2001). The pattern they conclude is that, beyond certain disturbance frequency, plant sprouting behavior is axillary, branch epicormic, stem epicormic, and basal in consequences of increasing disturbance severity (Figure 23). Such a sprouting response pattern (Bellingham and Sparrow 2000) is confirmed by true mountain-mahogany sprouting following fire in ponderosa pine forests along the Colorado Front Range.

I also found true mountain-mahogany basal sprouts had the greatest number and the longest length in the moderately burned shrubs in the first couple months after the Hayman Fire. Some studies illustrate that plants have the highest number of sprouts in the moderate disturbance than other levels of disturbance (Miller 1976, Brown and Simmerman 1986). True mountain-mahogany also reaches maximum growth rates after 60% chipping (Shepherd 1971). The results from the Hayman burn suggest moderate burned true mountain-mahogany had the most asexual reproductions.

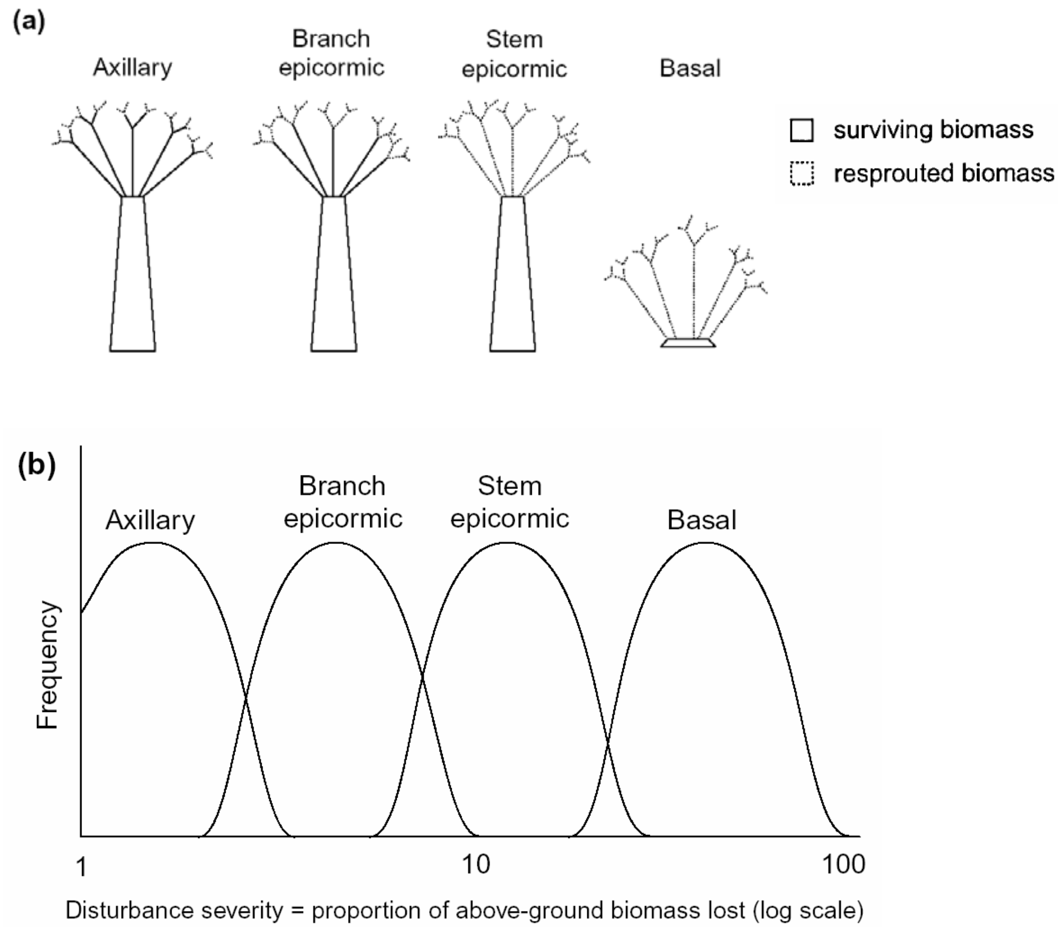

Figure 23. Sprouting response with increasing disturbance severity. (a) Possible surviving and sprouting patterns showing the loss and regenerate biomass, and (b) The relationship of sprouting response to disturbance severity. The diagram indicating the higher disturbance severity, the higher proportion of aboveground biomass lost. Reproduced from Bellingham and Sparrow (2000).

