DISSERTATION

DISTURBANCE IMPACTS ON UNDERSTORY PLANT COMMUNITIES OF THE COLORADO FRONT RANGE

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY PAULA J. FORNWALT ENTITLED DISTURBANCE IMPACTS ON UNDERSTORY PLANT COMMUNITIES OF THE COLORADO FRONT RANGE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

DISTURBANCE IMPACTS ON UNDERSTORY PLANT COMMUNITIES OF THE COLORADO FRONT RANGE

Pinus ponderosa – Pseudotsuga menziesii (ponderosa pine – Douglas-fir) forests of the Colorado Front Range have experienced a range of disturbances since they were settled by European-Americans approximately 150 years ago, including settlement-era logging and domestic grazing, and more recently, wildfire. In this dissertation, I explored the impacts of these disturbances on understory plant communities.

I investigated the long-term effects of settlement-era logging and grazing on forest understories by comparing understory composition at a historically logged and grazed site to that of a site that was protected from past use. I found little to no evidence of long-term logging and grazing impacts on understory richness, cover, and composition in upland forests. Long-term changes in richness, cover, and composition due to past logging and grazing were somewhat apparent in riparian forests, however, where these activities were likely the most intense.

I analyzed data collected before (1997) and after (2003 - 2007) the 2002 Hayman Fire to examine wildfire effects on understory communities. Some declines in species richness and cover were observed immediately following fire, but by 2007, richness and

cover often exceeded prefire conditions, even in severely burned areas. Fire-induced changes in community composition were apparent in all postfire years; regardless of fire severity, these changes were primarily due to new species recruitment, particularly short-lived native forbs, rather than due to a loss of prefire species. While exotic richness and cover generally increased as fire severity and time since fire increased, they remained low at the end of the study, and have not yet interfered with the recovery of the native understory community.

I conducted a literature review to examine the mechanisms through which Front Range understory species establish after fire *(i.e.*, by sprouting, establishing from soil-stored seed, and/or establishing from offsite seed). I found that postfire establishment mechanisms for many species are poorly understood, although some broad patterns did emerge. Short-lived forbs appear to establish postfire primarily through soil-stored seed, while sprouting is the most common postfire establishment mechanism for long-lived forbs, graminoids, and woody plants. Many species have multiple postfire establishment mechanisms, which helps to ensure their continued presence after fire.

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CHAPTER 1: INTRODUCTION

Pinus ponderosa – Pseudotsuga menziesii (ponderosa pine – Douglas-fir) forests of the Colorado Front Range have a long history of disturbance. Indeed, these forests have been repeatedly disturbed by fire for at least a thousand years (Brown 1999; Ehle and Baker 2003; Laurie Huckaby unpublished data). Other disturbances, such as insects, diseases, and wildlife grazing, are also a part of the region's historical disturbance regime (Veblen and Donnegan 2005).

A novel set of disturbances was brought to these forests by European-American settlers in the mid to late 1800s. Unregulated logging was widespread, and in many places, nearly all merchantable timber was removed (Jack 1900; Veblen and Donnegan 2005). Unregulated grazing by domestic cattle also occurred throughout the Front Range, and severe overgrazing was common, particularly in riparian areas (Gary and Currie 1977; Jack 1900; Veblen and Donnegan 2005). Unregulated logging and grazing ceased in the early 1900s when much of the *P. ponderosa – P. menziesii* forest in the Front Range was transferred to the United States Forest Service, and only a limited amount of regulated logging and grazing has occurred since.

Fire suppression also began shortly after European-American settlement, and continues today (Brown *et al*. 1999; Goldblum and Veblen 1992; Veblen and Donnegan 2005; Veblen *et al*. 2000). However, in recent years there has been a dramatic increase in

the area of *P. ponderosa – P. menziesii* forest burned by wildfire, despite considerable fire suppression efforts (McHugh and Gleason 2003; Anonymous 2000, 2002). In the last decade alone, more than 70,000 ha of montane Front Range forest have been burned by large (> 1000 ha) wildfires; the largest of these fires, the 2002 Hayman Fire, burned across 55,800 ha (Graham 2003).

In my dissertation, I explore how settlement-era logging and grazing, and the 2002 Hayman Fire, have impacted understory plant communities in Front Range *P. ponderosa – P. menziesii* forests.

In **Chapter 2**, I investigate the long-term impacts of settlement-era logging and grazing by comparing understory richness, cover, and composition within a logged and grazed *P. ponderosa – P. menziesii* forest to that of an environmentally similar area that was protected from past land use. Because grazing, and possibly logging, were often more intense in riparian areas than in uplands (Jack 1900; Veblen and Donnegan 2005), I also compared the two study areas separately by topographic category (north, south, and east/west slopes, ridgetops, and riparian areas). Field sampling for this study was conducted in 1997.

In June 2002, the Hayman Fire burned with mixed severity across the study areas described above. To complete the work presented in the next three chapters, I remeasured the understory community in the logged and grazed study area annually from 2003 to 2007 (the protected study area was intensively rehabilitated and salvage logged after the fire, and consequently was not remeasured). In **Chapter 3**, I explore the role of prefire community composition, fire severity, and time since fire in shaping postfire understory community development. Because fire is well-known for its ability to

promote exotic establishment and spread (Zouhar *et al.* 2008), in **Chapter 4** I focus my attention specifically on how fire severity and time since fire influenced the postfire response of exotic species. In **Chapter 5**, I review the published literature to examine the mechanisms through which each of the understory plant species identified in the pre- and post- Hayman Fire surveys are known to establish after fire.

I summarize my dissertation findings in **Chapter 6**, and discuss how my results provide a context for interpreting the role of disturbance in shaping *P. ponderosa – P. menziesii* understory plant communities of the Colorado Front Range.

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CHAPTER 2: EFFECTS OF PAST LOGGING AND GRAZING ON UNDERSTORY PLANT COMMUNITIES IN A *PINUS PONDEROSA – PSEUDOTSUGA MENZIESII* FOREST, COLORADO

ABSTRACT

Throughout *Pinus ponderosa – Pseudotsuga menziesii* (ponderosa pine – Douglas-fir) forests of the Colorado Front Range, intense logging and domestic grazing began at the time of European-American settlement in the mid to late 1800s and continued until the early 1900s. I investigated the long-term impacts of these settlement-era activities on understory plant communities by comparing understory composition at a historically logged and grazed site to that of an environmentally similar site that was protected from past use. I found that short-lived forb, long-lived forb, graminoid, and woody plant richness and cover rarely differed between sites in either upland or riparian areas. Multivariate analyses revealed little difference in species composition between sites on uplands, although compositional differences were apparent in riparian zones. My findings suggest that settlement-era logging and grazing have had little to no long-term impact on understories of upland Front Range *P. ponderosa – P. menziesii* forests, although they have had some long-term influence on riparian understories, where these activities were likely the most intense.

INTRODUCTION

Human activities have impacted nearly all of the world's ecosystems, and often these activities have adversely affected critical ecosystem components and processes (Vitousek *et al.* 1997). Throughout *Pinus ponderosa* (ponderosa pine) – dominated forests of the Rocky Mountains, intense land use including logging, domestic grazing, and fire suppression began at the time of European-American settlement in the 1800s (Cooper 1960; Dillon *et al.* 2005; Veblen and Donnegan 2005). Researchers have recently begun to investigate how this past land use has altered forest overstories from the pre-settlement condition by examining early photographs, written descriptions, and scientific studies, and also by reconstructing historical stand conditions from living and remnant woody material (*e.g.*, Brown and Cook 2006; Fulé *et al.* 1997; Kaufmann *et al.* 2001). Their findings suggest that past logging, grazing, and fire suppression have generally homogenized forest structure and increased stand density by removing the largest and oldest trees, encouraging tree establishment and growth, and decreasing tree mortality due to fire.

Past land use can also cause long-term departures from the pre-settlement condition in forest understories, although these changes are more difficult to assess because detailed information about the pre-settlement understory condition is often unavailable. Settlement-era photographs seldom focused on understory vegetation. Early reports and scientific papers describing the understory often list common species (*e.g.*, Cooper 1960; Leiberg 1904; Schneider 1911), but they rarely contain quantitative information. Annual growth rings and other 'natural records' are of limited use for reconstructing historical forest understories because most species are herbaceous and

decompose quickly (Swetnam *et al.* 1999). Any preserved plant material that may remain on site (*e.g.*, in soils, lake sediments, or packrat middens) is generally of limited spatial, temporal, and/or botanical resolution (but see Anderson *et al*. 2000 and citations therein; Kerns *et al*. 2003). Alternative approaches are therefore needed to provide detailed information about historical forest understories.

Areas that have been minimally disturbed by human activities can provide insight into the pre-settlement understory condition, and this approach has been implemented in several *P. ponderosa* – dominated ecosystems. In Utah, Madany and West (1983) compared an ungrazed relict site to a site that was grazed by livestock from the late 19th to the early 20th century, and found that past grazing had reduced herbaceous plant cover and increased the cover of woody species over the long-term. Gildar *et al.* (2004) compared the understory community of an Arizona site with 120 years of fire suppression to other sites where the historic fire regime has remained relatively intact, and found that plant community structure was related to fire history, but within-site variability was also an important driver. Similarly, Keeling *et al.* (2006) found evidence that fire suppression has altered *P. ponderosa – Pseudotsuga menziesii* (Douglas-fir) understories of Idaho and Montana to some degree, although environmental variability was a stronger force in shaping the understory community.

In montane forests of the Colorado Front Range, heavy settlement-era logging and domestic grazing began in the mid to late 1800s and continued until the early 1900s (Jack 1900; Veblen and Donnegan 2005). My objective was to investigate the long-term impacts of these activities by comparing the understory community within a logged and grazed *P. ponderosa – P. menziesii* forest to that of an environmentally similar site that

was protected from past land use. Fire suppression has occurred in both study sites since European-American settlement, so its effects cannot be discerned here. Because logging and grazing were often more intense in riparian areas than on upland slopes (Jack 1900; Veblen and Donnegan 2005), and because large within-site variability may mask more subtle effects of past land use (*e.g.*, Gildar *et al.* 2004), I also compared the two sites separately for each of five topographic categories (north, south, and east/west slopes; ridgetops; and riparian areas).

METHODS

Study area

This study was conducted in the southern Front Range of Colorado, approximately 60 km southwest of Denver (Figure 2.1). Forests here are dominated by *P. ponderosa* and *P. menziesii*, with *Juniperus scopulorum* (Rocky Mountain juniper), *Picea pungens* (blue spruce), and *Populus tremuloides* (quaking aspen) occurring intermittently. Precipitation averages 40 cm annually, most of which falls during the spring and summer (http://www.wrcc.dri.edu). January is the coldest month, with average highs of 7.3°C and average lows of -13.0°C; the warmest temperatures occur in July, when maximum daytime temperatures average 28.9°C (http://www.wrcc.dri.edu). Soils on upland slopes and ridgetops are gravelly coarse sandy loams derived from weathered Pike's Peak granite (USDA Forest Service 1992). In drainage bottoms, soils are also of granitic origin but are generally finer and more developed. Elevations range from 2100 to 2500 m in the areas sampled.

This area has experienced a considerable amount of human activity since it was settled by European-Americans in the mid to late 1800s, with the heaviest use coming from settlement-era loggers and ranchers. Widespread, unregulated logging occurred from the 1880s to the 1900s when several local lumber mills were established, and nearly all merchantable timber was removed (Figure 2.2; DeLay 1989; Jack 1900). Unregulated grazing by domestic cattle also occurred from the 1880s to the 1900s, and many areas were severely overgrazed (DeLay 1989; Gary and Currie 1977; Jack 1900). Unregulated logging and grazing largely ended in 1906 when the Pike National Forest was established, and only a limited amount of logging and grazing has occurred since. Prospectors flooded the area in the early 1890s when rumors of gold discovery first surfaced, but precious metals were never found and mining activity ceased within the decade (DeLay 1989). In the 1930s, the Civilian Conservation Corps planted *P. ponderosa* trees in select locations to help reforest heavily logged and grazed areas (DeLay 1989; Gary and Currie 1977). Since the 1930s, the region has been used mainly for recreation, and trails and campgrounds are abundant.

Study sites

Two adjacent ~30 km^2 study sites were established by Kaufmann *et al*. (2000), each with markedly different land use histories since European-American settlement (Figure 2.1). The 'managed' study site is located on the Pike National Forest, and land use history within the site is representative of the area. Historical records and tree-ring data indicate that the managed site was intensively logged in the mid-1890s, but it does not appear to have been logged since (DeLay 1989; Jack 1900; Laurie Huckaby unpublished data). Although there is not any direct evidence of grazing at the site,

records indicate that several families homesteaded ranches in the immediate vicinity during the settlement era (DeLay 1989; Riddle and Kane 1991), and it is likely that the timing and intensity of domestic grazing here coincided with that of the region. Grazing has not occurred here since the Pike National Forest was established (Sheila Lamb, South Park Ranger District, personal communication). Prospecting activities were limited to a handful of small isolated test pits that were dug during the mining era (Riddle and Kane 1991). There are no records of tree planting near the site and tree ages do not correspond with known planting periods (Kaufmann *et al.* 2000; Laurie Huckaby unpublished data). The site has been lightly used for recreation for several decades. A four-wheel-drive road runs near the site's southern edge and through its southwest corner. There are no designated trails within the site, although it does contain closed logging roads that are open to non-motorized recreation. A campground and a popular rock climbing area are less than a kilometer away.

The 'protected' study site is located in the forest surrounding Cheesman Lake, a reservoir on the South Platte River. The reservoir and the surrounding forest have been owned and managed by the Denver Water Board since 1894, and have been only minimally impacted by human activities. Prior to the 1894, the site likely received only limited use from loggers, ranchers or prospectors due to poor access (Riddle and Kane 1991). Some logging occurred during dam construction from 1894 to 1905, but was mostly below the current water line of the reservoir. Coincident with dam construction, a six-string fence was constructed around the property to exclude trespassing from loggers, prospectors, and domestic livestock. Cheesman Lake and the surrounding property have

been closed to public recreation since 1905, except for shoreline fishing and limited hiking. There is no record of tree planting on the property.

All wildfires within the two sites have been suppressed since the early 1900s. Fire scars indicate that a handful of 20th century wildfires burned in some plots (Brown *et al.* 1999), but were extinguished before they spread over more than a few hectares. However the 2002 Hayman Fire, which occurred after this study was completed, burned 55,800 ha including the study sites. Portions of the managed site experienced light prescribed burning in 1987 and 1990.

Thirty plots were established at both the protected and managed sites (Figure 2.1). To minimize environmental differences between sites, twenty-five plots at each site were located within an intensively sampled 4-km^2 (2 km x 2 km) area. The 4-km^2 areas are similar in elevation, topography and soils, and are separated by a distance of only 1 km. Plots within the 4-km^2 areas were randomly located and equally distributed among five topographic categories: north-facing slopes, east-or-west-facing slopes, south-facing slopes, ridgetops, and riparian areas. Five additional plots per site were also randomly established across the larger protected and managed landscapes, with one plot per topographic category. All plots were located in forested areas. North, east/west, and south plots were situated in upland areas with slopes between 15 and 35%; the long axis of the plot was aligned down the fall line. Ridgetop plots were also in upland areas (slope < 10%), with the long axis parallel to the ridge. Riparian plots were located above the banks of permanent streams, but could cross intermittent streams; plot aspect could vary, but slope had to be < 15%. The long axis of riparian plots was parallel to the

stream channel. Kaufmann *et al.* (2000) provide additional information about the study site selection process and plot establishment protocols.

Data collection

Field data were collected during June 1996 and June - July 1997. Although year-to-year variation in understory communities may occur due to differences in precipitation, monthly growing season (April - July) precipitation at Cheesman Lake did not differ between 1996 and 1997 (http://www.wrcc.dri.edu). Moreover, the variable 'year of sampling' was poorly correlated with understory composition in the ordination (results not shown).

Understory data were collected in each plot using the modified-Whittaker sampling design (Stohlgren *et al.* 1995). In this design, the main plot is 1000 m^2, and contains one 100-m^2 subplot, two 10-m^2 subplots, and ten 1-m^2 subplots nested within it. Vegetative cover for each species was ocularly estimated in the 1-m^2 subplots. Tree species were included only if they were less than breast height (1.37 m) tall. Species presence was recorded within the 10-m^2 subplots, the 100-m^2 subplot, and the 1000-m^2 plot. An average of 5% of the species in each plot could be identified only to genus, and another 4% could not be identified at all. All generic identifications were included in analyses, while unidentified specimens were excluded. I determined the growth form (forb, graminoid, shrub, tree) and lifespan (short-lived or long-lived) of each species using the USDA Plants Database (2007), local botanical keys, and my knowledge of the species. Short-lived species included annuals and biennials, as well as species considered to be biennial/perennial and annual/biennial/perennial. Only true perennials were considered long-lived. I then integrated growth form and lifespan information for each

species by further classifying it into one of four functional groups: short-lived forbs, long-lived forbs, graminoids, and woody plants. Short-lived graminoids were scarce and were not separated into their own category. Nomenclature follows the USDA Plants Database (2007), although varieties and subspecies were not distinguished.

Environmental attribute data were collected for each plot (Table 2.1). These attributes can be broadly grouped as describing a plot's (1) disturbance history; (2) topography; (3) distance to roads and streams; (4) overstory structure; (5) forest floor; and (6) sampling year. Three of the disturbance history variables, the age of the oldest tree, the year of the last fire, and the year of the last stand-replacing fire, were determined from tree age and fire scar data collected by Brown (1999) and Kaufmann *et al.* (2000). A fourth disturbance variable, land use history, indicated whether the plot was in the protected or managed site. Topographic variables included slope, elevation, and topographic category. Distance to the nearest stream and road (including former logging roads) was calculated from plot coordinates and GIS coverages obtained from the Pike National Forest. The overstory variables basal area and trees per hectare were calculated from diameter at breast height data collected for all live trees in a plot; only trees over 1.4 m tall were included in the calculation. Forest floor variables included the cover of duff, lichen, litter, moss, rock, soil, and wood, which were measured in the 1-m^2 subplots and averaged. Sampling year was 1996 or 1997.

Univariate analyses

I used univariate multi-response permutation procedures (MRPP) to test for differences in functional group richness and cover between sites. MRPP is a nonparametric procedure for detecting differences among two or more groups that is not

limited by assumptions of normally-distributed data or of homogeneous variances (McCune and Grace 2002; Mielke and Berry 2001). Richness within each functional group was calculated by tallying the number of short-lived forb, long-lived forb, graminoid, and woody species per 1000-m^2 plot. I calculated cover variables by averaging cover estimates for each species across the 1-m^2 subplots, then summing across a plot by functional group. I tested for functional group differences between sites overall using an α of 0.05. I also tested for differences between sites by topographic category; each of these tests was evaluated with a Bonferoni-adjusted α of 0.01 to maintain type I error (overall α of 0.05 divided by five topographic categories). I performed the analyses in Microsoft Excel using the procedure outlined in Mielke and Berry (2001) because univariate MRPP analyses cannot be easily conducted with most statistical packages.

Multivariate analyses

All multivariate analyses were conducted with PC-ORD version 5.0 (MjM Software Design, Glendon Beach, Oregon, USA) using the cover data for each species (averaged across the 1-m^2 subplots). I omitted all species whose cover was only measured in one or two plots following the recommendations of McCune and Grace (2002).

I conducted multivariate MRPP analyses using the Sørensen distance measure to test for differences in community composition between sites (McCune and Grace 2002). As with the univariate MRPP analyses, I tested for overall differences between sites (α = 0.05), and also for differences between sites for each of the topographic categories (α = 0.01).

I ordinated the understory cover dataset using non-metric multi-dimensional scaling (NMS) to investigate relationships between community composition and the measured environmental factors. All ordination runs used the Sørensen distance measure to calculate the distance matrix, a maximum of 500 iterations per run, and a stability criterion of 0.00001. I first assessed the dimensionality of the data set by running 250 preliminary ordinations with up to six axes and random starting configurations. I concluded that a three-dimensional solution was optimal because additional axes provided only slight reductions in stress, a measure of 'badness-of-fit'; results of a Monte Carlo test with 250 randomizations indicated that stress for this solution was lower than expected by chance ($p = 0.004$). I then ran a final three-dimensional ordination using the best final configuration from the preliminary three-dimensional runs as the starting configuration.