Although root reserves did not vary by fire severity (H_{O6}) in the Hayman Fire area, root TNC was higher in unburned shrubs than in burned shrubs (H_{O7}). Researchers who have examined sprouting versus storage have suggested the need to revise assumptions about sprouting vigor being primarily dependent on stored reserves (Cruz et al. 2003). Cruz et al. (2003) found that lignotuber stored carbohydrates are not correlated to sprout number, length, or biomass. The results of shrub sprouting associated with fire severity and shrub root reserves implies that fire severity, especially at the shrub scale, is a better predictor of true mountain-mahogany sprouting behavior following fire.

Fire influences shrub sprouting by reducing competition among plants (Vila and Terradas 1995). Pre-fire fuel reduction treatments and post-fire rehabilitation treatments (Figure 24) usually change the abiotic and biotic environment in the burned area. For example, pre-fire fuel reduction treatments usually remove or reduce flammable fuels. Post-fire rehabilitation using seeding and mulching creates the opportunity for exotic plant invasion or seeded grass growth (Kruse et al. 2004). In this study, true mountain-mahogany sprout number and length were significantly different between treatments (H_{O8} was rejected). The basal sprout number was larger in treated areas than in untreated areas one year after fire. Conversely, the epicormic sprout number was higher in untreated areas than in treated areas. Moreover, basal sprout lengths were higher in pre-fire treated areas than in post-fire treated areas. This might be caused by reduction in plant competition and fuel loading when applying prescribed burning treatments and thinnings. Results also indicated that pre- or post-fire treatments did not affect basal sprout number following fire, while pre-fire treatments seemed to lessen true mountain-mahogany epicormic sprouting.

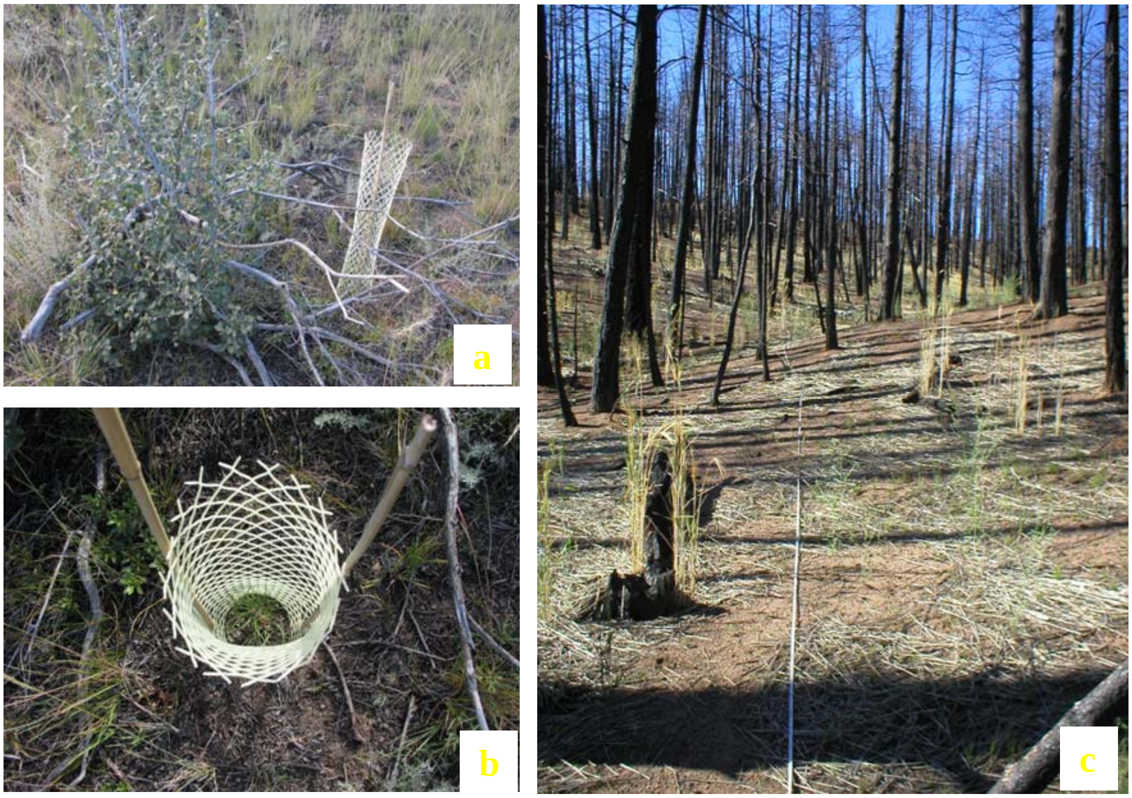

Figure 24. Post-fire rehabilitation treatments in Hayman Fire area, Colorado. (a) Planted ponderosa pine seedlings next to sprouted true mountain-mahogany, (b) Planted ponderosa pine seedling, and (c) Mulching.

Does this suggest pre-fire treatments are beneficial in controlling true mountain-mahogany epicormic sprouting? Do the results from treatment effects provide sufficient evidence in the responses of true mountain-mahogany sprouting following fire? Further analyses and more detailed examinations should be completed before answering these questions. For instance, the statistical model of testing cross-effects could be used to determine if there is interaction between treatment and other factors, such as fire severity, in affecting true mountain-mahogany sprouting. In particular, we may expect pre-fire treatments to alter behavior of wildfires and lead to differences in fire-induced plant mortality and subsequent sprouting. The effects of fire severity may be an underlying factor in the results from this study. Moreover, much of the post-fire treatments were focused in areas of high fire severity. To discover any insightful information between the effects, I did the preliminary analysis using treatment versus landscape scale fire severity, and treatment versus the shrub scale burn severity (SBSR). Preliminary results showed significant interactions between severity and pre- and post-fire treatment in true mountain-mahogany sprout length and number. Results also implied severity might be the causal effect in true mountain-mahogany sprouting, not treatment.

Post-fire quick-sprouted shrubs competing with resources, such as light, water, and nutrients may alter the establishment of pine seedling following fire (Neeman et al. 1992, Chen and Liang 2000). Ponderosa pine seedlings were only found in the low fire severity area four years after Hi Meadow burn, and no ponderosa pine seedling was found in high severity or unburned areas. Since we lack information on the ponderosa pine seedling distribution patterns in both high fire severity and unburned areas, the hypothesis H_{O9} could not be tested. Seed source usually plays an essential role for pine natural regeneration following fires. In the high fire severity area, most of the ponderosa pine were killed by fire, and the seed sources from either canopy seed bank or soil seed bank were consumed and eliminated. In this study, I found ponderosa pine seedling height differed in relation to the distance from sprouted true mountain-mahogany (H_{O10}). This may result from the nitrogen fixation ability of true mountain-mahogany. Sprouted true mountain-mahogany retards soil erosion and nutrient losses, and creates a suitable environmental condition for pine seedlings. Results of my study provide evidence of ponderosa pine seedlings growing faster in the area closer to sprouted true mountain-mahogany than those located farther away.