Correlation coefficients between each environmental variable and the three NMS axes were calculated, and environmental variables that were correlated with one or more axes ($|r| \geq 0.4$) were overlaid on the ordination as vectors. The angle and length of the vector denotes the direction and strength of the relationship. If an NMS axis was correlated with multiple environmental variables, interrelationships among the axis scores and the environmental variables were further explored with multiple regression in SAS 9.1 (SAS Institute Inc., Cary, North Carolina, USA). Nonsignificant variables were iteratively excluded from the regression until only significant ($p < 0.05$) variables remained. The categorical variables land use history and topographic category were treated as ranked quantitative variables for these procedures. For land use history, I assigned a value of 1 to the protected plots and 2 to the managed plots. Topographic

categories were assigned a value from 1 to 5 based on my *a priori* perception of water availability; riparian plots were assigned a value of 1 (most mesic), north plots a 2, east/west plots a 3, south plots a 4, and ridgetop plots a 5 (most xeric).

When multivariate MRPP indicated significant differences in community composition between sites, I conducted indicator species analyses (ISA) to determine if any species were representative of a particular site (McCune and Grace 2002). This analysis combines information about the frequency and abundance of a species in a group of plots relative to other groups to generate an indicator value (IV) for the species in each group. An IV of 0 denotes that the species is not present within a group while an IV of 100 denotes that the species is both exclusive to and always present in a group. For all analyses, I tested the significance of each IV using a Monte Carlo simulation with 5000 randomizations. A species was a significant indicator if $IV \geq 25$ and $p < 0.05$.

RESULTS

I identified 237 species within the 60 plots, with 152 species present in both sites. Thirty-two of the species were short-lived forbs, 119 were long-lived forbs, 44 were graminoids, and 33 were woody plants. Nine species were identified to genus only and could not be classified into functional groups due to variability within the genus. Dominant understory species included *Artemisia ludoviciana* (white sagebrush), *Geranium caespitosum* (pineywoods geranium), *Mertensia lanceolata* (prairie bluebells), and *Muhlenbergia montana* (mountain muhly); these species were found on 90% or more of the plots at both sites. Only a handful of exotic species were found, the most frequent

of which were *Taraxacum officinale* (common dandelion) and *Verbascum thapsus* (common mullein). A detailed analysis of exotics is reported in Fornwalt *et al.* (2003).

Univariate analyses

Few differences in functional group richness or cover were found between the two sites. Overall, the protected site had greater woody plant richness and cover than the managed site, although the two sites did not differ overall in the richness or cover of short-lived forbs, long-lived forbs, or graminoids (Table 2.2). When the two sites were compared by topographic categories, only woody cover differed, and this difference was limited to riparian areas (Table 2.2).

Multivariate analyses

Multivariate MRPP demonstrated that significant differences in species composition existed between the protected and managed sites overall ($p < 0.001$). However, analyses by individual topographic categories revealed that differences were restricted to riparian areas ($p = 0.004$); community composition did not differ between the protected and managed sites for any of the four upland categories (north: $p = 0.119$; east/west: $p = 0.133$; south: $p = 0.013$; ridgetop: $p = 0.225$).

The three-dimensional NMS ordination represented 79.1% of the total variation in the understory cover distance matrix, with axis one, two and three explaining 30.1%, 16.1%, and 32.8% of the variation, respectively (Figure 2.3; final stress = 15.77; instability < 0.00001). Protected plots separated from managed plots along axis one, with moderate overlap. Plots also separated along axis three by topographic category, with the riparian plots distributed in the top half of the ordination diagram and upland plots in the bottom half. Axis one was correlated with the environmental variables land

use history, elevation, trees per hectare, and tree basal area, while axis three was correlated with topographic category; axis two was not correlated with any environmental variables ($|r| \geq 0.4$; Figure 2.3; Table 2.3). When interrelationships between axis one and the four correlated environmental variables were further explored with multiple regression, land use history and trees per hectare were significant in the final model, but elevation and tree basal area were not ($p = 0.001$, $p < 0.001$, $p = 0.519$, and $p = 0.341$, respectively). Land use history and trees per hectare were correlated to each other to some degree ($r = 0.317$), although each was also correlated to axis one when the other was explicitly controlled for using partial correlations (land use: $r = 0.408$; trees per hectare: $r = 0.601$).

ISA identified three indicator species for the protected site and six for the managed site (Table 2.4); species indicative of the protected site included *Allium cernuum* (nodding onion), *Artemisia frigida* (prairie sagewort), and *Bouteloua gracilis* (blue grama), while species associated with the managed site included *Arctostaphylos uva-ursi* (kinnikinnick), *Carex rossii* (Ross' sedge), *Fragaria* spp. (strawberry), *Juniperus communis* (common juniper), and *Potentilla fissa* (bigflower cinquefoil). ISA for individual topographic categories was only conducted for riparian areas because multivariate MRPP indicated that composition was similar between sites for the four upland categories. Riparian areas in the protected site were identified by *Schizachyrium scoparium* (little bluestem; IV at protected site = 77; IV at managed site = 1; $p = 0.015$), while the managed site was identified by *Fragaria* spp. (IV at protected site = 2; IV at managed site = 94; $p = 0.005$).

DISCUSSION

Given this area's intensive settlement-era use, I expected to find that major differences in understory communities between protected and managed sites still persisted today. I did not. Rather, the overall comparisons between protected and managed sites provide only modest indications that heavy logging and grazing from the late 1800s to the early 1900s have caused long-term changes to forest understories — differences in functional group richness and cover between sites were few, and while multivariate MRPP and NMS ordination suggest that community composition differed somewhat between sites, the relatively short list of indicator species implies that the abundance of most species was similar (Figure 2.3; Tables 2.2, 2.4).

Although overall compositional differences between the protected and managed sites were not overwhelming, they nonetheless may be due to both direct and indirect impacts of past land use. For example, grazing often directly reduces the abundance of palatable species while allowing unpalatable species to increase (Smith 1967). The list of indicator species for the protected and managed sites is consistent with this finding. *Artemisia frigida* and *Bouteloua gracilis*, indicators of the protected site, are palatable to livestock but can decline under continuous heavy grazing, while indicators of the managed site, especially *Arctostaphylos uva-ursi* and *Juniperus communis*, are not typically grazed by cattle (Table 2.4; USDA Forest Service 2007). Logging and grazing can also encourage overstory tree regeneration and growth, and therefore they may indirectly alter understory composition over the long-term by favoring shade-tolerant species (Belsky and Blumenthal 1997 and citations therein; see Bakker and Moore 2007 for an exception). Indeed, the managed site tended to have greater overstory tree density

than the protected site (Figure 2.3; Table 2.1; Kaufmann *et al.* 2000); furthermore, the species indicative of the protected site are relatively shade-intolerant species that thrive in open Front Range forests, while some indicators of the managed site generally occur in shadier environments (Table 2.4; Powell 1987; USDA Forest Service 2007).

When I compared the protected and managed sites by topographic category, I found that the degree of understory community change due to past logging and grazing varied greatly with topography. I found little to no evidence of long-term logging and grazing impacts in upland areas; functional group richness and cover were similar between the protected and managed sites (Table 2.2), and differences in community composition between sites were not detected in the multivariate MRPP analyses. Impacts of past logging and grazing were somewhat more apparent in riparian areas (Figure 2.3; Table 2.2). Given the history of human use in Front Range riparian areas, it is not surprising that I found greater understory differences in these locations than in their upland counterparts. Throughout the Rocky Mountains, riparian areas were generally more heavily grazed by livestock than uplands (Belsky and Blumenthal 1997), and Jack (1900) and Gary and Currie (1977) both noted heavy grazing damage along streams only a few kilometers from my sites. Unfortunately, early written documents never indicate whether riparian zones were more thoroughly logged than upland slopes, although this is probable since they tend to support a greater number of large trees (Kaufmann *et al.* 2000). I do know that logs were not floated down streams and rivers near the sites, a practice that occurred elsewhere in the region (Delay 1989; Jack 1900). Early settlers also preferred riparian areas for setting up camps and homesteads; the remains of one such dwelling can be found in one of the managed riparian plots.

Taken as a whole, the results presented here suggest that Front Range understory communities were generally resilient to settlement-era logging and grazing impacts over the long-term. These results highlight the fact that many of the native understory species are tolerant of a range of disturbances and growing environments. Grazing is part of the Front Range's natural disturbance regime, although grazing by wildlife was probably never as intense as livestock grazing (Veblen and Donnegan 2005). The majority of species also exhibit regeneration strategies that promote survival or rapid re-establishment after disturbance, such as sprouting, seedbanking, and long-distance seed dispersal (Chapter 5). Finally, although many of the species prefer open, high-light environments, many of them can inhabit shady forests as well (USDA Forest Service 2007).

A weakness of my study is the fact that the study sites are unreplicated. Unfortunately, this was unavoidable because the area surrounding Cheesman Lake contained one of the only known *P. ponderosa – P. menziesii* forests in the Front Range that had not been subjected to logging and grazing, and even it was lost as a research resource in the 2002 Hayman Fire. Although the protected and managed sites do differ slightly in elevation, the elevational effect probably is minimal because the elevation ranges at the sites overlap substantially, and elevation was not significant in the regression analyses. Moreover, the two sites are adjacent to one another, separated only by a fence, and both are situated in the middle of the elevational range for the *P. ponderosa – P. menziesii* vegetation type. Despite this inescapable constraint on the study design, results lead me to conclude that settlement-era logging and grazing have had only modest influences on understories of Front Range *P. ponderosa – P. menziesii*

forests, and this influence is largely restricted to riparian areas. Additional site-specific comparisons of this kind are needed to determine how applicable my conclusions may be to other *P. ponderosa* – dominated landscapes in the Rocky Mountains.

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Table 2.1. Environmental attributes measured in protected and managed plots.

Variable	Protected	Managed
Disturbance variables		
Land use history	1	2
Year of last fire	1587-1963	1851-1990
Year of last stand-replacing fire	1531-1851	1723-1851
Year of oldest tree germination	1522-1887	1617-1883
Topographic variables		
Topographic category	1-5	1-5
Slope (%)	0-36	0-35
Elevation (m)	2098-2346	2242-2494
Distance variables		
Distance to nearest stream (m)	14-809	0-432
Distance to nearest road (m)	37-2169	0-1040
Overstory variables		
Trees per ha	91-1176	184-2621
Tree basal area (m^2 per ha)	4.6-28.2	10.4-40.6
Forest floor variables		
duff (%)	0-46	0-11
lichen (%)	0-15	0-8
litter (%)	20-92	32-76
moss (%)	0-9	0-26
rock (%)	0-32	0-18
soil (%)	1-75	4-48
wood (%)	0-11	0-19
Sampling variables		
Year measured	1996-1997	1996-1997

Table 2.2. Means and standard deviations for species richness and cover by functional groups. Differences in functional group richness and cover between the protected and managed sites are indicated in bold (for overall test, $\alpha = 0.05$; for topographic category tests, $\alpha = 0.01$ to adjust for multiple comparisons).

	Richness (1000 m^2)			Cover (%)		
	Protected	**Managed**	**p-value**	**Protected**	**Managed**	**p-value**
Short-lived forbs						
Overall	5.8 ± 0.6	5.0 ± 0.7	0.441	0.4 ± 0.1	0.5 ± 0.1	0.451
Riparian	9.0 ± 1.5	7.7 ± 1.9	0.494	1.2 ± 0.4	1.1 ± 0.3	0.844
North	3.0 ± 0.5	3.5 ± 0.9	0.610	0.0 ± 0.0	0.3 ± 0.1	0.080
East/West	6.5 ± 1.1	4.2 ± 1.5	0.281	0.2 ± 0.1	0.2 ± 0.1	0.896
South	4.8 ± 0.7	7.5 ± 0.9	0.061	0.2 ± 0.1	0.5 ± 0.2	0.093
Ridgetop	5.7 ± 1.2	2.3 ± 0.9	0.084	0.2 ± 0.1	0.3 ± 0.2	0.550
Long-lived forbs						
Overall	24.8 ± 1.3	26.2 ± 1.4	0.852	8.4 ± 1.3	8.2 ± 1.2	1.000
Riparian	34.0 ± 3.1	38.5 ± 3.1	0.268	17.0 ± 4.4	16.4 ± 3.7	0.844
North	25.5 ± 2.4	24.0 ± 1.9	0.896	7.6 ± 1.9	7.5 ± 2.1	1.000
East/West	23.3 ± 0.8	21.8 ± 1.8	0.191	6.2 ± 0.9	4.9 ± 1.3	0.429
South	17.7 ± 1.8	21.8 ± 1.4	0.188	3.7 ± 0.8	6.8 ± 1.4	0.132
Ridgetop	23.5 ± 1.5	24.8 ± 1.5	0.844	7.6 ± 0.9	5.6 ± 0.9	0.204
Graminoids						
Overall	9.3 ± 0.5	8.3 ± 0.6	0.188	7.9 ± 0.9	7.3 ± 1.1	0.727
Riparian	12.8 ± 1.6	13.0 ± 1.0	1.000	10.1 ± 3.0	10.3 ± 3.7	1.000
North	8.3 ± 1.1	6.8 ± 1.1	0.481	3.6 ± 0.5	4.9 ± 1.5	0.281
East/West	8.7 ± 0.5	6.3 ± 0.8	0.061	8.5 ± 1.1	6.5 ± 2.1	0.141
South	7.3 ± 0.6	7.3 ± 0.6	1.000	5.8 ± 1.4	5.4 ± 1.2	0.671
Ridgetop	9.5 ± 0.8	8.2 ± 0.4	0.307	11.5 ± 1.9	9.2 ± 2.5	0.351
Woody plants						
Overall	**7.2 ± 0.5**	**9.3 ± 0.8**	**0.015**	**6.9 ± 1.3**	**12.0 ± 1.5**	**0.010**
Riparian	10.3 ± 1.9	16.2 ± 1.7	0.041	**7.1 ± 2.8**	**22.4 ± 3.0**	**0.009**
North	7.8 ± 0.8	7.7 ± 0.7	1.000	12.8 ± 2.7	12.5 ± 3.8	0.671
East/West	6.0 ± 0.3	7.8 ± 0.8	0.041	4.7 ± 2.9	8.4 ± 1.9	0.169
South	5.5 ± 0.3	7.3 ± 1.0	0.091	1.5 ± 0.8	8.0 ± 2.7	0.018
Ridgetop	6.5 ± 0.6	7.7 ± 0.8	0.292	8.3 ± 2.9	8.7 ± 1.2	0.541

Table 2.3. Environmental variables and their correlation with the three NMS ordination axes. Only variables with $|r| \geq 0.4$ for one or more axes are shown (values are in bold).

	Correlation (r)		
Variable	**Axis 1**	**Axis 2**	**Axis 3**
Land use history	**0.500**	-0.097	0.010
Topographic category	-0.294	-0.328	**-0.510**
Elevation (m)	**0.466**	-0.364	-0.139
Trees per ha	**0.652**	0.037	0.290
Tree basal area (m^2 per ha)	**0.492**	-0.008	0.376

Table 2.4. Indicator species of protected and managed study sites. Only species with an indicator value (IV) ≥ 25 and a Monte Carlo p-value < 0.05 were considered indicators of a particular site.

Species	IV Protected	IV Managed	p-value
Protected site			
Allium cernuum	34	6	0.040
Artemisia frigida	37	8	0.043
Bouteloua gracilis	68	10	<0.001
Managed site			
Arctostaphylos uva-ursi	16	56	0.004
Carex rossii	27	63	0.002
Fragaria	1	30	0.030
Juniperus communis	0	33	0.001
Potentilla fissa	3	48	<0.001

Figure 2.1. Location of protected (●) and managed (▲) plots in the Colorado Front Range.

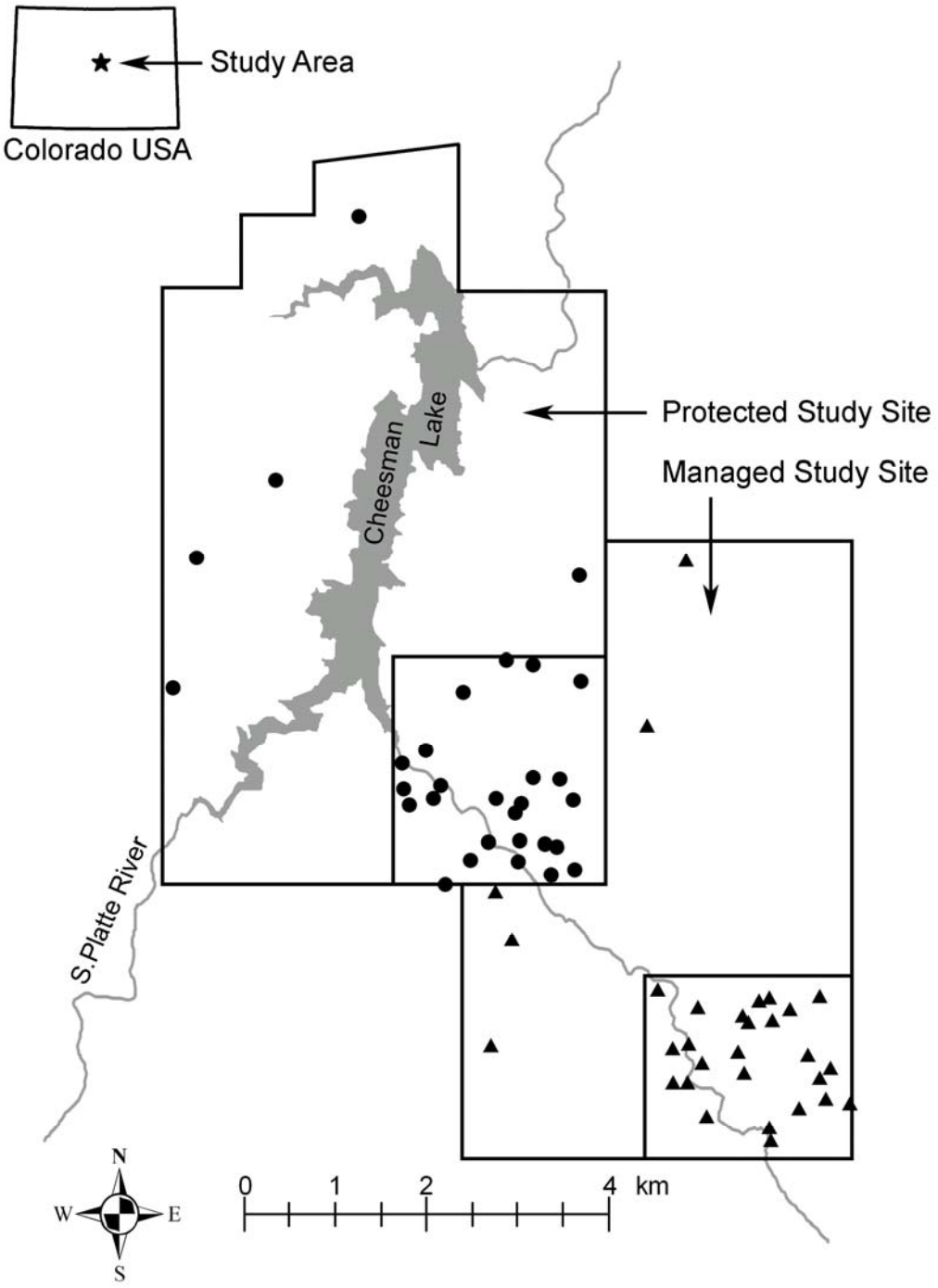
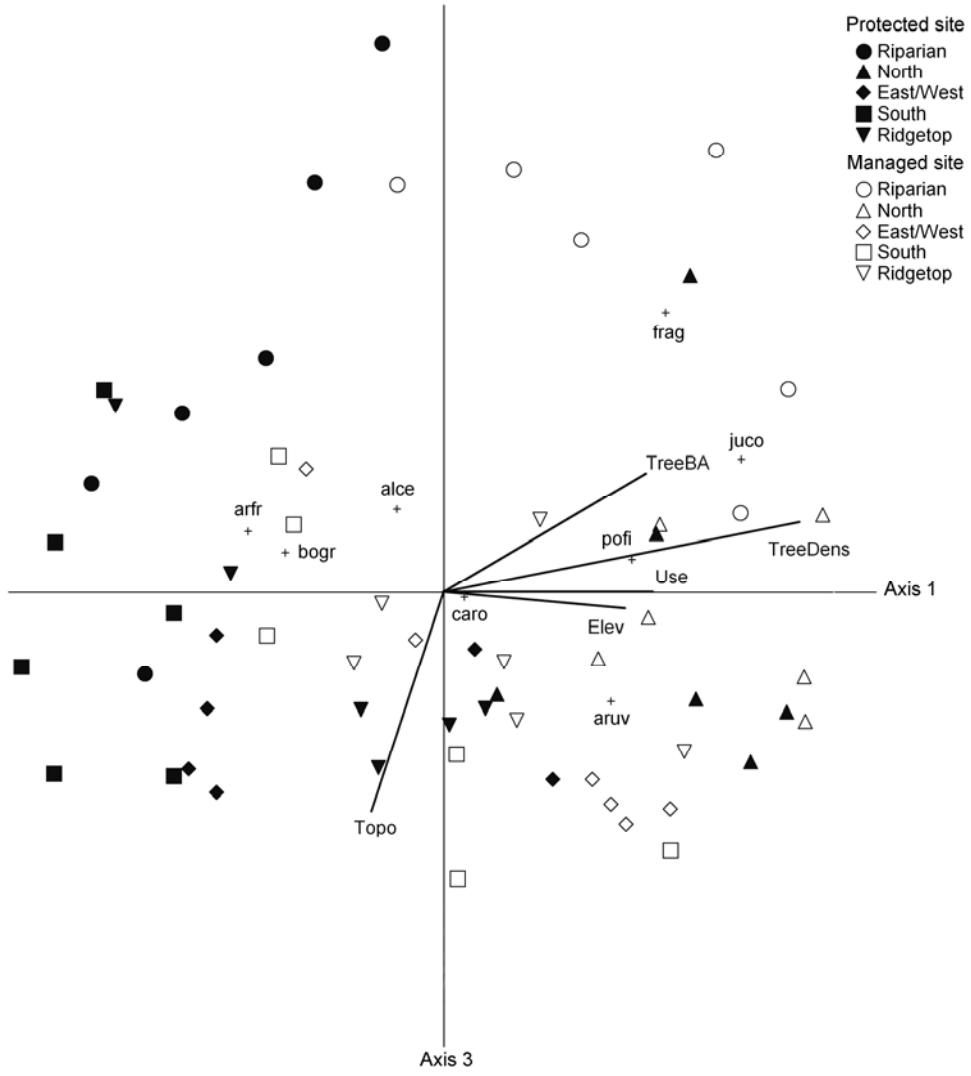


Figure 2.2. This 1910 photo depicts the remains of a *Pinus ponderosa – Pseudotsuga menziesii* stand after a settlement-era timber harvest near the managed study site. Photo courtesy of the Pike National Forest.