True mountain-mahogany is a sprouting, understory shrub species in ponderosa pine forests along the Colorado Front Range. Fire historical studies in the Colorado Front Range ponderosa pine forests have showed that the historical fire regime was a mixed-severity fire regime (Brown et al. 1999, Kaufmann et al. 2000a, Kaufmann et al. 2000b, Huckaby et al. 2001, Kaufmann et al. 2001, Ehle and Baker 2003), which created patchy, uneven age pine forests over time. A mixed-severity fire regime is the most complex type of fire regime and the least understood (Schoennagel et al. 2004). Plant adaptation to fires of different severity becomes more complex and unlikely to be understood if we do not have adequate and ample studies in fire effects and plant responses. My study provides accounts of shrub sprouting responses under different fire severities in both larger (landscape) and finer (shrub) scales. True mountain-mahogany in this study sprouted after the fire suggests that they are well adapted to fire of various intensities, and thus, both high and low intensity fires must have occurred in this region in the past. I expect shrubs in a mixed-severity fire regime to be better adapted to fire of various intensities given that different types of fires are characteristic in a mixed-severity fire regime than in high- or low- severity fire regimes.

CONCLUSION

Sprouting is a key mechanism for true mountain-mahogany to regenerate following fires. True mountain-mahogany is an obligate sprouter exhibiting various sprouting behaviors throughout different fire severities in the early recovery stage following fires. In this study, I provided descriptive information of shrub sprouting behavior under different fire severities. I also provided quantitative evidence in sprout number and length at both landscape and finer scale fire severities. I addressed the possible misleading information in landscape fire severity maps; therefore, a finer scale "Shrub Burn Severity Rating (SBSR)" class was introduced and practiced on true mountain-mahogany in this study. The SBSR class more reliably reflected shrub sprouting behavior under a continuum of fire severities. Whether the finer scale fire severity is appropriate for use in forest management activities still needs to be examined in other applications with various plant species.

Little is known about the functioning of mixed-severity fire regime forests. We also lack knowledge of the role and importance of shrub species in the development of ponderosa pine forest ecosystems in general, but particularly in mixed-severity fire regimes. Ponderosa pine forests in the Colorado Front Range comprise a mixed-severity fire regime with true mountain-mahogany as the dominant undergrowth shrub species. True mountain-mahogany sprout after the fire indicates that they are well adapted to various fire intensities.

In ponderosa pine forests in the Colorado Front Range, true mountain-mahogany root reserves do not contribute significant effects on sprouting. The sprouting responses also show a discrepancy from pre- and post-fire fuel treatments. Fire severity seems to be the most important abiotic predictor of true mountain-mahogany sprouting behavior after fire.

The spatial relationship between ponderosa pine seedlings and sprouted shrubs in the Colorado Front Range is not well answered in this study, although preliminary results show possible tree-shrub interactions that deserve further study. Other areas of future interest include the contribution of sprouted shrubs to fuel loading at various forest development stages and impacts on potential fire behavior. Future studies about characteristics of forest structure, fuel loads, and flammability contributed by sprouted shrubs following fires are important for increasing our understanding of fire behavior in multi-layered, non-uniform fuel complexes.

REFERENCES

Agee, J. K. 1998. The landscape ecology of western forest fire regimes. Northwest Science **72**:24-34.

Alexander, R. R. 1987. Classification of the forest vegetation of Colorado by habitat type and community type. USDA Forest Service Rocky Mountain Forest and Range Experiment Station. Research Note RM-478. 14p.

Arno, S. F. 2000. Chapter 5: Fire in western forest ecosystem. Pages 97-120 *in* J. K. Brown and J. K. Smith, editors. Wildland fire in ecosystems -- effects of fire on flora. USDA Forest Service Rocky Mountain Research Station. RMRS-GTR-42-Vol. 2.

Arno, S. F., D. J. Parsons, and R. E. Keane. 2000. Mixed-severity fire regimes in the northern Rocky Mountains: consequences of fire exclusion and options for the future. Pages 225-232 *in* D. N. Cole, S. F. McCool, W. T. Borrie, and J. O'Loughlin, editors. Wilderness science in a time of change conference-Volume 5: Wilderness ecosystems, threats, and management. Proceedings RMRS-P-15-VOL-5. Ogden, Utah. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula, Montana.

Association of Official Agricultural Chemists. 1965. Official methods of analysis of the AOAC, 10th edition, Washington, D.C.

Bell, D. T., A. J. M. Hopkins, and J. S. Pate. 1984. Fire in the Kwongan. Pages 178-204. *in* J. S. Pate and J. S. Beard, editors. Plant life on the Sandplain. University of Western Australia Press, Nedlands, Western Australia.

Bellingham, P. J., and A. S. Sparrow. 2000. Resprouting as a life history strategy in woody plant communities. Oikos **89**:409-416.

Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology & Evolution **16**:45-51.

Bond, W. J., and J. J. Midgley. 2003. The evolutionary ecology of sprouting in woody plants. International Journal of Plant Sciences **164**:103-114.

Bosela, M. J., and F. W. Ewers. 1997. The mode of origin of root buds and root sprouts in the clonal tree *Sassafras albidum* (*Lauraceae*). American Journal of Botany **84**:1466-1481.

Bowen, B. J., and J. S. Pate. 1993. The significance of root starch in postfire shoot recovery of the resprouter *Stirlingia Latifolia* R. Br. (*Proteaceae*). Annals of Botany **72**:7-16.

Bradley, A. F., N. V. Noste, and W. C. Fischer. 1991. Fire ecology of forests and woodlands. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Ogden, Utah. General Technical Report INT-287. 128p.

Brown, J. K., and D. G. Simmerman. 1986. Appraising fuels and flammability in western aspen: a prescribed fire guide. USDA Forest Services, Intermountain Research Station, Ogden, Utah. General Technical Report INT-205. 48p.

Brown, J. K., and J. K. Smith. 2000. Wildland fire in ecosystems -- effects of fire on flora. USDA Forest Service Rocky Mountain Research Station. RMRS-GTR-42-Vol. 2.

Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology **14**:513-532.

Busso, C. A., R. M. Boo, and D. V. Pelaez. 1993. Fire effects on bud viability and growth of *Stipa tenuis* in semiarid Argentina. Annals of Botany **71**:377-381.

Chen, M. Y., and L. M. Liang. 2000. The natural regeneration of *Pinus taiwanensis* and *Pinus morrisonicola* following disturbances in Guandaushi forest ecosystem. Quarterly Journal of Forest Research of Taiwan **22**:13-22.

Cirne, P., and F. R. Scarano. 2001. Resprouting and growth dynamics after fire of the clonal shrub *Andira legalis* (*Leguminosae*) in a sandy coastal plain in south-eastern Brazil. Journal of Ecology **89**:351-357.

Colorado State Forest Service. 2000. The upper South Platte Watershed protection and restoration project. *in*. Colorado State Forest Service - Colorado State University World Wide Web: http://www.colostate.edu/Depts/CSFS/platte/southplatte.html.

Cruz, A., B. Perez, and J. M. Moreno. 2003. Plant stored reserves do not drive resprouting of the lignotuberous shrub *Erica australis*. New Phytologist **157**:251-261.

Davis, J. N. 1990. General ecology, wildlife use, and management of the mountain mahoganies in the Intermountain West. Pages 1-13. *in* K. L. Johnson, editor. Proceedings of the Fifth Utah Shrub Ecology Workshop: The Genus *Cercocarpus*, Utah State University, Logan, Utah.

de Rouw, A. 1993. Regeneration by sprouting in slash and burn rice cultivation, Taï rain forest, Côte d'Ivoire. Journal of Tropical Ecology **9**:387-408.

Ehle, D. S., and W. L. Baker. 2003. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. Ecological Monographs **73**:543-566.

Espelta, J. M., J. Retana, and A. Habrouk. 2003. Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. Forest Ecology and Management **179**:401-414.

Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in North Florida longleaf pine savannas. Ecological Monographs **65**:441-476.