Figure 2.3. Axis one versus three of an NMS ordination of species cover in protected and managed plots. Environmental variables that were correlated with the ordination axes ($|r| \geq 0.4$) are overlaid as vectors (Table 2.3). Environmental variables include: TreeBA = tree basal area; TreeDens = trees per hectare; Use = land use history (protected or managed); Elev = elevation; Topo = topographic category. Species indicative of the protected and managed sites are also shown (Table 2.4): alce = *Allium cernuum*; arfr = *Artemisia frigida*; bogr = *Bouteloua gracilis*; aruv = *Arctostaphylos uva-ursi*; caro = *Carex rossii*; frag = *Fragaria* spp.; juco = *Juniperus communis*; pofi = *Potentilla fissa*.



CHAPTER 3: UNDERSTORY PLANT COMMUNITY DEVELOPMENT FOLLOWING THE 2002 HAYMAN FIRE, COLORADO

ABSTRACT

The 2002 Hayman Fire, Colorado, burned 55,800 ha of *Pinus ponderosa – Pseudotsuga menziesii* (ponderosa pine – Douglas-fir) forest, and created severely burned patches with complete overstory mortality, as well as less severely burned patches where overstory trees survived. Also burned in the fire were 25 pre-existing 1000-m^2 plots that had been surveyed for understory plant composition and cover in 1997. These plots were located in both upland and riparian areas, and burned with a range of severities. I examined the short-term impacts of this fire on understory plant community development by remeasuring the plots annually from 2003 to 2007. In lightly burned, moderately burned, and severely burned upland plots, fire-induced changes in individual species' abundances, species richness and cover, and community composition were apparent through time. Although some declines in species richness and cover were observed immediately following fire, by postfire year five, they met or exceeded prefire levels, even in severely burned plots. For all fire severities, the changes in community composition that were observed were primarily due to postfire species recruitment, particularly native short-lived forbs, rather than due to a loss of prefire species. Because of the opportunistic nature of this study, only lightly burned riparian areas were studied

here, as prefire riparian plots in more severely burned areas were insufficiently replicated. Postfire changes in species' abundances, community composition, and plant richness and cover in lightly burned riparian plots were minimal. I conclude that the Hayman Fire has had largely favorable impacts on understory plant communities in upland plots, regardless of fire severity. In lightly burned riparian plots, however, fire effects were neutral. Although only a small area within the Hayman Fire perimeter was sampled in this study, I suspect that my findings are representative of much of the burn.

INTRODUCTION

Mixed severity fire is a key disturbance process in many Rocky Mountain forests (Arno *et al.* 1995; Barrett *et al*. 1991; Brown *et al.* 1999; Ffolliott *et al.* 2008; Lentile *et al.* 2005; Turner *et al.* 1997, 1999; Veblen *et al.* 2000). Such fires are characterized by their extreme variability in behavior and effects. A single fire event includes lightly or moderately burned patches where overstory mortality and forest floor consumption are minimal, as well as severely burned patches where all trees are killed and the canopy and forest floor are largely consumed (Arno 2000; Brown 2000).

Mixed severity fires often have profound, yet diverse, influences on the development of postfire understory plant communities. For example, fire severity had varied impacts on a suite of biotic responses measured one to three years after the 1988 Yellowstone Fires, including forb, graminoid, and shrub cover, sprout densities of common prefire species, and seedling densities of opportunistic native and exotic species (Turner *et al*. 1999). Similarly, Keyser (2007) found that understory cover and composition varied greatly through time and among fire severities after the 2000 Jasper

Fire, South Dakota. Indeed, lingering fire severity effects on understory plant communities have been detected as much as thirty years after fire (Bataineh *et al.* 2006).

In the Colorado Front Range, interest in understory development after mixed severity wildfire has been mounting, primarily due to a recent string of large (>1000 ha) blazes that have burned tens of thousands of hectares of montane Front Range forest in the last decade. The largest of these fires, the 2002 Hayman Fire, burned 55,800 ha alone. Approximately half of the Hayman Fire area burned as a severe fire with complete overstory mortality, much of it in a single day of extreme weather; the other half of the area burned with a finer, more heterogeneous mosaic of severities (Finney *et al.* 2003).

Prefire understory plant data collected in upland and riparian plots within the Hayman Fire perimeter provide a unique opportunity to investigate understory development after a mixed severity wildfire. I remeasured these prefire plots annually from 2003 to 2007 to address the following questions:

- What was the impact of the Hayman Fire on the abundances of common understory species, and did impacts vary with fire severity and over time?
- Did total and functional group (short-lived forb, long-lived forb, graminoid, and woody plant) understory plant richness and cover change as a result of the fire, and how do these changes relate to fire severity and time since fire?
- Did the Hayman Fire have any immediate impact on understory species composition in lightly burned, moderately burned, and/or severely burned areas, and did prefire and postfire communities within each of these areas become more similar or less similar as time passed?

METHODS

Study area and study design

I conducted my study in a 4-km^2 portion of the Pike National Forest, Colorado, approximately 60 km southwest of Denver (Figure 3.1). Forests within the study area are dominated by *Pinus ponderosa* (ponderosa pine) and *Pseudotsuga menziesii* (Douglas-fir) forest, while understories are a diverse community of graminoids, forbs, and shrubs (Fornwalt *et al.* 2009; Kaufmann *et al.* 2000; Chapter 2). Soils are gravelly coarse sandy loams derived from weathered Pikes Peak granite (USDA Forest Service 1992). Elevations within the study area range from 2300 to 2500 m. Average annual precipitation is around 40 cm, most of which falls during afternoon thunderstorms in July and August (http://www.wrcc.dri.edu).

The 4-km^2 study area and the plots within it were originally established and measured in 1996 and 1997 by Kaufmann *et al.* (2000). Five plots were established in each of five topographic environments, for a total of 25 plots: north-facing slopes, south-facing slopes, east- or west-facing slopes, ridgetops, and riparian areas. All plots were 1000 m^2 (20 x 50 m) and were located in forested areas. North, south, and east/west plots were situated on upland slopes with the long axis of the plot aligned down the fall line. Ridgetop plots were also in upland areas, with the long axis parallel to the ridge. Riparian plots were located in low-lying valley bottoms or draws near intermittent or perennial streams, with the long axis of the plot parallel to the stream channel.

In 2002, the Hayman Fire burned 55,800 ha (Graham 2003), including the 4-km^2 study area (Figure 3.1). This fire, which is the largest fire known to burn in Colorado to date, was ignited on the afternoon of June 8, 2002. Low fuel moistures, heavy,

continuous fuel loadings, and strong, gusty winds allowed the Hayman Fire to burn over 24,000 ha on June 9, mostly as a high severity fire with complete overstory mortality (Finney *et al.* 2003; Figure 3.1). Less extreme weather conditions followed the next day and persisted for the following three weeks, causing the fire to burn with a finer, more heterogeneous mosaic of low, moderate, and high severity fire until it was contained on June 28. The 4-km^2 study area is situated in a transitional zone between these two fire behaviors (Figure 3.1). As a result, it contains an edge of a large high severity fire patch created on June 9, as well as smaller low, moderate, and high severity patches (Figure 3.1).

In 2003, I successfully relocated and remeasured all of the original plots. The location of the plots was reconstructed using prefire data such as plot UTM coordinates and overstory stem maps, as well as postfire evidence such as the remains of plot corner stakes and aluminum tree tags. Plots were also remeasured in 2004, 2005, 2006, and 2007.

Data collection

Prefire and postfire understory composition and cover data were collected for each plot using the modified Whittaker sampling design (Stohlgren *et al.* 1995). In this method, the primary 1000-m^2 plot has several subplots nested within it. One 100-m^2 subplot is located in the center of the main plot, and two 10-m^2 subplots are located in diagonally opposite corners. Ten 1-m^2 subplots are located around the perimeter of the main plot and the 100-m^2 subplot. Vegetative cover was ocularly estimated for each understory plant species in the ten 1-m^2 subplots. Cumulative additional species were recorded for each of the 10-m^2 subplots, the 100-m^2 subplot, and the remainder of the

1000-m^2 plot. All graminoid, forb, and shrub species were included in the surveys, but tree species were not. Nomenclature follows the USDA Plants Database (2008), although varieties and subspecies are not distinguished. Approximately 11% of the observations made in each plot could be identified only to genus; another 1% could not be identified at all. Generic observations were generally limited to a small number of genera for which individual species could not be consistently distinguished, either because hybridization is common (e.g., *Rosa*), or because species are difficult to determine when sampled outside peak phenological development (e.g., *Carex*, *Chenopodium*). Generic observations were included in analyses, while unidentified observations were excluded. Voucher specimens are stored at the USDA Forest Service Rocky Mountain Research Station in Fort Collins, Colorado.

Direct fire effects on the overstory and forest floor were assessed for each plot in 2003. Percent overstory mortality equaled the percent of prefire live trees over 1.37 m tall (determined by Kaufmann *et al.* 2000 when the plots were established) that were dead in 2003. Additional overstory fire effects including scorch height, bole char height, percent crown scorch, and percent crown consumption were also measured on each tree. Postfire overstory canopy cover was determined using a spherical densiometer by averaging eight systematic measurements taken in each plot. We assessed fire effects on the forest floor by noting the degree of char (unburned, partially blackened, fully blackened, partially consumed, and fully consumed) on prefire litter, small wood, and large wood in each of the ten 1-m^2 modified Whittaker subplots; freshly fallen litter and wood were disregarded. We also recorded the percent of bare soil and litter cover in the subplots.

Postfire rehabilitation treatment maps created by the USDA Forest Service indicate that four plots were aerially seeded in the fall of 2002 (Robichaud *et al.* 2003). The seed used in the rehabilitation treatment was a certified weed-free mixture of 70% *Hordeum vulgare* (barley) and 30% ×*Triticosecale rimpaui* (triticale, wheat-rye hybrid), and was applied at a rate of ~280 seeds/m^2 (Robichaud *et al.* 2003). Both *H. vulgare* and *T. rimpaui* are exotic annual grasses. Preliminary data analysis suggest that seeded grasses were most abundant in the plots in 2003, but even in this year seeded grass cover was negligible (< 0.1%). Furthermore, seeded grass cover did not differ between the four seeded and the twenty-one unseeded plots for any year except 2003 (2003: $p = 0.004$; all other years: $p = 1.000$). In light of these findings, I did not feel it was necessary to analyze the 'seeded' and 'unseeded' plots separately in this study.

Data classification

Prior to analyses, plots were classified into groups that reflected both their fire severity and topographic position. Plots where less than 50% of the overstory trees died in the fire were categorized as burning with low severity, while plots that burned with moderate severity had 50% mortality or more but had only modest levels of crown and forest floor consumption. High severity plots were those with 100% tree mortality and complete or nearly complete crown and forest floor consumption. Topographic position for each plot was defined as either upland (i.e., north, south, east-west, and ridgetop) or riparian based on its original topographic designation; previous work in these plots found few differences in prefire understory richness and composition among upland categories, although upland and riparian plots differed considerably (Fornwalt *et al.* 2003, 2009; Chapter 2). Using this new classification scheme, my dataset contains ten low severity,

six moderate severity, and four high severity upland plots, and four low severity, one moderate severity, and no high severity riparian plots. Direct fire effects on the overstory and forest floor for upland low, moderate, and high severity plots, and for riparian low severity plots, are presented in Table 3.1. Moderate and high severity riparian plots are not included in this table or in any subsequent analyses because they are not sufficiently replicated. All prefire data were assigned a year of 1997 even though some plots were measured in 1996 because growing season precipitation and understory community composition did not differ between the two prefire years (Fornwalt *et al.* 2003, 2009; Chapter 2).

Species were classified into one of four functional groups based on life history and growth form characteristics; these functional groups included short-lived forbs, long-lived forbs, graminoids, and woody plants. Classifications were made based on the USDA Plants Database (2008) and local botanical keys (Harrington 1964; Weber and Wittmann 2001). Generic identifications were assigned to functional groups only when the classification was appropriate for all species known to occur in Colorado *P. ponderosa – P. menziesii* forests. Short-lived forbs included annuals and biennials, as well as species categorized as annual/perennial, biennial/perennial and annual/biennial/perennial. Short-lived graminoids were scarce and were not separated into their own category.

Data analyses

Common species. The impacts of fire on the abundances of common understory species were examined using repeated measures analysis of variance (ANOVA) in SAS 9.1.3 (SAS Institute Inc., Cary, North Carolina, USA). Common species were defined as

those occurring in more than 50% of the 1000-m^2 plots in at least one year. For upland plots, I separately modeled the presence or absence of each species in the 1000-m^2 plots against the factors year, fire severity, and year * fire severity. For riparian plots, where only low severity plots are available for analysis, I modeled species presence or absence against the factor year. All analyses used the spatial power covariance matrix, which assumes that there is a higher level of correlation between two repeated observations closer in time than between two observations further apart. When year or year * fire severity was significant ($p < 0.05$), pairwise differences between years were further examined using least squares means with a Tukey-Kramer adjustment for multiple comparisons.

Model results were then used to classify each common understory species as increasing, decreasing, or unchanged in abundance after the Hayman Fire. Species that increased in abundance had a significant year or year * fire severity effect, and were 'more present' in one or more postfire years than in the prefire year, while species that decreased in abundance also had a significant year or year * fire severity effect, but were 'more present' in the prefire year than in one or more postfire years. Species that were unchanged in abundance had nonsignificant year and year * fire severity effects, or, if effects were significant, then prefire and postfire abundances did not vary for any postfire year.

Species richness and cover. The impacts of fire on measures of species richness and cover were also examined using repeated measures ANOVA. Total species richness was calculated by tallying the number of species in each 1000-m^2 plot. Total species cover was calculated by summing the cover of all species in each 1-m^2 subplot and

averaging across the ten subplots per plot. Species richness and cover within the four functional groups were calculated in a similar manner. As before, analyses of upland data were conducted by separately modeling each richness/cover measure against the factors year, fire severity, and year * fire severity, while analyses of riparian data were conducted by modeling each measure against the factor year. Cover data were square-root transformed prior to analysis to improve the distribution and homogeneity of residuals.

Species composition. Compositional differences among years and fire severities were analyzed using multi-response permutation procedures (MRPP) and blocked multi-response permutation procedures (MRBP) in PC-ORD 5.19 (MjM Software Design, Glendon Beach, Oregon, USA). MRPP and MRBP are nonparametric procedures for testing for multivariate differences among two or more levels of a factor. However, these procedures cannot handle multifactor designs, such as the one used above for upland plots. To overcome this, I first used MRPP to investigate fire severity effects on upland species composition for each year. MRPP analyses were conducted using species presence-absence data for the 1000-m^2 plots, with rare species (those occurring in 5% of the plots or less) omitted to reduce noise in the dataset. MRPP used the Sørensen distance measure to calculate the matrix of distances (*i.e.*, compositional dissimilarities) between plots. MRPP results indicated that species composition did not vary among fire severities in 1997 ($p = 0.258$), although composition did vary among fire severities in all postfire years but 2007 (2003 $p = 0.027$; 2004 $p = 0.035$; 2005 $p = 0.002$; 2006 $p = 0.002$; 2007 $p = 0.052$). Therefore, I separately examined temporal changes in composition for low severity, moderate severity, and high severity upland plots using MRBP, with plot

serving as the blocking factor to control for repeated measures. Compositional changes in low severity riparian plots over time were likewise examined with MRBP. Following a significant overall test, pairwise differences between years were examined using an alpha of 0.05. Adjustments for multiple comparisons (*e.g.*, using the *post hoc* Bonferoni method) were not made because they would have precluded detecting any differences between years in upland high severity and riparian low severity areas. This is due to the size of the minimum p-value that can be calculated using permutation methods when sample sizes are small (Clarke 1993). For instance, with a sample size of four (this is the sample size for upland high severity and riparian low severity areas), the minimum p-value that can be obtained for a pairwise comparison is 0.029. While this minimum p-value would be adequate for detecting differences using an unadjusted alpha of 0.05, it would be inadequate for detecting differences with a Bonferoni-adjusted alpha of 0.003 (0.05/15 multiple comparisons).

I further examined compositional differences among years using the non-metric multi-dimensional scaling (NMS) ordination procedure in PC-ORD 5.19. The following procedure was conducted separately for low severity, moderate severity, and high severity upland plots and for low severity riparian plots, using species presence-absence data for the 1000-m^2 plots (omitting rare species, as before). First, I assessed the dimensionality of the dataset by running 250 preliminary ordinations using a step-down in dimensionality procedure (*i.e.*, one- through six-dimensional solutions were calculated for each of the 250 runs) and a random starting configuration. Each ordination run used the Sørensen distance measure to calculate the distance matrix, a maximum of 500 iterations per run, and a stability criterion of 0.00001. The optimal preliminary

ordination was the one whose configuration minimized the number of dimensions in the solution while also minimizing stress, a measure of 'badness-of-fit', and where the Monte Carlo p-value from 250 runs with randomized data was less than 0.05. I then ran a final ordination with the optimal preliminary ordination configuration used as the starting configuration. The final ordination was rigidly rotated to align year with axis one. The correlation between year and axis one was calculated while accounting for repeated measures.

RESULTS

A total of 247 understory species were found in the 24 1000-m^2 plots across all years. Of these, 22.7% were short-lived forbs, 47.8% were long-lived forbs, 16.6% were graminoids, and 8.9% were woody plants. 4.0% of species were identified to genus only and could not be classified into functional groups due to variability within the genus. Exotic species were a relatively minor component of the understory before and after fire. A detailed analysis of exotic species response to the Hayman Fire is reported in Chapter 4.

Hayman Fire effects on understory communities in upland forests

Common species. 58 species in upland plots were identified as being common (i.e., they occurred in more than 50% of the 1000-m^2 plots in at least one year; Table 3.2). Of these, 62.1% were unchanged in abundance before versus after the fire, while 29.3% increased in abundance for one or more postfire years, and 8.6% decreased in abundance.