Goto, Y., T. Yoshitake, M. Okano, and K. Shimada. 1996. Seedling regeneration and vegetative resprouting after fires in *Pinus densiflora* forests. Vegetatio **122**:157-165.

Graham, R. T., editor. 2003. Hayman fire case study. USDA Forest Service Rocky Mountain Research Station. RMRS-GTR-114.

Greenland, D., J. Burbank, J. Key, L. Klinger, J. Moorhouse, S. Oaks, and D. Shankman. 1985. The bioclimates of the Colorado Front Range. Mountain Research and Development **5**:251-262.

Greenwood, L. R., and J. D. Brotherson. 1978. Ecological relationships between pinyon-juniper and true mountain mahogany stands in Uintah Basin, Utah. Journal of Range Management **31**:164-167.

Hodgkinson, K. C. 1998. Sprouting success of shrubs after fire: height dependent relationships for different strategies. Oecologia **115**:64-72.

Hoffman, G. R., and R. R. Alexander. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. USDA Forest Service Research Paper RM-276. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Fort Collins, Colorado.

Huckaby, L. S., M. R. Kaufmann, J. M. Stoker, and P. J. Fornwalt. 2001. Landscape patterns of montane forest age structure relative to fire history at Cheesman in the Colorado Front Range. USDA Forest Service Rocky Mountain Forest and Range Experiment Station. RMRS-P-22:19-27.

Huddle, J. A., and S. G. Pallardy. 1996. Effects of soil and stem base heating on survival, resprouting and gas exchange of *Acer* and *Quercus* seedlings. Tree Physiology **16**:583-589.

Jain, T. B., and R. T. Graham. 2003. Fire severity classification: uses and abuses. *in* 5th Symposium on Fire and Forest Meteorology Joint With 2nd International Wildland Fire Ecology and Fire Management Congress, Orlando, Florida.

Johansen, D. A. 1940. Plant microtechnique, 1st edition. McGraw Hill Inc, New York.

Kabeya, D., A. Sakai, K. Matsui, and S. Sakai. 2003. Resprouting ability of *Quercus crispula* seedlings depends on the vegetation cover of their microhabitats. Journal of Plant Research **116**:207-216.

Kauffman, J. B. 1991. Survival by sprouting following fire in tropical forests of the eastern Amazon. Biotropica **23**:219-224.

Kauffman, J. B., and R. E. Martin. 1990. Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra-Nevada mixed conifer ecosystems. Forest Science **36**:748-764.

Kaufmann, M. R., P. J. Fornwalt, L. S. Huckaby, and J. M. Stoker. 2001. Cheesman Lake - a historical Ponderosa pine landscape guiding restoration in the South Platte Watershed of the Colorado Front Range. USDA Forest Service. RMRS-P-22:9-18.

Kaufmann, M. R., L. Huckaby, and P. Gleason. 2000a. Ponderosa pine in the Colorado Front Range: long historical fire and tree recruitment intervals and a case for landscape heterogeneity. Pages 153-160 *in* Joint Fire Science Conference and Workshop, Boise, Idaho.

Kaufmann, M. R., C. M. Regan, and P. M. Brown. 2000b. Heterogeneity in Ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. Canadian Journal of Forest Research **30**:698-711.

Kruse, R., E. Bend, and P. Bierzychudek. 2004. Native plant regeneration and introduction of non-natives following post-fire rehabilitation with straw mulch and barley seeding. Forest Ecology and Management **196**:299-310.

Malanson, G. P., and L. Trabaud. 1988. Vigor of post-fire resprouting by *Quercus Coccifera* L. Journal of Ecology **76**:351-365.

Matlack, G. R., D. J. Gibson, and R. E. Good. 1993. Regeneration of the shrub *Gaylussacia baccata* and associated species after low-intensity fire in an Atlantic coastal plain forest. American Journal of Botany **80**:119-126.

Medin, D. E. 1960. Physical site factors influencing annual production of true mountain mahogany, *Cercocarpus montanus*. Ecology **41**:454-460.