Fire-induced changes in species abundances were readily apparent for many of the common short-lived forbs, with 71.4% of them becoming more abundant after the fire

for one or more postfire years (Table 3.2). For many of these species, the duration of the postfire increase lengthened as fire severity increased. The remaining 28.6% of species did not vary in abundance before versus after the fire.

Abundances of common long-lived forb and graminoid species were much less responsive to fire (Table 3.2). 77.4% of the common long-lived forb species did not vary in abundance before versus after the fire; for the remaining species, 16.1% increased in abundance during one or more postfire years, while 6.5% decreased in abundance. Similarly, 75.0% of the common graminoid species were unchanged in abundance after the fire, while 12.5% increased and 12.5% decreased after fire in one or more years. For both long-lived forbs and graminoids, increases in species' abundances occurred throughout the postfire sampling period, although none of the species increased for all five postfire years. Decreases, however, were only observed in early postfire years, with species returning to prefire levels by 2005. Furthermore, decreases typically only occurred after severe fire.

40.0% of the common woody plant species did not change in abundance as a result of the Hayman Fire, while 20.0% increased in abundance for one or more postfire years, and 40.0% decreased in abundance (Table 3.2). Decreases in abundances persisted for the entire postfire period.

Species richness and cover. Total understory species richness and cover in upland plots varied with year and with the interaction between year and fire severity, but not with fire severity *per se* (Table 3.3; Figures 3.2, 3.3). For all fire severities, total richness was unchanged by fire during the first two to three postfire years, and then subsequently exceeded prefire levels. Total cover decreased initially after fire in lightly

and moderately burned plots but returned to prefire levels by 2004 and remained there for the duration of the study. In severely burned plots, total cover also decreased initially after fire and returned to prefire levels from 2004 to 2006, but then exceeded prefire levels in 2007.

The impacts of time since fire and fire severity on functional group richness were diverse (Table 3.3; Figure 3.4). More short-lived forb species were found in each of the five postfire years than were found before the fire, with the magnitude and timing of the postfire increases varying among fire severities. Long-lived forb richness was similar to prefire richness in the years immediately after the fire, but then exceeded prefire richness in the later postfire years. Although graminoid richness varied significantly with time, differences among years were limited to the postfire sampling period; no differences between prefire and postfire richness were observed. Lastly, woody plant richness did not vary through time or among fire severities.

Understory cover within all four functional groups varied with time, but only short-lived forb cover also varied with fire severity (Table 3.3; Figure 3.5). The postfire cover of short-lived forbs increased in lightly burned plots only in 2004; in contrast, moderately and severely burned plots saw a postfire increase in three of the five postfire years. Long-lived forb cover was unchanged by fire from 2003 to 2005, and then increased in 2006 and 2007. For graminoids, cover was lower after the fire than before for the first two postfire years, but returned to prefire levels from 2005 to 2007. Woody plant cover was lower after the fire than before the fire in all postfire years.

Species composition. Multivariate MRBP revealed that understory species composition varied with time for all fire severities ($p < 0.001$ in all cases; Table 3.4). In

lightly burned areas, the understory community present in a particular year was distinct from the one present in all other years — no two years were compositionally similar. In moderately and severely burned areas, prefire composition also differed from postfire composition for all postfire years, although there was some compositional similarity among postfire years.

Three-dimensional NMS ordinations also suggested that composition varied among years for all fire severities, with prefire plots separating from postfire plots to some extent along axis one (Table 3.5; Figures 3.6, 3.7, and 3.8). In the low severity ordination, some overlap between prefire and postfire plots is clearly visible, while in the moderate and high severity ordinations, prefire and postfire plots appear completely separated in ordination space. The correlations between axis one scores and year echo this trend, as the correlation is weaker in the low severity ordination ($r^2 = 0.226$) than in moderate and high severity ordinations ($r^2 = 0.849$ and 0.703, respectively). Furthermore, in moderate and high severity plots earlier postfire years (*e.g.*, 2003 and 2004) also appear somewhat separated in ordination space from later postfire years (*e.g.*, 2006 and 2007); such a pattern is not evident in the low severity ordination, however. Successional vectors of individual plots through time also suggest that prefire and postfire community composition diverged as time passed in moderately and severely burned plots.

Hayman Fire effects on understory communities in riparian forests

Common species. Riparian plots contained 80 common species (Table 3.6). Of these, 92.5% did not vary in abundance before versus after the fire, while 7.5% increased

and none decreased. Species that increased in abundance after fire were predominately short-lived forbs.

Species richness and cover. Total species richness and cover did not vary over time in lightly burned riparian forests ($p = 0.361$ and 0.135, respectively; Figure 3.9). Functional group richness and cover also changed little over the course of this study (Figure 3.10). Differences in functional group richness were limited to short-lived forbs ($p = 0.007$); long-lived forb, graminoid, and woody plant richness did not vary across years ($p = 0.658$, 0.307, and 0.858, respectively). Short-lived forb richness differed somewhat among postfire years but did not differ before versus after the fire. The cover of short-lived forbs, long-lived forbs, and graminoids varied among years ($p = 0.008$, <0.001, and 0.025, respectively), although there were no significant pairwise differences in short-lived forb or graminoid cover after adjustments for multiple comparisons were made. Differences in long-lived forb cover were observed only among postfire years. Woody plant cover did not vary through time ($p = 0.103$).

Species composition. Results of MRBP indicate that prefire species composition differed from postfire composition in all postfire years, although some compositional similarities among postfire years were evident (Table 3.7). By comparison, the three-dimensional NMS ordination showed that plots did not separate by year in ordination space, suggesting that plots were similar in composition among prefire and postfire years (Figure 3.11); correlations between axis one and year support this interpretation ($r^2 = 0.072$).

DISCUSSION

Hayman Fire effects on understory communities in upland forests

Over 60% of the common understory species identified in upland areas were unchanged in abundance by the Hayman Fire during the first five postfire years, regardless of fire severity (Table 3.2). Most of these species were long-lived forbs, although short-lived forbs, graminoids, and woody plants were also represented. Examples of widespread species whose abundances were unchanged by fire include *Bouteloua gracilis* (blue grama), *Geranium caespitosum* (pineywoods geranium), *Heterotheca villosa* (hairy false goldenaster), *Koeleria macrantha* (prairie Junegrass), and *Ribes cereum* (wax currant). Given that forests in the area burned by the Hayman have a long history of mixed severity fire (Brown *et al.* 1999), this level of postfire resiliency is not surprising. Indeed, many of the species that occurred in my Hayman Fire plots are known to readily sprout or reestablish from seed even after severe fire (Chapter 5). Rapid reestablishment of the prefire understory community has been found in other Rocky Mountain forests, and underscores its importance in shaping postfire succession in fire dependent ecosystems (Anderson and Romme 1991; Laughlin and Fulé 2008; Turner *et al.* 1997; Lyon and Stickney 1976).

Furthermore, an additional 30% of the common upland species increased in abundance after the Hayman Fire in one or more postfire years, most of which were short-lived forbs (Table 3.2). Increases in short-lived forbs after fire have been observed worldwide, including in *P. ponderosa* – dominated forests (Crawford *et al*. 2001; Huisinga *et al*. 2005; Laughlin and Fulé 2008). Species that increased in abundance after the fire were largely incidental in the prefire community, with only four species

completely absent from prefire surveys: *Conyza canadensis* (Canadian horseweed), *Laennecia schiedeana* (pineland horseweed), *Lactuca serriola* (prickly lettuce), and ×*Triticosecale rimpaui* (triticale). *T. rimpaui* is a sterile annual that was intentionally seeded as part of postfire rehabilitation efforts (Robichaud *et al*. 2003), while *C. canadensis*, *L. serriola*, and *L. schiedeana* potentially established from both offsite and onsite seed sources (Dauer *et al*. 2007; Thompson *et al*. 1997; Weaver 2001; Weaver and Downs 2003; Chapter 5). Unfortunately, several of the species that increased in abundance after fire are exotic. Exotic species appeared to be especially stimulated in severely burned areas (Table 3.2; Chapter 4). However, their cover remains low at this point in time, so I do not consider them a major ecological threat at present (Chapter 4).

Few of the common species that increased in abundance at some point after the Hayman Fire exhibited a 'boom and bust' postfire cycle, suggesting that they may remain key members of the postfire community for the foreseeable future (Table 3.2). However, there were a handful of exceptions, the most notable of which is *Corydalis aurea* (scrambled eggs). *C. aurea* was largely absent from the prefire landscape, but it was ubiquitous one year after fire, particularly in severely burned areas. By postfire year three, however, it had largely disappeared from the landscape once again. This species probably establishes after fire from long-lived seeds in the soil seedbank (Crane *et al*. 1983; Chapter 5), and likely plays a critical role in early postfire soil stabilization in Front Range forests. The exotic species *Lactuca serriola* has also been documented as transient in the postfire landscape, although this species has not yet begun to decline in my plots (Crane *et al.* 1983; Stickney and Campbell 2000; Chapter 5).

Although over 90% of the common species had neutral or favorable responses to the Hayman Fire, nearly 10% did exhibit a decline in abundance in one or more postfire

years (Table 3.2). These decreases were largely ephemeral and were mostly limited to severely burned areas. Indeed, only one common understory species, *Juniperus communis* (common juniper), declined across all years and fire severities. *J. communis* is a resinous species that is easily ignited by fire, yet it lacks a mechanism for rapid postfire recovery (Edlin 1958; Hobbs *et al*. 1984; Chapter 5). Declines in *J. communis* after fire have occurred in ecosystems across the world (Diotte and Bergeron 1989; Hobbs *et al.* 1984; Keyser 2007). Given its susceptibility to fire, the widespread prefire abundance of *J. communis* within the Hayman Fire area may be partly an artifact of 20th century fire suppression (and also settlement-era grazing; see Chapter 2), in which case its reduced postfire abundance may be more in line with the historical condition.

Given the paucity of common species that declined in abundance after the Hayman Fire, it follows that total species richness also probably did not decline. Indeed this was the case, even in severely burned areas. Rather, prefire and postfire species richness were comparable during early postfire years, then increased during the last few years of this study (Figure 3.3a). These changes were primarily attributable to increases in short-lived forb richness, and, to a lesser extent, to increases in long-lived forb richness (Figure 3.4 a, b).

The compositional differences among years after low, moderate, and high severity fire are also largely attributable to the recruitment of short-lived and long-lived forbs postfire, rather than to a loss of prefire species (Tables 3.2, 3.4; Figures 3.6, 3.7, 3.8). Furthermore, ordination diagrams suggest that compositional change was directional, particularly in moderately and severely burned plots, with prefire and postfire community composition becoming more dissimilar as time since the Hayman Fire passed. This

directionality of compositional change is likely reflecting the continued accumulation of new species in these plots over the five years.

Total understory cover did decline initially after the fire for all fire severities, driven primarily by reductions in graminoid and woody plant cover (Figures 3.3b, 3.5 b, d). However, the decline in total cover was rapidly reversed as short-lived forb, long-lived forb, and graminoid cover increased to, or even surpassed, prefire cover over the following years (Figure 3.5 a, b, c). These results demonstrate the overall resiliency that herbaceous cover can have even after severe fires; indeed, similar phenomena have documented in other Rocky Mountain ecosystems (Keyser 2007; Turner *et al*. 1999). Woody plant cover, however, appears to be much slower to recover after fire, and was still below prefire levels in the fifth postfire year for all fire severities (Figure 3.5d). The relatively slow recovery of woody plants is likely due to a number of factors, including the inability of some species to sprout after fire, such as *J. communis*, as I discussed above. Even species that rapidly sprout after fire, like *Cercocarpus montanus* (alderleaf mountain mahogany), often take several years to regain their large prefire size (Liang 2005).

Hayman Fire effects on understory communities in riparian forests

Postfire changes in understory plant communities were minimal in lightly burned riparian areas. I observed little to no variation in species richness and cover over the course of this study (Figures 3.9, 3.10). Compositional differences among years, while statistically significant, were subtle and appear to be driven primarily by the recruitment of a handful of species that were rare or absent before the fire — particularly short-lived forbs — rather than by the loss of prefire species (Tables 3.6, 3.7; Figure 3.11). The

relative stability of the riparian understory community is likely due to the low fire severity in the areas studied here. After the Hayman Fire, litter and wood lying on the forest floor remained unburned in places; where fire did occur, this material was typically blackened but rarely consumed (Table 3.1). Some prefire plants also remained unburned, and those that did burn tended to recover readily, primarily by sprouting. Establishment of new species was likely limited by the high levels of litter and canopy cover that remained in the postfire environment (Table 3.1; Xiong and Nilsson 1999).

Concluding remarks: ecological impacts of the Hayman Fire on understory communities

The 2002 Hayman Fire is the largest and most severe fire known to burn in Colorado to date. Prefire data collected five years prior to the 2002 Hayman Fire have provided a valuable reference condition for interpreting its ecological impact on understory plant communities during the first five postfire years. The results presented here suggest that the Hayman Fire was not an 'ecological catastrophe' from an understory plant community perspective (Keane *et al*. 2008). Rather, my results suggest that the Hayman Fire has had largely neutral or favorable impacts on understory communities during the first five postfire years, even in severely burned areas.

Given that only a small portion of the Hayman Fire was sampled in this study, how applicable are my findings to the entire area burned by the fire? In general, I suspect that they are representative of much of the Hayman Fire area. In particular, I expect that upland and riparian portions of the burn characterized by low severity fire, and upland portions characterized by moderate severity fire, will have postfire vegetation responses similar to those reported here. This expectation also holds for small upland patches of high severity fire, as well as the edges of large high severity patches. However,

extrapolation of my results to the interiors of large high severity patches should be done with caution, as these areas are not represented by my plots (Figure 3.1). The duration and depth of extreme soil heating can be greater within large severe fire patches than within small severe fire patches, potentially resulting in more damage to the belowground organs that enable sprouting plants to regenerate after fire (Keane *et al*. 2008; Ryan 2002; Turner *et al*. 1997). Soil seedbanks may likewise be more damaged in the interior of large severe fire patches. Also, seed dispersal by wind and animals may be slower in large severe fire patches due to greater distances from seed sources located in unburned areas (Keane *et al*. 2008).

That being said, understory communities throughout many of the Hayman's large severe fire patches appear to be recovering similarly to those in the severely burned areas I measured. Within large severe fire patches I have observed numerous native species sprouting vigorously, while other species appear to be readily establishing from soil-stored and offsite seed sources. Exotic species are certainly present within large patches of severe burn, particularly in areas where extensive postfire rehabilitation activities were conducted (Robichaud *et al*. 2003; Robichaud and Wagenbrenner 2008), yet generally they appear to be no more abundant than they were within my severely burned plots.

It is expected that large and severe fires will continue to occur in Front Range *P. ponderosa – P. menziesii* forests due to the elevated fuel loadings created by a century of fire suppression and other human activities, as well due to the projected impacts of climate change. Fortunately, this fire-adapted understory community seems capable of persisting, if not flourishing, after all but possibly the largest, most intense burns.

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Table 3.1. Direct effects of the 2002 Hayman Fire on the overstory and forest floor, by topographic category and fire severity. All measurements were made in 2003. Values are means ± standard errors. Litter, small wood, and large wood characteristics are for prefire material; freshly fallen material was disregarded. Both prefire and postfire litter, however, are included in litter cover estimates.

	Upland			Riparian
	Low severity (n = 10)	**Moderate severity (n = 6)**	**High severity (n = 4)**	**Low severity (n = 4)**
Overstory				
Mortality (%)	20.9 ± 4.1	66.7 ± 4.1	100.0 ± 0.0	33.0 ± 5.9
Canopy cover[a] (%)	54.1 ± 3.8	52.3 ± 4.7	34.0 ± 3.8	67.9 ± 9.6
Scorch height (m)	5.0 ± 0.9	6.9 ± 0.7	9.5 ± 0.4	4.0 ± 1.0
Bole char height (m)	2.3 ± 0.5	4.7 ± 0.6	9.4 ± 0.4	1.4 ± 0.5
Crown scorch (%)	36.1 ± 6.4	37.4 ± 3.0	0.8 ± 0.5	42.4 ± 4.2
Crown consumption (%)	9.9 ± 3.1	49.8 ± 4.4	99.2 ± 0.5	7.5 ± 2.4
Total crown damage (%)	46.0 ± 6.8	87.0 ± 2.5	100.0 ± 0.0	50.0 ± 6.5
Forest floor				
Litter cover (%)	41.2 ± 3.7	49.8 ± 6.7	3.4 ± 2.2	49.8 ± 12.7
Bare soil cover (%)	46.5 ± 4.1	34.3 ± 6.0	86.5 ± 3.9	26.2 ± 8.4
Litter characteristics	unburned to fully blackened	partially blackened to fully consumed	partially blackened to fully consumed	unburned to fully blackened
Small wood (<7.6 cm) characteristics	unburned to fully blackened	partially blackened to partially consumed	fully blackened to fully consumed	unburned to fully blackened
Large wood (>7.6 cm) characteristics	unburned to partially consumed	partially blackened to partially consumed	fully blackened to partially consumed	unburned to partially blackened

[a] Canopy cover is contributed by foliage, stems, and branches.

Table 3.2. Response of common upland understory species to the Hayman Fire based on the results of an ANOVA modeling species presence or absence in 1000-m^2 plots against year, fire severity, and year * fire severity. Species that increased in response to the Hayman Fire are those that were more abundant (*i.e.*, they were found in more 1000-m^2 plots) after the fire than before the fire for one or more postfire years; species that decreased were more abundant before the fire than after. Fire severity impacts are discussed only if year * fire severity was significant.

Species	Response to Hayman Fire
Short-lived forbs	
Androsace septentrionalis	Unchanged
Artemisia campestris	Unchanged
B*ahia dissecta*	Increased after fire in all years but 2003
Chenopodium	Increased after fire in all years
Corydalis aurea	Increased after fire in 2003, 2004 and 2006
Conyza canadensis	Increased in 2007 after low severity fire; increased in all years but 2004 after moderate severity fire; increased from 2005 to 2007 after high severity fire
Erysimum capitatum	Unchanged
Ipomopsis aggregata	Unchanged
Laennecia schiedeana	Increased after fire in 2005 and 2007
Lactuca serriola[a]	Increased in 2003 and 2007 after low severity fire; increased in all years but 2004 after moderate severity fire; increased from 2005 to 2007 after moderate and high severity fire
Machaeranthera bigelovii	Increased after fire from 2005 to 2007
Phacelia heterophylla	Increased after fire in all years
Tragopogon dubius[a]	Increased in 2007 after low severity fire; increased in 2005 and 2007 after moderate severity fire; increased from 2005 to 2007 after high severity fire
Verbascum thapsus[a]	Increased in 2005 and 2007 after low severity fire; increased in all years after moderate severity fire; increased in all years but 2003 after high severity fire
Long-lived forbs	
Achillea millefolium	Unchanged after low and moderate severity fire; decreased after severe fire from 2003 to 2004
Allium cernuum	Unchanged
Antennaria parvifolia	Unchanged
Arabis fendleri	Unchanged
Artemisia frigida	Increased after fire in 2007
Artemisia ludoviciana	Unchanged
Campanula rotundifolia	Unchanged
Eriogonum alatum	Unchanged
Erigeron compositus	Decreased after fire in 2003
Erigeron subtrinervis	Increased after fire from 2006 to 2007

Species	Response to Hayman Fire
Erigeron vetensis	Unchanged
Fragaria	Unchanged
Geranium caespitosum	Unchanged
Heterotheca villosa	Unchanged
Hieracium fendleri	Unchanged
Mertensia lanceolata	Unchanged
Noccaea montana	Unchanged
Packera fendleri	Unchanged
Pediocactus simpsonii	Unchanged
Penstemon glaber	Increased after fire in all years but 2003
Penstemon secundiflorus	Unchanged
Penstemon virens	Unchanged
Potentilla fissa	Unchanged
Potentilla hippiana	Unchanged
Pulsatilla patens	Unchanged
Scutellaria brittonii	Unchanged
Sedum lanceolatum	Unchanged
Silene scouleri	Increased after fire in 2005 and 2007
Solidago	Unchanged
Taraxacum officinale[a]	Increased after fire from 2006 to 2007
Yucca glauca	Unchanged
Graminoids	
Bouteloua gracilis	Unchanged
Carex	Unchanged
Elymus elymoides	Unchanged
Koeleria macrantha	Unchanged
Muhlenbergia montana	Unchanged after low and moderate severity fire; decreased in 2003 after severe fire
Poa fendleriana	Unchanged
Schizachyrium scoparium	Unchanged
×*Triticosecale rimpaui*[ab]	Increased after low severity fire in 2003 and 2005; unchanged after moderate severity fire; increased after high severity fire in 2003
Woody plants	
Arctostaphylos uva-ursi	Unchanged after low and moderate severity fire; decreased after severe fire in all years
Cercocarpus montanus	Unchanged
Juniperus communis	Decreased after fire in all years
Ribes cereum	Unchanged
Rubus idaeus	Increased after fire in all years but 2003

[a] This species is exotic to the continental United States.
[b] This species was intentionally seeded after the Hayman Fire.