Menges, E. S., and C. V. Hawkes. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications **8**:935-946.

Menges, E. S., and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. Bulletin of the Torrey Botanical Club **122**:282-297.

Miller, M. 1976. Shrub sprouting response to fire in a Douglas-fir/western larch ecosystem. M.S. Thesis. University of Montana, Missoula, Montana.

Moore, R. 1992. Soil survey of Pike National Forest, Eastern Part, Colorado, parts of Douglas, El Paso, Jefferson, and Teller counties. 0102-B-06, USDA Forest Service and Soil Conservation Service; in cooperation with Colorado Agricultural Experiment Station, Washington, D.C.

Moreno, J. M., and W. C. Oechel. 1991. Fire intensity and herbivory effects on postfire resprouting of *Adenostoma fasciculatum* in southern California chaparral. Oecologia **85**:429-433.

National Wildfire Coordinating Group. 1994. Fire effects guide. USDA, Forest Service Publication. FFES #2394, National Interagency Fire Center, Boise, Idaho.

Neeman, G., H. Lahav, and I. Izhaki. 1992. Spatial pattern of seedlings 1 year after fire in a mediterranean pine forest. Oecologia **91**:365-370.

Olson, M. S., and W. J. Platt. 1995. Effects of habitat and growing-season fires on resprouting of shrubs in longleaf pine savannas. Vegetatio **119**:101-118.

Omi, P. N., E. Martinson, M. Kalkhan, and G. Chong. 2000. Spatial interactions among fuels, wildfire, and invasive plants. Joint Fire Science Program Project Proposal.

Ott, L., and M. Longnecker. 2001. An introduction to statistical methods and data analysis, 5th edition. Duxbury, Pacific Grove, California.

Pase, C. P., and A. W. Lindenmuth, Jr. 1971. Effects of prescribed fire on vegetation and sediment in oak-mountain mahogany chaparral. Journal of Forestry **69**:800-805.

Pelaez, D. V., R. M. Boo, O. R. Elia, and M. D. Mayor. 1997. Effect of fire intensity on bud viability of three grass species native to central semi-arid Argentina. Journal of Arid Environments **37**:309-317.

Pyne, S. J. 1984. Introduction to wildland fire: Fire management in the United States. John Wiley & Sons Inc, New York.

Radloff, D. L. 1983. Wildland classification with multivariate analysis and remote sensing techniques. Ph.D. dissertation. Colorado State University, Fort Collins, Colorado.

Ralphs, M. H., D. C. Schen, and F. Busby. 1975. Prescribed burning -- effective control of sagebrush and open juniper. Utah Science **36**:94-98.

Sakai, A., S. Sakai, and F. Akiyama. 1997. Do sprouting tree species on erosion-prone sites carry large reserves of resources? Annals of Botany **79**:625-630.

Scheiner, S. M., and J. Gurevitch, editors. 2001. Design and analysis of ecological experiments, 2nd edition. Oxford University Press, New York.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across rocky mountain forests. Bioscience **54**:661-676.

Shepherd, H. R. 1971. Effects of clipping on key browse species in southwestern Colorado. Colorado Division of Game, Fish and Parks Technical Publication Number 28.

Smith, D. 1981. Removing and analyzing total nonstructural carbohydrates from plant tissue. College of Agricultural and Life Sciences, University of Wisconsin, Madison, Wisconsin.

Smith, D., G. M. Paulsen, and C. A. Raguse. 1964. Extraction of total available carbohydrates from grass and legume tissue. Plant Physiology **39**:960-962.

Stanton, F. 1974. Wildlife guidelines for range fire rehabilitation. U.S. Department of the Interior, Bureau of Land Management, Denver, Colorado. Technical Note 6712. 90p.

Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio **117**:113-121.

Stutz, H. C. 1990. Taxonomy and evolution of *Cercocarpus* in the western United States. Pages 15-26. *in* K. L. Johnson, editor. Proceedings of the Fifth Utah Shrub Ecology Workshop: The Genus *Cercocarpus*, Utah State University, Logan, Utah.