Table 3.3. ANOVA results for the effects of year, fire severity, and year * fire severity on measures of understory richness and cover in upland plots. Significances ($p < 0.05$) are in bold.

Understory response	Year (p-value)	Fire severity (p-value)	Year * fire severity (p-value)
Total richness (1000m^2)	**<0.001**	0.079	**0.014**
Total cover (%)	**<0.001**	0.410	**0.008**
Functional group richness (1000m^2)			
Short-lived forbs	**<0.001**	0.856	**<0.001**
Long-lived forbs	**<0.001**	**0.010**	0.276
Graminoids	**0.017**	0.406	0.278
Woody plants	0.283	0.611	0.525
Functional group cover (%)			
Short-lived forbs	**<0.001**	**0.010**	**<0.001**
Long-lived forbs	**<0.001**	0.497	0.137
Graminoids	**<0.001**	0.564	0.093
Woody plants	**<0.001**	0.460	0.448

Table 3.4. Pairwise comparison p-values of understory species composition between prefire and postfire years in upland plots, as determined by MRBP using species presence-absence data for the 1000-m^2 plots. Significant differences ($p < 0.05$) are indicated in bold. Years with different group letters differ in species composition.

a). Low severity (overall p < 0.001)

	1997	2003	2004	2005	2006	2007
1997		**<0.001**	**0.001**	**<0.001**	**0.004**	**<0.001**
2003			**0.006**	**<0.001**	**<0.001**	**<0.001**
2004				**0.001**	**0.002**	**0.001**
2005					**0.002**	**0.007**
2006						**0.001**
2007						
Groups	A	B	C	D	E	F

b). Moderate severity (overall p < 0.001)

	1997	2003	2004	2005	2006	2007
1997		**0.009**	**0.008**	**0.008**	**0.008**	**0.008**
2003			**0.016**	**0.008**	**0.008**	**0.009**
2004				**0.009**	**0.008**	**0.008**
2005					**0.017**	**0.018**
2006						0.088
2007						
Groups	A	B	C	D	E	E

c). High severity (overall p < 0.001)

	1997	2003	2004	2005	2006	2007
1997		**0.030**	**0.030**	**0.030**	**0.030**	**0.030**
2003			0.304	**0.030**	**0.031**	**0.030**
2004				**0.030**	**0.034**	**0.031**
2005					**0.036**	0.188
2006						0.051
2007						
Groups	A	B	B	C	D	CD

Table 3.5. Final stress of the upland low, moderate, and high severity and the riparian low severity NMS ordinations, and r^2 correlations depicting the amount of variation in the original species presence-absence distance matrix that is explained by the ordination axes.

		r^2			
Fire severity	**Stress**	**Axis one**	**Axis two**	**Axis three**	**Total**
Upland					
Low severity	18.279	0.218	0.382	0.170	0.770
Moderate severity	16.237	0.405	0.117	0.302	0.824
High severity	10.101	0.273	0.170	0.452	0.894
Riparian					
Low severity	8.845	0.358	0.252	0.321	0.932

Table 3.6. Response of common riparian understory species to the Hayman Fire based on the results of an ANOVA modeling species presence or absence in 1000-m^2 plots against year. Species that increased in response to the Hayman fire are those that were more abundant (i.e., they were found in more 1000-m^2 plots) after the fire than before the fire for one or more postfire years; species that decreased were more abundant before the fire than after.

Species	Response to Hayman Fire
Short-lived forbs	
Aliciella pinnatifida	Unchanged
Androsace septentrionalis	Unchanged
Arabis hirsuta	Unchanged
Artemisia campestris	Unchanged
Axyris amaranthoides[a]	Unchanged
Bahia dissecta	Unchanged
Carduus nutans[a]	Unchanged
Chenopodium	Unchanged
Chenopodium capitatum	Unchanged
Cirsium canescens	Unchanged
Corydalis aurea	Unchanged
Conyza canadensis	Increased after fire in all years but 2003
Cryptantha virgata	Unchanged
Erysimum capitatum	Unchanged
Ipomopsis aggregata	Unchanged
Laennecia schiedeana	Increased after fire in 2007
Lactuca serriola[a]	Increased after fire from 2005 to 2007
Machaeranthera bigelovii	Unchanged
Phacelia heterophylla	Unchanged
Rudbeckia hirta	Unchanged
Silene antirrhina	Unchanged
Tragopogon dubius[a]	Unchanged
Verbascum thapsus[a]	Unchanged
Long-lived forbs	
Achillea millefolium	Unchanged
Allium cernuum	Unchanged
Antennaria parvifolia	Unchanged
Apocynum androsaemifolium	Unchanged
Arabis fendleri	Unchanged
Artemisia ludoviciana	Unchanged
Astragalus miser	Unchanged
Campanula rotundifolia	Unchanged
Chamerion angustifolium	Unchanged
Cirsium arvense[a]	Unchanged
Cystopteris fragilis	Unchanged
Epilobium ciliatum	Unchanged

Species	Response to Hayman Fire
Erigeron subtrinervis	Unchanged
Fragaria	Unchanged
Galium boreale	Unchanged
Geranium caespitosum	Unchanged
Heterotheca villosa	Unchanged
Hieracium fendleri	Unchanged
Lithospermum multiflorum	Unchanged
Linaria vulgaris[a]	Unchanged
Maianthemum stellatum	Unchanged
Mertensia ciliata	Unchanged
Mertensia lanceolata	Unchanged
Monarda fistulosa	Unchanged
Packera fendleri	Unchanged
Penstemon glaber	Unchanged
Penstemon virens	Unchanged
Potentilla fissa	Unchanged
Pseudocymopterus montanus	Unchanged
Pulsatilla patens	Unchanged
Scutellaria brittonii	Unchanged
Senecio eremophilus	Unchanged
Silene scouleri	Increased after fire in 2004 and 2006
Solidago	Unchanged
Symphyotrichum porteri	Unchanged
Taraxacum officinale[a]	Unchanged
Thalictrum fendleri	Unchanged
Viola adunca	Unchanged
Graminoids	
Agrostis scabra	Increased after fire from 2004 to 2006
Bromus ciliatus	Unchanged
Bromus inermis[a]	Unchanged
Carex	Unchanged
Elymus elymoides	Increased after fire from 2005 to 2006
Elymus trachycaulus	Unchanged
Koeleria macrantha	Unchanged
Muhlenbergia montana	Unchanged
Poa fendleriana	Unchanged
Poa pratensis[a]	Unchanged
Woody plants	
Acer glabrum	Unchanged
Arctostaphylos uva-ursi	Unchanged
Betula occidentalis	Unchanged
Juniperus communis	Unchanged
Prunus virginiana	Unchanged

Species	Response to Hayman Fire
Ribes cereum	Unchanged
Rosa	Unchanged
Rubus idaeus	Unchanged
Symphoricarpos albus	Unchanged

[a] This species is exotic to the continental United States.

Table 3.7. Pairwise comparison p-values of understory species composition between years in lightly burned riparian plots, as determined by MRBP using species presence-absence data for the 1000-m^2 plots. Overall $p < 0.001$. Significant differences ($p < 0.05$) are indicated in bold. Years with different group letters differ in species composition.

	1997	**2003**	**2004**	**2005**	**2006**	**2007**
1997		**0.044**	**0.033**	**0.030**	**0.030**	**0.029**
2003			**0.036**	**0.031**	**0.031**	**0.036**
2004				0.067	**0.031**	0.074
2005					**0.039**	0.096
2006						0.051
2007						
Groups	A	B	C	C	D	CD

Figure 3.1. Location of the 25 1000-m^2 plots within the 4-km^2 study area and within the Hayman Fire. Hayman Fire severity was determined by the USDA Forest Service from a SPOT 4 satellite image (Graham 2003), and largely correlates with the fire severity observed in our plots.

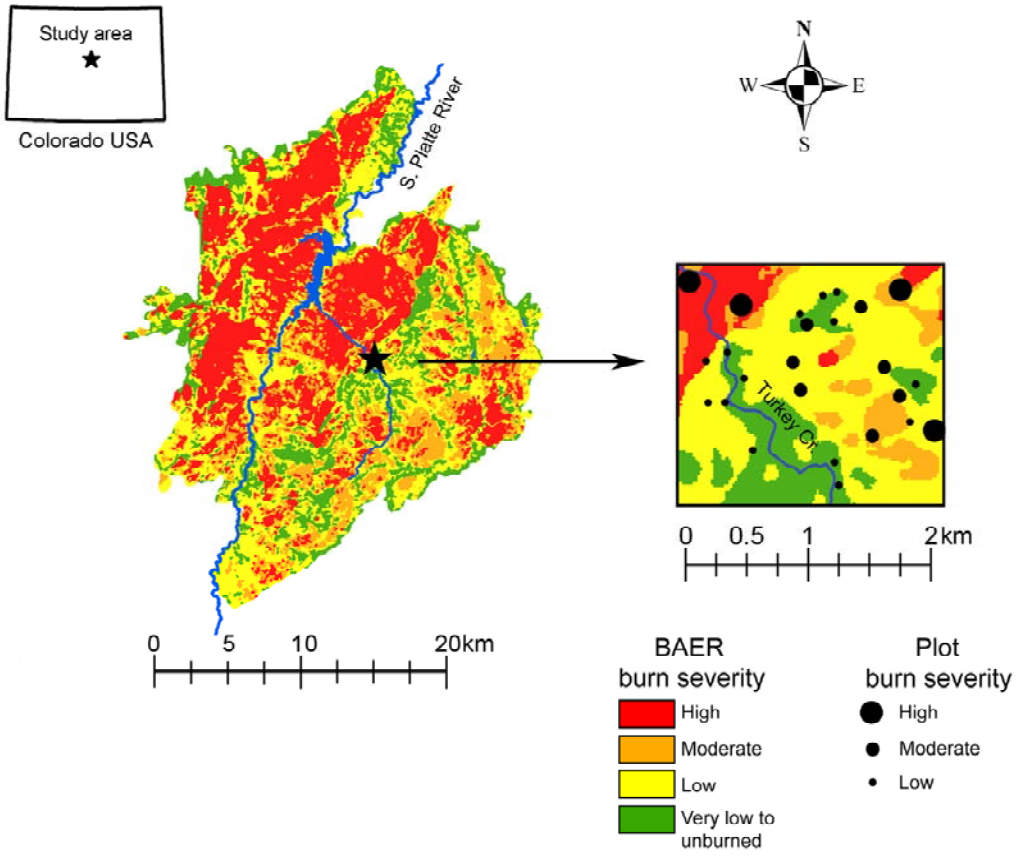


Figure 3.2. Changes in the forest understory as a result of the 2002 Hayman Fire. Photographs were taken on a severely burned ridgetop within the 4-km^2 study area. The rapid postfire recovery of *Cercocarpus montanus* and *Yucca glauca* are particularly apparent in this photo series. 2002 photo by Merrill Kaufmann; all other photos by Paula Fornwalt.

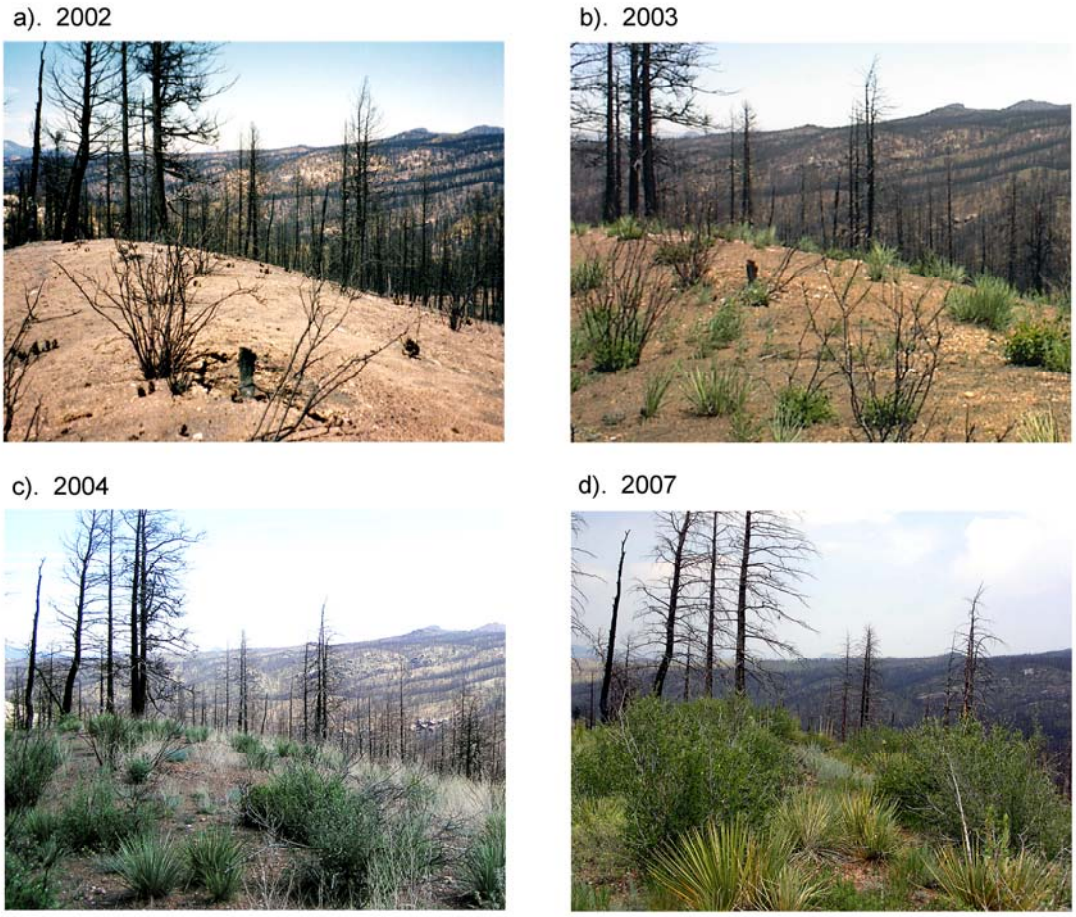


Figure 3.3. Means ± standard errors for (a) total species richness and (b) total cover in upland areas. Prefire data were collected in 1997 and postfire data were collected from 2003-2007, one to five years after the Hayman Fire. Different letters indicate differences among years.

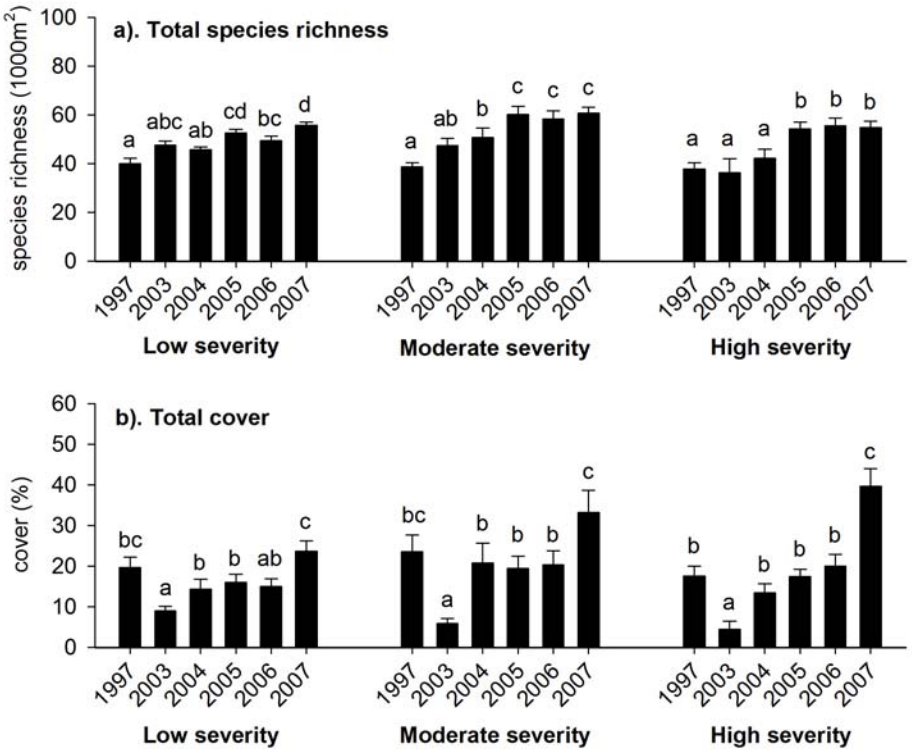


Figure 3.4. Means ± standard errors for the richness of (a) short-lived forbs, (b) long-lived forbs, (c) graminoids, and (d) woody plants in upland areas. Data are shown separately for low, moderate, and high fire severities only when fire severity * year was significant. Different letters indicate differences among years (NS = no differences among years).

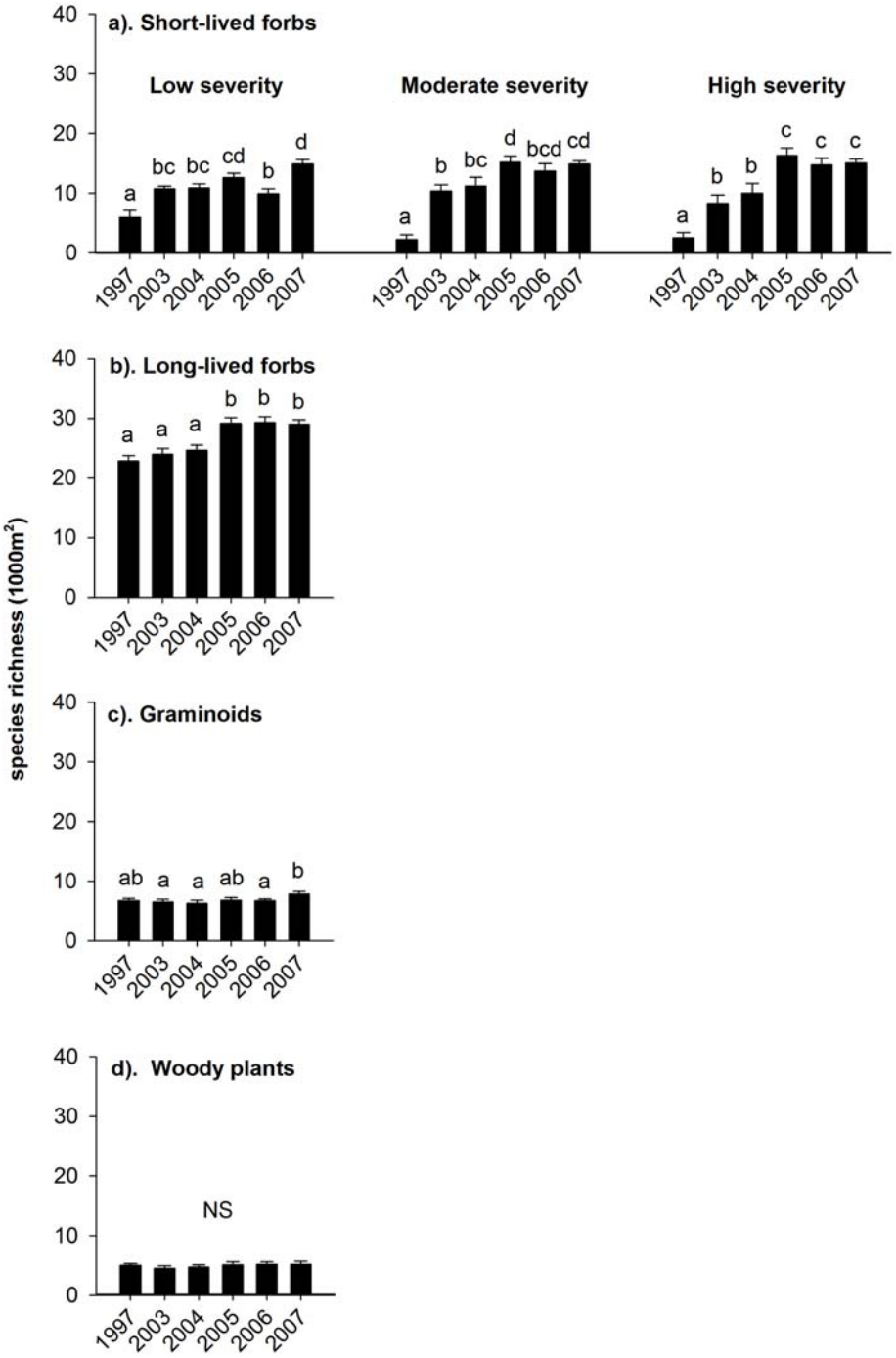


Figure 3.5. Means ± standard errors for the cover of (a) short-lived forbs, (b) long-lived forbs, (c) graminoids, and (d) woody plants in upland areas. Data are shown separately for low, moderate, and high fire severities only when fire severity * year was significant.

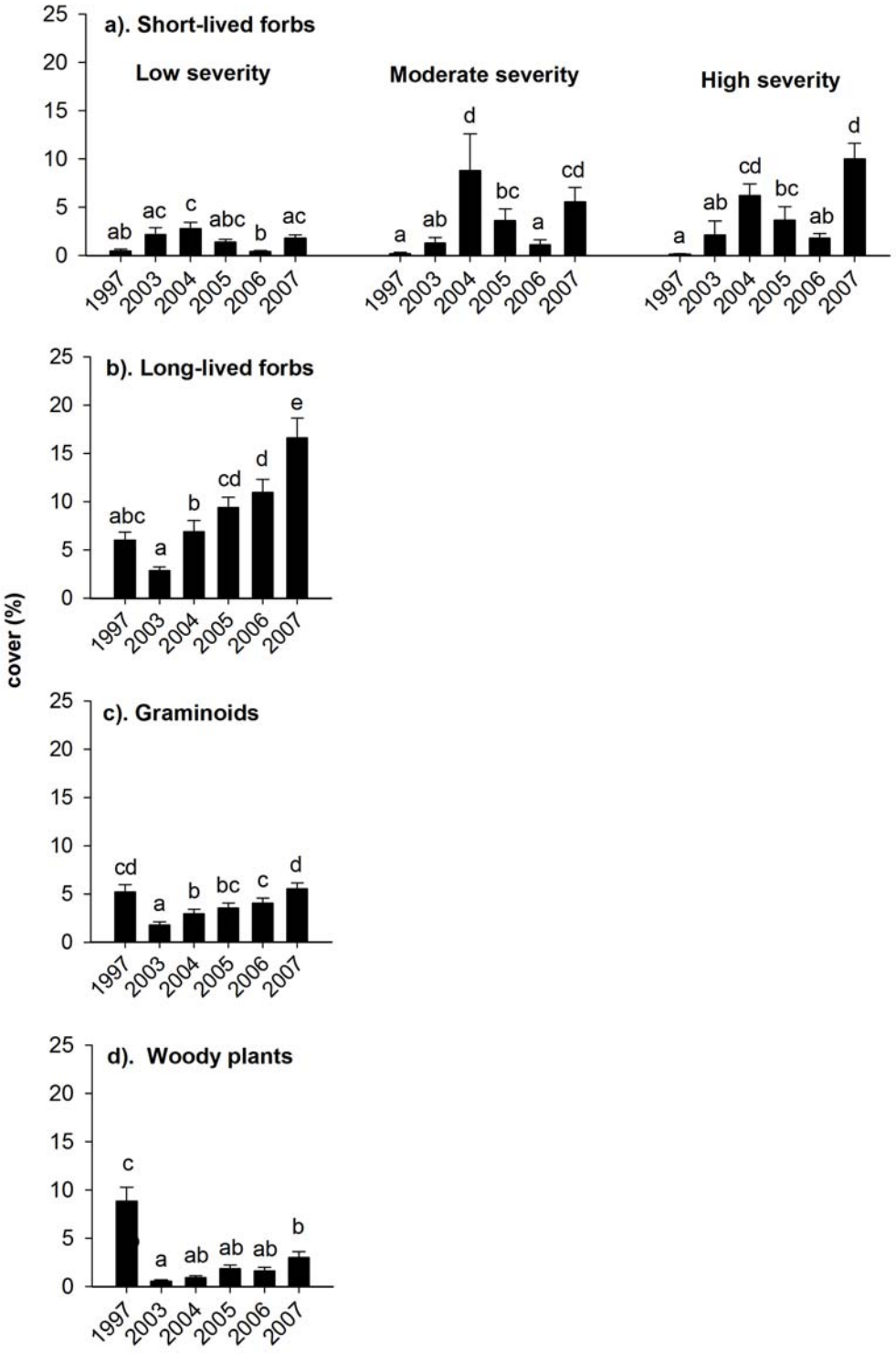
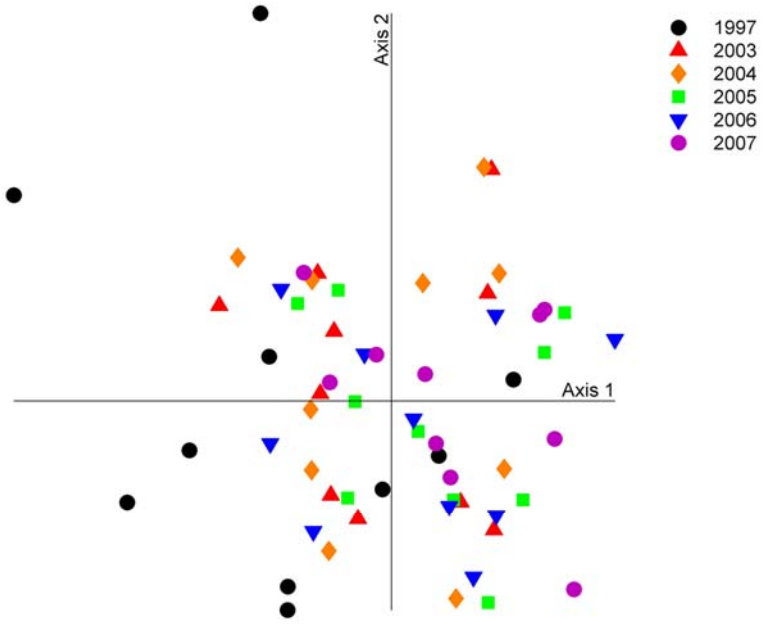


Figure 3.6. (a) Axis one versus two of an NMS ordination of understory species presence-absence in lightly burned upland 1000-m^2 plots. (b) A sample of successional vectors for three representative plots, illustrating their magnitude and direction of compositional change through time.

a). Ordination of all plots



b). Successional vectors for three representative plots

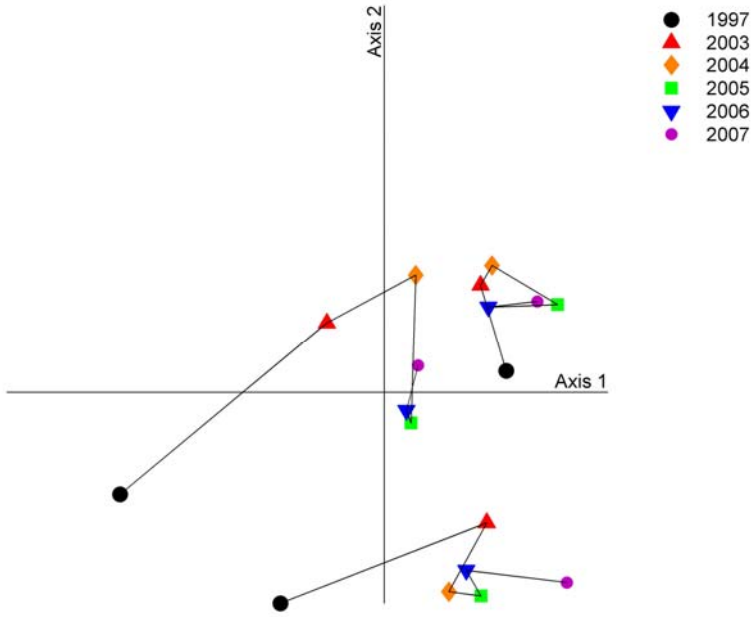


Figure 3.7. (a) Axis one versus three of an NMS ordination of understory species presence-absence in moderately burned upland 1000-m^2 plots. Plots sampled in 1997, 2003-2004, and 2006-2007 are enclosed by loops. (b) A sample of successional vectors for three representative plots, illustrating their magnitude and direction of compositional change through time.

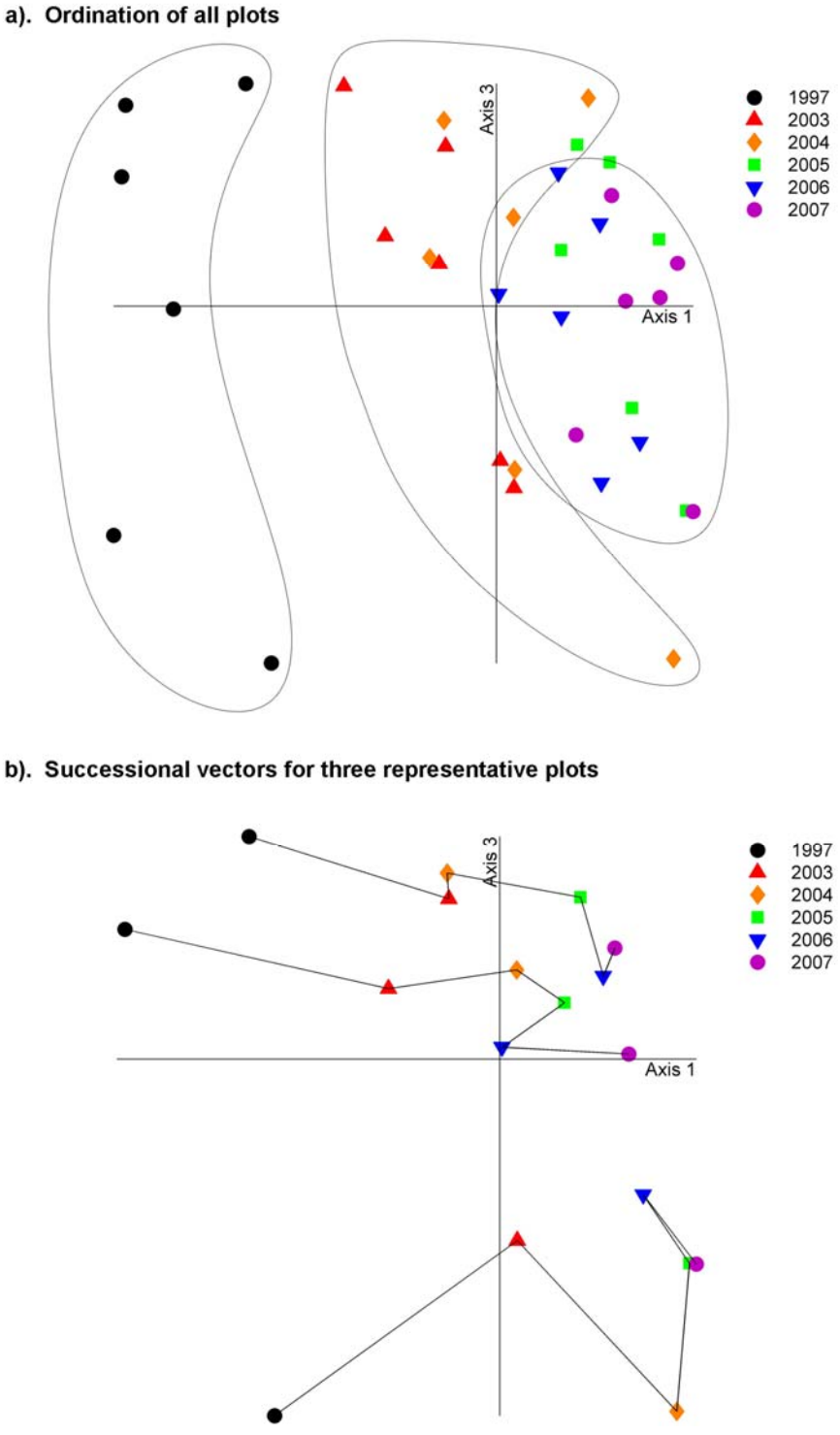
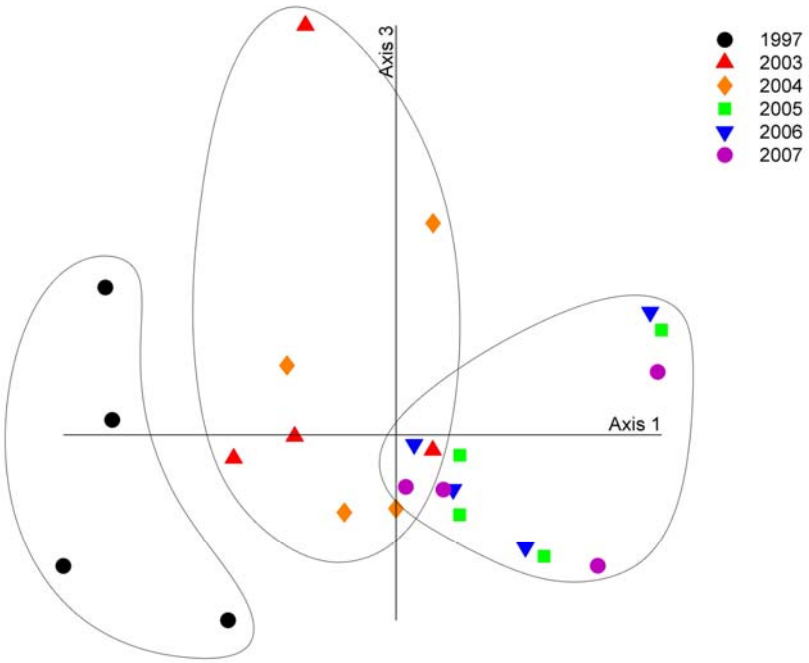


Figure 3.8. (a) Axis one versus three of an NMS ordination of understory species presence-absence in severely burned upland 1000-m^2 plots. Plots sampled in 1997, 2003-2004, and 2006-2007 are enclosed by loops. (b) A sample of successional vectors for three representative plots, illustrating their magnitude and direction of compositional change through time.

a). Ordination of all plots



b). Successional vectors for three representative plots

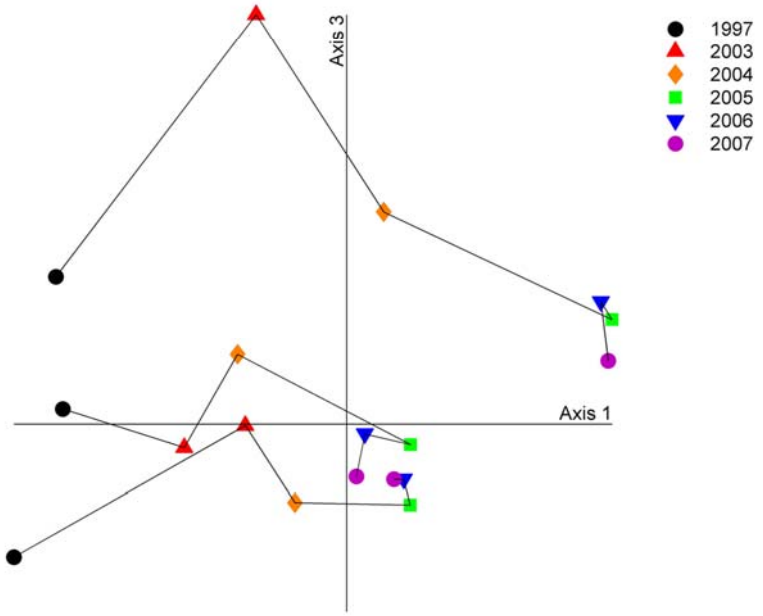


Figure 3.9. Means ± standard errors for (a) total species richness and (b) total cover in lightly burned riparian areas. There were no differences among years for either variable.

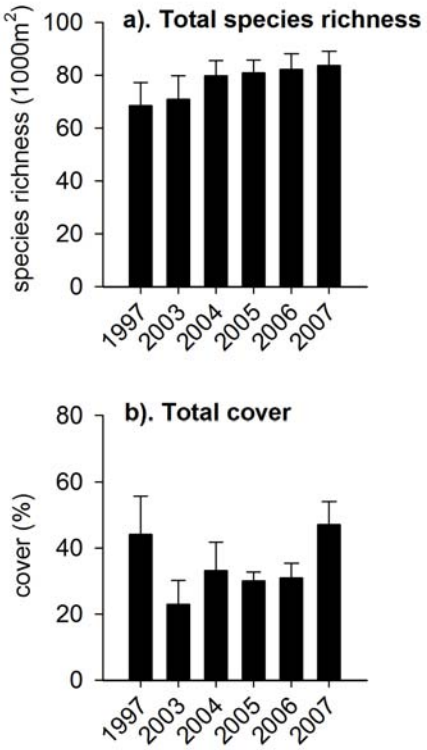


Figure 3.10. Means ± standard errors for the richness and cover of (a) short-lived forbs, (b) long-lived forbs, (c) graminoids, and (d) woody plants in lightly burned riparian areas. NS = no differences among years.