Trlica, M. J. 1977. Distribution and utilization of carbohydrate reserves in range plants. Pages 73-96 *in* R. E. Sosebee and others, editors. Rangeland plant physiology. Society for Range Management, Denver, Colorado.

Turley, D., B. A. Roundy, and S. C. Walker. 1999. Twig demography of true mountain mahogany (*Cercocarpus montanus* Scop.). Pages 168-170. *in* E. D. McArthur, W. K. Ostler, and C. L. Wambolt, editors. Proceedings: Shrubland Ecotones. USDA Forest Service, Ephraim, Utah.

USDA Forest Service. 2001. Fire effects information system. *in* Rocky Mountain Research Station World Wide Web: http://www.fs.fed.us/database/feis/.

Verdaguer, D., and F. Ojeda. 2002. Root starch storage and allocation patterns in seeder and resprouter seedlings of two cape *Erica* (*Ericaceae*) species. American Journal of Botany **89**:1189-1196.

Vila, M., and J. Terradas. 1995. Effects of competition and disturbance on the resprouting performance of the Mediterranean shrub *Erica Multiflora* L. (*Ericaceae*). American Journal of Botany **82**:1241-1248.

Waugh, W. J. 1990. Stagnation and decadence of C*ercocarpus montanus* in a southeastern Wyoming big game exclosure. Pages 89-96. *in* K. L. Johnson, editor. Proceedings of the Fifth Utah Shrub Ecology Workshop: the genus *Cercocarpus*, Utah State University, Logan, Utah.

Young, D. L. 1973. First-year effects of fire, clipping, and herbicide on the quantity and quality of current annual growth of two species of shrubs. M.S. Thesis. Colorado State University, Fort Collins, Colorado.

Young, D. L., and J. A. Bailey. 1975. Effects of fire and mechanical treatment on *Cercocarpus montanus* and *Ribes cereum*. Journal of Range Management **28**:495-497.

Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events - the effect of a short interval between fires in California chaparral and coastal scrub. Ecology **64**:809-818.

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Treatment effects on true mountain-mahogany post-fire sprouting in Colorado Front Range ponderosa pine forests

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Abstract

Pre-fire fuel reduction treatments and post-fire rehabilitation treatments usually change abiotic and biotic environments in the burned area, including the growing conditions for understory shrub species in forests. Pre-fire fuel treatments usually reduce flammable fuels, and post-fire rehabilitation may create the opportunity for exotic plant invasion or seeded grass growth, with unknown impacts on understory shrub species. We examined the influences of prescribed burns, thinnings, and seeding on true mountain-mahogany (*Cercocarpus montanus* Raf.) sprouting behavior following the 2002 Hayman Fire, Colorado. We hypothesized that pre-fire fuel treatments and post-fire rehabilitation treatments do not influence true mountain-mahogany sprout length and number at the early vegetation recovery stage after fire. Results from the Hayman Fire showed that the basal sprout number was larger in treated areas (grouped pre- and post-fire treatments) than in untreated areas one year after fire. Conversely, the epicormic sprout number was higher in untreated areas than in treated areas. Moreover, basal sprout lengths were higher in pre-fire treated areas than in post-fire treated areas in the year of fire. However, results also indicated that basal sprout number was not significantly different between pre-fire treatments and post-fire treatments, while pre-fire treatments seemed to lessen true mountain-mahogany epicormic sprouting. We found that there were no typical sprouting response patterns to treatments. We also found that treatments and fire severity (measured at landscape- and individual shrub-scales) interacted significantly in true mountain-mahogany sprouting responses following fire. Our study implied that in a mixed-severity fire regime, such as the ponderosa pine forests in the Colorado Front Range, potential effects of management treatments may be more complicated and less predictable insofar as impacts on understory shrubs. Further study is required into the role of shrub understories in contributing to the flammability and post-fire recovery of mixed severity fire regimes.