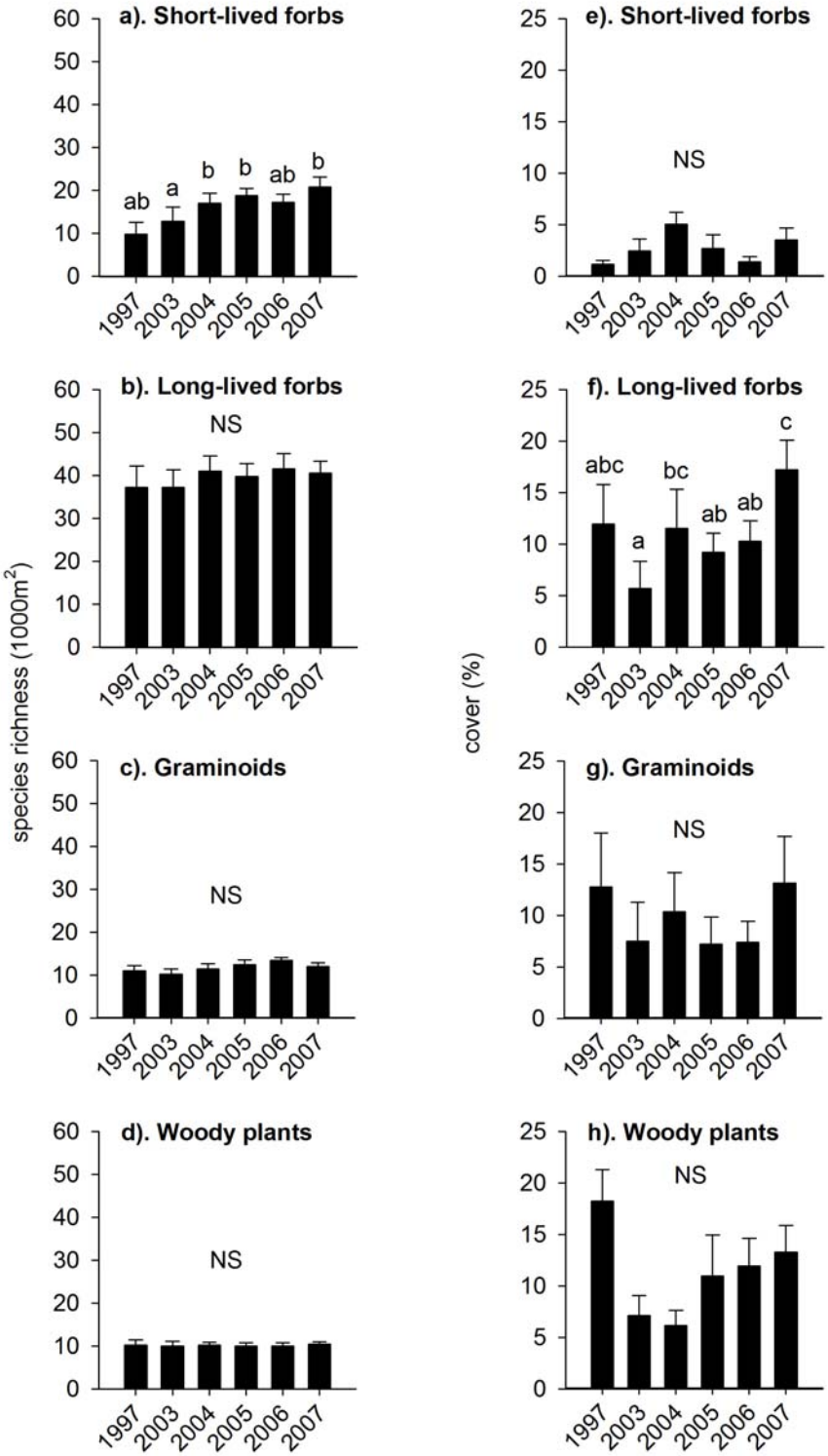
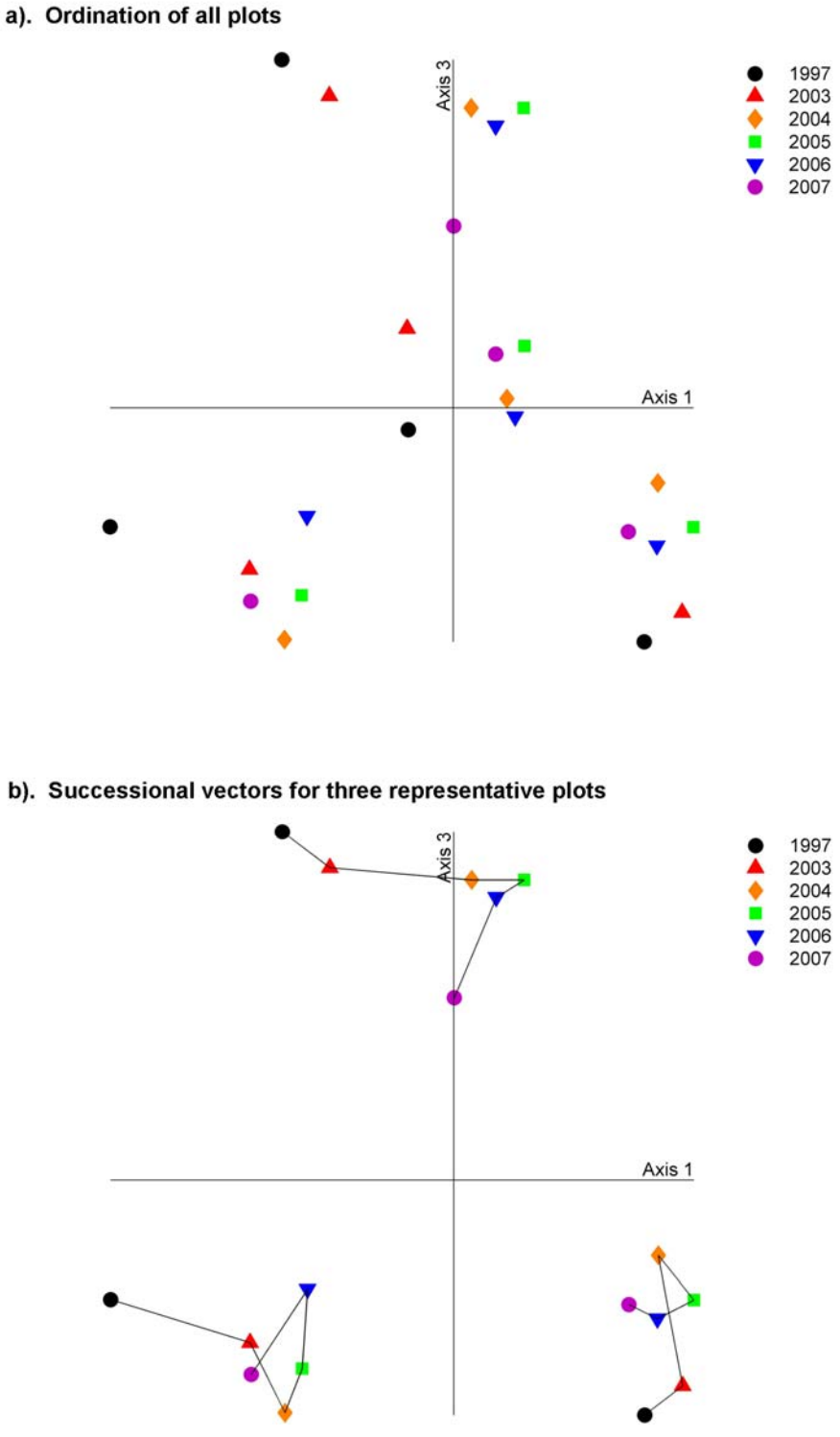


Figure 3.11. (a) Axis one versus three of an NMS ordination of understory species presence-absence in lightly burned riparian 1000-m^2 plots. (b) A sample of successional vectors for three representative plots, illustrating their magnitude and direction of compositional change through time.



CHAPTER 4: IMPACTS OF MIXED SEVERITY WILDFIRE ON EXOTIC PLANTS IN THE COLORADO FRONT RANGE

ABSTRACT

The 2002 Hayman Fire burned with mixed severity across 55,800 ha of montane Colorado forest, including pre-existing understory plots originally measured in 1997. I remeasured understory plant composition and cover in these plots annually from 2003 to 2007 to examine the influence of this wildfire on exotic plants. I found that (1) exotic richness and cover generally increased as fire severity and time since fire increased; (2) the exotic species that were present in a plot before the fire were also largely present in the plot after the fire, regardless of fire severity; (3) many new species in a plot were present elsewhere in the study area before the fire, although some new species were truly new invaders that were not found in any prefire surveys; (4) lightly burned riparian forests were not more susceptible to exotic invasion after fire than surrounding uplands that burned with similar severity; and (5) native and exotic richness and cover were positively correlated or uncorrelated for all fire severities and years. My findings suggest that exotic species were stimulated by the 2002 Hayman Fire, especially in the most severely burned areas. However, exotic richness and cover remain low as of 2007, and the positive or non-significant correlations between native and exotic richness and cover suggest that exotics have not yet interfered with the development of the native understory

community. Therefore, I conclude that exotic species are not a major ecological threat at present, but continued monitoring is necessary to evaluate if they will pose a threat in future years.

INTRODUCTION

Fire is a key ecological process in coniferous forests of western North America, and it historically played critical roles in regulating stand densities, decreasing surface fuel loads, and sustaining understory biodiversity and cover (Agee 2003; Arno 1976; Laughlin *et al.* 2004). However, today's forests differ considerably from historical ones in many regards, and fire is now performing novel functions. For example, in forests where exotic plant species have invaded or have the potential to invade, fire is now playing a role in promoting their establishment and spread (Zouhar *et al.* 2008 and citations therein).

Fire characteristics such as fire severity often influence exotic plant establishment in burned coniferous forests. Exotics are typically least stimulated in lightly burned forests and most stimulated in severely burned forests (Crawford *et al.* 2001; Freeman *et al.* 2007), although not all severely burned sites become heavily invaded (Huisinga *et al.* 2005). The response of exotic plants after fire also often varies with time since disturbance (Klinger *et al.* 2006; Nelson *et al.* 2008). Furthermore, there can be a significant interaction between fire severity and time since fire, as found by Keeley *et al.* (2003). They monitored postfire exotic response in Sierra Nevada forests one and three years after fire, and found that exotic richness and cover were not stimulated by low or

high severity fire in the first postfire year, but in the third year, exotic richness and cover escalated in the high severity but not the low severity sites.

Site-related characteristics, such as the degree of prefire exotic establishment, can also impact exotic invasion after fire. For example, unburned riparian areas often have greater exotic richness and cover than adjacent upland areas (DeFerrari and Naiman 1994; Stohlgren *et al.* 2005), and so they may be more vulnerable to increased postfire invasion than uplands that burned with similar severity. The composition of the prefire exotic community can also influence postfire exotic establishment, as not all exotic species are equally invasive in recently disturbed areas. Some species are well-adapted to disturbance, and where these species were present in the prefire community, fire often provides them with a foothold to expand (Dodge *et al.* 2008; Ferguson *et al.* 2007; Keeley and McGinnis 2007). In contrast, less fire-adapted species may decline after fire; for these species, well-timed prescribed fires are often an effective method of control (DiTomaso *et al.* 1999 and citations therein).

Exotic species can threaten native plant communities, and even drive localized native species extinctions in extreme cases (Alvarez and Cushman 2002; Minchinton *et al.* 2006; Walker and Vitousek 1991). Simple correlations between measures of native and exotic plant abundance (*e.g.*, richness, cover, density) can provide insight into whether or not exotics are negatively impacting native species. If exotics are outcompeting natives, there would likely be a negative correlation between natives and exotics; on the other hand, a positive correlation may indicate that natives and exotics are responding similarly to environmental conditions. This approach has been employed by

many researchers (Brown and Peet 2003; Parker *et al.* 1993; Stohlgren *et al.* 1999), although rarely in the context of fire (but see Keeley *et al.* 2003).

In this study, I analyzed data collected before and after the 2002 Hayman Fire, Colorado, to examine its influence on exotic plant assemblages. Prefire data were collected in 1997, five years before fire, and postfire data were collected annually from 2003 through 2007. Specifically, I addressed the following questions:

- Did fire severity and time since fire influence exotic richness and cover in burned forests?
- Was there mainly a return of exotic species that were already present before the fire, or was there a true invasion of new species after fire?
- Were riparian forests more vulnerable or less vulnerable to postfire exotic invasion than upland forests that burned with a similar severity?
- Were native and exotic richness and cover correlated (either positively or negatively), and did fire severity or time since fire influence the strength or the direction of this correlation?

METHODS

Study area and study design

I conducted my study in a 4 km^2 portion of the Pike National Forest, Colorado, approximately 60 km southwest of Denver. Forest overstories within the study area are dominated by *Pinus ponderosa* (ponderosa pine) and *Pseudotsuga menziesii* (Douglas-fir), and forest understories are a diverse assemblage of graminoids, forbs, and shrubs (Fornwalt *et al.* 2009; Kaufmann *et al.* 2000; Chapter 2). Soils are well-drained gravelly

coarse sandy loams derived from weathered Pikes Peak granite (USDA Forest Service 1992). Elevations within the study area range from 2300 to 2500 m. Precipitation averages 40 cm annually, most of which falls during the spring and summer (http://www.wrcc.dri.edu). January is the coldest month, with average highs of 7.3°C and average lows of -13.0°C; the warmest temperatures occur in July, when maximum daytime temperatures average 28.9°C (http://www.wrcc.dri.edu).

The study area and the plots within it were originally established and measured in 1996 and 1997 by Kaufmann *et al.* (2000). Five plots were established in each of five topographic environments, for a total of 25 plots: north-facing slopes, south-facing slopes, east- or west-facing slopes, ridgetops, and riparian areas. All plots were 1000 m^2 (20 x 50 m) and were located in forested areas. North, south, and east/west plots were situated on upland slopes with the long axis of the plot aligned down the fall line. Ridgetop plots were also in upland areas, with the long axis parallel to the ridge. Riparian plots were located in low-lying valley bottoms or draws near intermittent or perennial streams, with the long axis of the plot parallel to the stream channel.

In 2002, the Hayman Fire burned 55,800 ha (Graham 2003), including this study area (Figure 3.1). Approximately half of the Hayman Fire area burned as a stand replacing crown fire, much of it in a single day of extreme weather. The other half burned as a mixed severity fire, creating a mosaic of burn severities on the landscape. My study area is situated in a transitional zone between these two fire behaviors, and therefore contains components of each. In 2003, I successfully relocated and remeasured all of the original plots. Plots were also measured in 2004, 2005, 2006, and 2007.

Data collection

Understory plant data were collected using the modified-Whittaker sampling design (Stohlgren *et al.* 1995). This method uses a primary 1000-m^2 plot with several subplots nested within it. One 100-m^2 subplot is located in the center of the main plot, and two 10-m^2 subplots are located in diagonally opposite corners. Ten 1-m^2 subplots are located around the perimeter of the main plot and the 100-m^2 subplot. Vegetative cover for each understory plant species was ocularly estimated in the ten 1-m^2 subplots. The presence of cumulative additional understory species was recorded for each of the 10-m^2 subplots, the 100-m^2 subplot, and the remainder of the 1000-m^2 plot. All graminoid, forb, and shrub species were included in the surveys, but tree species were not. Approximately 11% of the plant observations were identified only to genus, while 1% were not identified at all. Generic observations were generally due to a small number of genera for which I did not attempt to distinguish individual species, either because hybridization is common (*e.g.*, *Rosa*), or because species are difficult to determine when sampled outside peak phenological development (*e.g.*, *Carex*, *Chenopodium*). Generic observations were included in the analyses, while unidentified observations were excluded. Nomenclature follows the USDA Plants Database (USDA 2008), although varieties and subspecies are not distinguished. I determined the nativity (native or exotic to the continental United States) using the *Flora of North America* and the USDA Plants Database (Flora of North America Editorial Committee 1993+; USDA 2008). Nativity was determined for generic identifications only when the classification was appropriate for all species known to occur in montane Front Range forests. Voucher specimens are stored at the USDA Forest Service Rocky Mountain Research Station in Fort Collins, Colorado.

Plot attribute, overstory, and forest floor data were collected for each plot. Slope, aspect, and elevation were documented when the plots were established (Kaufmann *et al.* 2000). At this time, diameter at breast height, species, height, and live or dead status were also measured for all trees over 1.37 m tall (Kaufmann *et al.* 2000). Live or dead status for all trees was assessed again in 2003 and percent overstory mortality due to fire was calculated for every plot. In all years, percent cover of abiotic variables including litter, duff, and bare soil were ocularly estimated in the 10 1-m^2 subplots. Percent overstory canopy cover was also assessed in all postfire years using a spherical densiometer. Densiometer measurements were systematically recorded at eight points in each plot and averaged. Prefire canopy cover measurements were not taken but were estimated using a regression of canopy cover versus basal area, which was developed with a dataset collected in nearby unburned plots ($n = 44$; $r^2 = 0.481$; Paula Fornwalt unpublished data).

Postfire rehabilitation treatment maps created by the USDA Forest Service indicate that four plots were aerially seeded in the fall of 2002. The seed used in the rehabilitation treatment was a certified weed-free mixture of 70% *Hordeum vulgare* (barley) and 30% ×*Triticosecale rimpaui* (triticale, a wheat-rye hybrid), and was applied at a rate of ~280 seeds/m^2 (Robichaud *et al.* 2003). Both *H. vulgare* and *T. rimpaui* are exotic, non-persistent, annual grasses. Seeded grasses were most abundant in the plots in 2003, and were found in each of the four 'seeded' plots, as well as in ten of the twenty-one 'unseeded' plots. However, even in 2003 seeded grass cover was negligible (< 0.1%), although preliminary analyses revealed that it was statistically greater in seeded than in unseeded plots ($p = 0.004$). In all other years, seeded grass cover did not differ

between unseeded and seeded plots ($p = 1.000$). In light of these findings, I concluded that it was not necessary to analyze the seeded and unseeded plots separately in this study.

Statistical analyses

To aid in analysis, plots were classified into groups that reflected both their fire severity and topographic position. Plots where less than 50% of the overstory trees died in the fire were categorized as having burned with low severity, while plots that burned with moderate severity had more than 50% mortality but did not experience much crown consumption. High severity plots were those with 100% mortality and complete or nearly complete crown consumption. Topographic position was defined as either upland (*i.e.*, north, south, east-west, and ridgetop) or riparian based on the plot's original topographic designation; previous work in these plots found few differences in prefire understory composition among upland categories, although upland plots differed considerably from riparian ones (Fornwalt *et al.* 2003, 2009; Chapter 2). Prefire and postfire overstory canopy cover and cover of forest floor components for low, moderate, and high severity upland plots and for low severity riparian plots are shown in Table 4.1. Moderate and high severity riparian plots are not included in this table or in any subsequent analyses because they are not sufficiently replicated. All prefire data were assigned a year of 1997 even though some plots were measured in 1996 because growing season precipitation and plant community composition did not differ between the two prefire years (Fornwalt *et al.* 2003, 2009; Chapter 2).

I used repeated measures ANOVA in SAS 9.1.3 (SAS Institute Inc., Cary, North Carolina, USA) to examine how time since fire, fire severity, and topographic position

influenced several metrics of the exotic community. The metric *total exotic richness* was calculated by tallying the number of exotic species in each 1000-m^2 plot. Total exotic richness was further divided into the *richness of 'legacy' exotic species* and the *richness of 'new' exotic species*. Legacy species were those found in a plot's pre-Hayman survey, while new exotic species were those found in a plot only after the fire. An exotic species could be a 'legacy' species in one plot but a 'new' species in another depending on whether or not it was recorded in the prefire survey. *Total exotic cover* per 1000-m^2 plot was calculated by summing the cover of all exotic species in each 1-m^2 subplot and averaging across the subplots. I first analyzed exotic response in upland areas by separately modeling each of the four dependent exotic variables described above against the independent variables year, fire severity, and year * fire severity. I then analyzed exotic response in low severity riparian areas by modeling each exotic variable against year. Finally, I compared low severity riparian and low severity upland areas by modeling total exotic richness and cover against year, topographic position, and year * topographic position. All of these repeated measures analyses used the spatial power covariance matrix, which assumes that there is a higher level of correlation between two repeated observations closer in time than between two observations further apart. Nonsignificant independent variables ($p \geq 0.05$) were iteratively excluded until only significant variables remained. Significant independent variables were further examined for pairwise differences between variable levels using least squares means with a Tukey-Kramer adjustment for multiple comparisons. Cover data were square-root transformed to improve the distribution and homogeneity of residuals.

Repeated measures ANOVAs were also used to determine the correlation between total exotic and total native richness and cover. Two separate models were constructed: I modeled total native richness against total exotic richness, year, fire severity, total exotic richness * year, total exotic richness * fire severity, and total exotic richness * year * fire severity, and I modeled total native cover against total exotic cover, year, fire severity, total exotic cover * year, total exotic cover * fire severity, and total exotic cover * year * fire severity. Upland and riparian plots were combined for these analyses. All nonsignificant ($p \geq 0.05$) variables were iteratively excluded from the models as before. If an interaction term was significant, I constructed separate models for each level of the categorical variable in the interaction term (*e.g.*, if total exotic cover * year was a significant predictor of total native cover, I conducted separate linear regressions of total native cover versus total exotic cover for each year). Cover variables were square-root transformed prior to analysis.

RESULTS

Twenty-one exotic plant species were identified over the six years of this study (Table 4.2), accounting for 8.5% of all understory species found. Ten of the exotic species are annual, biennial, or short-lived perennial forbs; three perennial forbs, three annual graminoids, and five perennial graminoids were also found. Five of the exotic species are noxious weeds in the state of Colorado: *Bromus tectorum* (cheatgrass), *Carduus nutans* (nodding thistle), *Cirsium arvense* (Canada thistle), *Linaria vulgaris* (butter and eggs), and *Verbascum thapsus* (common mullein).

V. thapsus was the most widespread exotic species; when averaged over all years it was found in 81% of plots (Table 4.2). The two next most widespread species, *Taraxacum officinale* (common dandelion) and *Lactuca serriola* (prickly lettuce), were found in an average of 62% and 56% of plots, respectively (Table 4.2). All other exotic species occurred in less than 50% of plots on average. *V. thapsus* also had the greatest cover of any exotic species, averaging 0.3% cover across all plots and years and accounting for over 40% of total exotic cover. *Poa pratensis* (Kentucky bluegrass) and *T. officinale* were the next most abundant species in terms of cover, averaging 0.1% cover each. Cover of all other exotics averaged < 0.1% each.

Exotic richness and cover in upland sites

Prior to the 2002 Hayman Fire, upland plots contained an average of 1.1 exotic species per 1000-m^2 plot, whereas after the fire, they contained an average of 3.8 species. Total exotic richness was related to year ($p < 0.001$), fire severity ($p = 0.002$), and year * fire severity ($p < 0.001$). In low severity plots, total exotic richness after fire increased relative to prefire levels only in 2007, but in moderate and high severity plots, total exotic richness was greater after fire than before in four of the five postfire years (Figure 4.1a). Furthermore, total exotic richness after fire in moderate and high severity plots generally increased as time since fire increased, although not always significantly so. Comparing fire severities, I found that total exotic richness did not differ between low, moderate, and high severity plots in 1997, 2003, or 2004, but from 2005 to 2007, total richness of exotic species in moderate and high severity areas was nearly always greater than in low severity areas (Figure 4.1a).

On average, 18% of the exotics occurring in postfire plots were legacy species originally found in the plot's prefire survey, while 82% were new species not previously found. Richness of exotic legacy species was not related to year ($p = 0.358$), fire severity ($p = 0.233$), or year $*$ fire severity ($p = 0.991$), indicating that postfire plots contained most of the species originally found before the fire, regardless of time since fire or fire severity (Figure 4.1b). However, the richness of new exotic species per plot was related to year ($p < 0.001$), fire severity ($p < 0.001$), and year $*$ fire severity ($p = 0.002$), with postfire trends through time and among fire severities closely following the trends observed for total exotic richness (Figure 4.1c).

Total exotic cover in upland areas averaged < 0.1% prior to the Hayman Fire. Total exotic cover increased postfire, although it only averaged 0.5% across all years and fire severities. As with total exotic richness, total exotic cover was significantly related to year ($p < 0.001$), fire severity ($p = 0.017$), and year $*$ fire severity ($p = 0.010$). In lightly burned areas, total exotic cover after fire never varied from prefire cover, but in moderately and severely burned areas, a postfire increase was apparent in one or more years (Figure 4.2). Total exotic cover did not differ among fire severities in 1997, 2003, or 2004, but was greater in moderate and/or high severity plots than in low severity plots from 2005 through 2007.

Exotic richness and cover in lightly burned riparian areas

Neither total exotic richness nor total exotic cover in low severity riparian plots varied over time ($p = 0.522$ and $p = 0.296$, respectively); across all years, the exotic community in these plots averaged 6.6 species and 1.6% cover. 55% of the postfire exotic species in a plot were legacy species, while 45% were new species not previously

found. The richness of legacy and new exotic species also did not vary over time ($p = 0.707$ and 0.843, respectively). Relative to lightly burned upland plots, lightly burned riparian plots had greater total exotic richness and cover over the course of the study ($p < 0.001$ and $p = 0.003$ in both cases), although trends in richness and cover through time for the two topographic positions were similar (year * topographic category: $p = 0.097$ and $p = 0.286$, respectively).

Correlations between natives and exotics

Total native richness was related to total exotic richness ($p = 0.002$), year ($p < 0.001$), and total exotic richness * fire severity ($p = 0.005$), but not to fire severity, total exotic richness * year, or total exotic richness * year * fire severity ($p = 0.301$, 0.498, and 0.105, respectively). The relationship between total native and total exotic richness was positive and significant for all fire severities (Figure 4.3a-c).

Total native cover was related to total exotic cover ($p = 0.003$), year ($p < 0.001$), and total exotic cover * year ($p = 0.025$), but not to fire severity, total exotic cover * fire severity, or total exotic cover * year * fire severity ($p = 0.507$, 0.829 and 0.531, respectively). Total native and total exotic cover were significantly and positively correlated in 1997, 2003, 2004, 2006, and 2007 (Figure 4.4a-d, f), and non-significantly but positively correlated in 2005 (Figure 4.4e).

DISCUSSION

Impacts of fire severity and time since fire on exotic species in uplands

Total exotic richness and cover in upland areas were highly dependent on fire severity (Figures 4.1a, 4.2). Exotics were least stimulated by fire in lightly burned areas

where less than 50% of the forest overstory was killed, while they were most stimulated in moderately and severely burned areas where overstory mortality was 50% or more. These findings are consistent with a growing body of research on exotic invasions in burned *P. ponderosa* forests. For example, Crawford *et al.* (2001) document a dramatic increase in exotic cover with increasing burn severity following wildfires in *P. ponderosa* forests of Arizona. They found that exotic cover two years after fire increased from 0% in nearby unburned stands to 59% in moderately burned stands and 116% in severely burned stands. Freeman *et al.* (2007) found more moderate influences of fire severity on exotics in recently burned *P. ponderosa* forests; in their study of seven western wildfires, exotic cover ranged from ~1% in unburned stands to ~2% in lightly burned stands and ~3% in severely burned stands, which is generally consistent with the findings presented here. Mechanisms to explain exotic plant response after fire have been repeatedly linked to the postfire availability of resources such as light and bare mineral soil, which are critical for exotic establishment and growth (Freeman *et al.* 2007; Keeley *et al.* 2003). The lightly burned stands measured in this study had nearly twice the canopy cover and half the exposed soil cover as severely burned stands (Table 4.1), suggesting that these important resources may also be driving exotics in this system.

Most studies on exotic response after mixed severity wildfire are conducted for only one or two years, so little is known about longer-term dynamics. Although exotic plant richness and cover in the study area were low for all years (even in the most heavily invaded locations), the data presented here suggest that exotics became increasingly abundant in moderately and severely burned sites as time since fire passed. In contrast, exotics in lightly burned areas changed little over the course of this study (Figures 4.1a,

4.2). Again, abundant levels of light and bare soil probably explain much of these postfire temporal patterns; even five years after fire, severely burned forests still had nearly 60% bare soil cover, and overstory canopy cover (from dead tree branches) was only 17% (data not shown). Annual variability in precipitation may also be driving temporal patterns to some extent (Keeley *et al.* 2005), although precipitation was below average in all postfire years (http://www.wrcc.dri.edu).

The dearth of long-term research on exotic plant response after mixed severity wildfire makes it difficult to predict how exotics in the Hayman Fire will behave in the future. Other ongoing factors that also influence exotic abundance, such as development within the wildland-urban interface, forest restoration treatments, and climate change, further complicate predictions. That being said, my data suggest that the level of invasion in lightly burned areas of the Hayman Fire will remain relatively unchanged in the foreseeable future. However, exotics may continue to expand in areas where the Hayman Fire burned hottest. Continued monitoring of exotic species within mixed severity wildfires such as the Hayman is needed if long-term patterns of postfire exotic invasion are to be better understood.

The importance of 'legacy' and 'new' species in postfire exotic invasions

I found that, regardless of fire severity and topographic position, the exotic species that were present in a plot before the fire were also largely present in the plot after the fire (Figure 4.2a). Only two species found in the prefire survey, *Bassia scoparia* (burningbush) and *Poa annua* (annual bluegrass), were never found in postfire surveys (Table 4.2), and these species were only found in one prefire plot each. The high rate of exotic return is likely because most of the common prefire exotic species are able to

survive or rapidly re-establish from seed after disturbance. For example, the perennial species *Bromus inermis* (smooth brome), *Cirsium arvense*, *Linaria vulgaris*, and *Poa pratensis* are all capable of sprouting after disturbance (USDA Forest Service 2008), while *Verbascum thapsus* seeds are able to persist in the soil seedbank for 100 years or more (Kivilaan and Bandurski 1981). Furthermore, most 'new' species in a plot were present elsewhere in the study area before the fire, which may have enabled them to quickly establish in new plots postfire (Table 4.2). These findings provide evidence that the prefire exotic community at both the local scale and the landscape scale strongly influences the composition of the postfire exotic community at a given location.

However, some new exotic species were truly new invaders that were not found in any prefire surveys (Table 4.2). The most notable of these are *Lactuca serriola*, ×*Triticosecale rimpaui*, and *Bromus tectorum*. While *L. serriola* likely established via long-distance seed dispersal (Weaver and Downs 2003), both *T. rimpaui* and *B. tectorum* are known to have been introduced in the Hayman Fire during postfire rehabilitation activities. *T. rimpaui* was intentionally seeded to help stabilize the soil in severely burned areas (Robichaud *et al.* 2003), while *B. tectorum* was unintentionally dispersed as a contaminant of postfire rehabilitation materials (Chong *et al.* 2003). The arrival of *B. tectorum* is particularly disturbing, as it is an aggressive invader that can rapidly establish and spread in an area, especially after disturbances such as fire. For example, three years after a fire in Mesa Verde National Park, Colorado, *B. tectorum* occurred in only 5% of the postfire sampling locations, but eight years after fire dense cheatgrass stands were found throughout the burn (Floyd *et al.* 2006). Heavy *B. tectorum* establishment such as was found in Mesa Verde National Park often has dire ecological consequences, such as

increased fuel production and fire frequency and decreased native species diversity and cover (Knapp 1996).

Exotic invasion in lightly burned riparian areas

Riparian areas are often 'hotspots' of exotic plant invasion in unburned forests due to an abundance of limiting resources, for example water and soil nutrients (DeFerrari and Naiman 1994; Stohlgren *et al.* 1999, 2005). Indeed, the prefire data show that unburned riparian areas in Colorado *P. ponderosa* forests may contain more than twice as many exotic species as the surrounding uplands (see also Fornwalt *et al.* 2003). Given the affinity of exotic species for riparian habitats, I expected that these areas would become more invaded after fire, yet there was no significant increase in exotic richness or cover during any of the five postfire years. While riparian areas contained greater exotic richness and cover than uplands both before and after the fire, the insignificant interaction term year * topographic category indicated that trends through time were similar for lightly burned upland and riparian areas. This suggests that lightly burned riparian areas were not any more susceptible to exotic invasion after fire than surrounding upland forests that burned with a similar severity. It is important to reiterate that riparian analyses are limited to lightly burned areas only, because an insufficient number of the prefire riparian plots happened to fall within areas of greater fire severity to provide adequate sample sizes. Clearly, more work is needed to untangle the relationship between fire severity and time since fire in these very sensitive and important ecosystems.

Correlations between native and exotic richness and cover

The positive or non-significant correlations observed between native and exotic richness and cover suggest that exotic species have not yet impacted the recovering native plant community. While simple correlations such as this do not prove a cause-and-effect relationship between exotics and natives, the relatively low richness and cover of exotics and the ample amount of bare soil available for both native and exotic plant establishment provide support for my interpretation. Instead, my results suggest that conditions favorable for native species are also favorable for exotics, a phenomenon that has been well-documented in observational studies conducted in a variety of disturbed and undisturbed systems and across multiple spatial scales (*e.g.*, Brown and Peet 2003; Keeley *et al.* 2003; Stohlgren *et al.* 1999).

Conclusions

Exotic species were favored by the 2002 Hayman Fire, especially in the most severely burned areas. However, exotic richness and cover remain low at this point in time, and native and exotic richness and cover remain positively or non-significantly correlated, so I do not consider them a major ecological threat at present. Continued monitoring is necessary to evaluate if they will pose a threat in future years. Although other portions of the Hayman Fire may be more invaded than my study area, for example, along roads, in severely burned riparian areas, and in areas that were intensively rehabilitated after the fire, I suspect that my findings are representative of much of the burn.

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Table 4.1. Mean prefire (1997) and postfire (2003-2007) percent cover of overstory and forest floor components (± standard error), by fire severity and topographic category.

Year	Overstory	Forest floor[a]		
	Canopy cover[b]	Understory cover[c]	Litter cover	Bare soil cover
Upland, low severity fire (n = 10 plots; overstory mortality = 21%)				
Prefire	51.0 ± 2.3	19.7 ± 2.6	48.2 ± 1.9	30.2 ± 1.8
Postfire	52.6 ± 4.2	15.6 ± 2.5	39.5 ± 2.8	41.8 ± 3.1
Upland, moderate severity fire (n = 6 plots; overstory mortality = 67%)				
Prefire	56.9 ± 1.1	23.6 ± 4.1	63.4 ± 4.3	13.7 ± 2.9
Postfire	42.5 ± 5.2	20.0 ± 5.1	41.6 ± 5.0	33.1 ± 4.0
Upland, high severity fire (n = 4 plots; overstory mortality = 100%)				
Prefire	52.8 ± 5.4	17.6 ± 2.4	54.4 ± 2.3	21.2 ± 4.8
Postfire	23.6 ± 4.9	19.0 ± 6.4	5.5 ± 1.8	71.7 ± 6.3
Riparian, low severity fire (n = 4 plots; overstory mortality = 33%)				
Prefire	56.7 ± 3.0	44.1 ± 11.6	53.0 ± 6.2	11.8 ± 4.3
Postfire	68.8 ± 8.0	32.9 ± 7.0	42.4 ± 7.1	21.9 ± 6.4

[a] The sum of the forest floor variables may exceed 100% because of overlap among the elements.
[b] Canopy cover is contributed by foliage, stems, and branches.
[c] Understory cover includes all vascular understory plant species (native + exotic).

Table 4.2. Exotic species documented before and after the 2002 Hayman Fire, and percent of 1000-m^2 plots containing each exotic species, by year.

Species	Growth form[a]	Percent of plots (n = 24)					
		1997	2003	2004	2005	2006	2007
Agropyron cristatum	P graminoid	0	0	8	0	0	0
Axyris amaranthoides	A forb	0	13	4	0	0	0
Bassia scoparia	A forb	4	0	0	0	0	0
Bromus inermis	P graminoid	13	13	13	21	17	25
Bromus tectorum[b]	A graminoid	0	0	0	0	0	21
Camelina microcarpa	A/B forb	0	4	4	0	0	0
Carduus nutans[b]	B/P forb	4	0	13	21	38	33
Cirsium arvense[b]	P forb	4	38	33	33	38	50
Dactylis glomerata	P graminoid	0	4	0	0	0	0
Descurainia sophia	A/B forb	0	0	0	4	4	4
Lactuca serriola	A/B forb	0	58	54	79	58	88
Linaria vulgaris[b]	P forb	13	13	46	25	29	21
Phleum pratense	P graminoid	0	0	4	0	4	4
Poa annua	A graminoid	4	0	0	0	0	0
Poa pratensis	P graminoid	25	17	17	17	17	17
Polygonum convolvulus	A forb	0	4	0	0	0	0
Sonchus asper	A forb	0	0	4	0	0	0
Taraxacum officinale	P forb	50	38	50	63	83	88
Tragopogon dubius	A/B forb	13	8	38	54	54	79
×*Triticosecale rimpaui*	A graminoid	0	54	29	50	4	8
Verbascum thapsus[b]	B forb	38	79	92	96	83	100

[a] Determined using the USDA Plants Database (USDA 2008) and local botanical keys. A = annual; B = biennial; P = perennial.

[b] A noxious weed in the state of Colorado.

Figure 4.1. Mean and standard errors for exotic richness in upland plots, by year and fire severity. The bars in (a) are shaded to reflect the relative contributions of legacy (black) and new (grey) exotic species to total exotic richness. Legacy species are those species that were found in an individual plot before the fire, while new species are species that were not present in a plot before the fire but were present after the fire. Different letters indicate significant differences in richness among years for an individual fire severity class ($p < 0.05$).

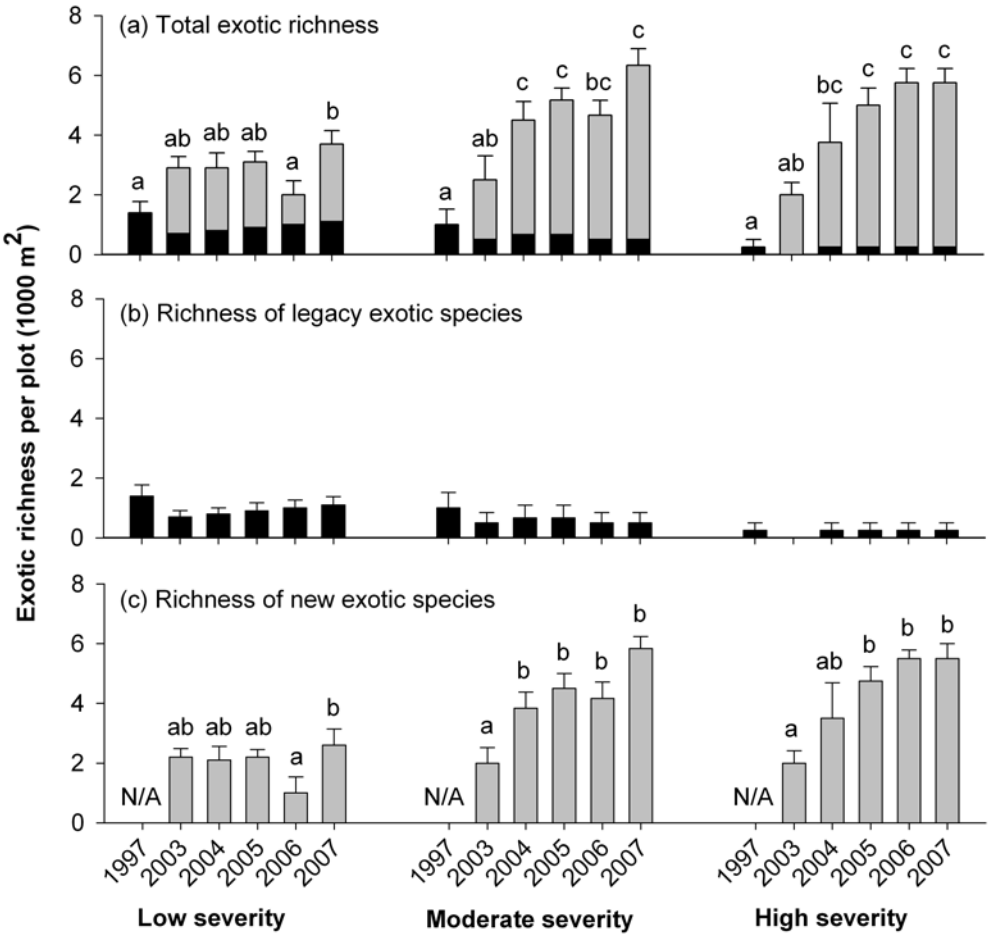


Figure 4.2. Mean and standard errors for total exotic cover in upland plots, by year and fire severity. Different letters indicate significant differences among years for an individual fire severity class ($p < 0.05$).

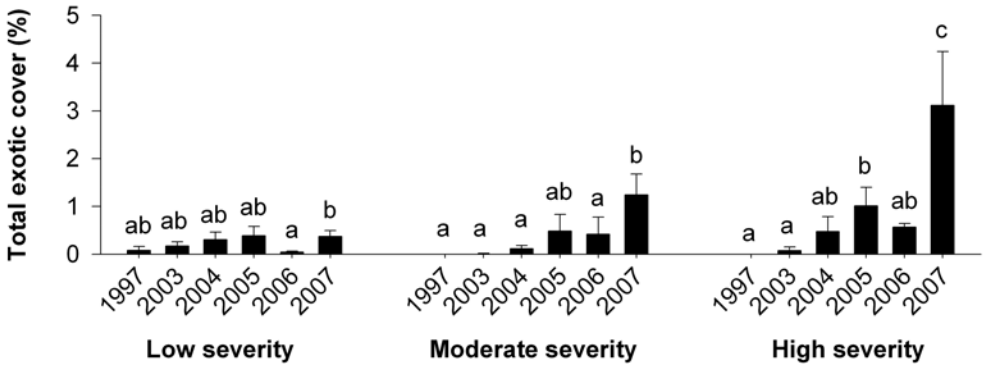


Figure 4.3. Scatterplots depicting the relationship between native and exotic richness in 1000-m^2 plots, by fire severity. The data are combined across all years because the interaction terms total exotic richness * year and total exotic richness * year * fire severity were not significant in the model.

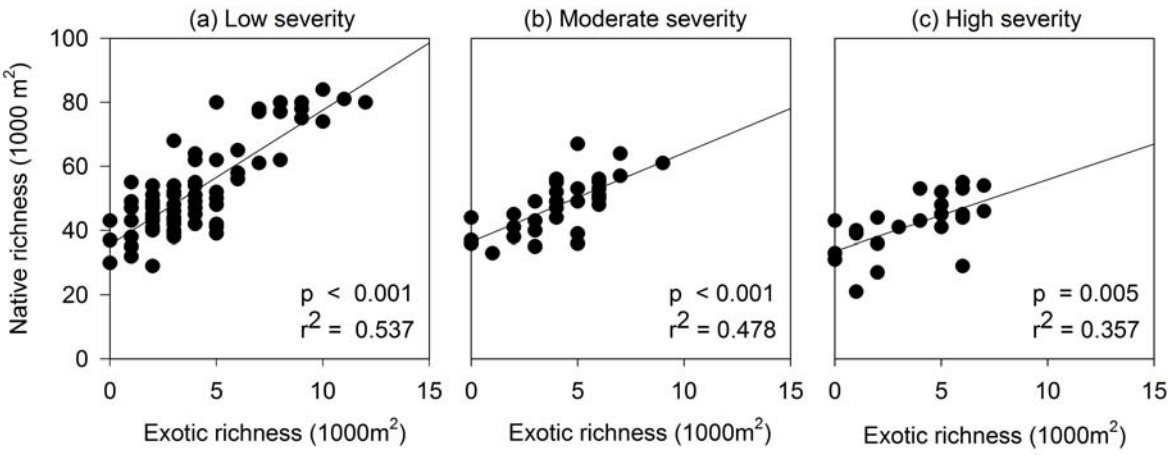
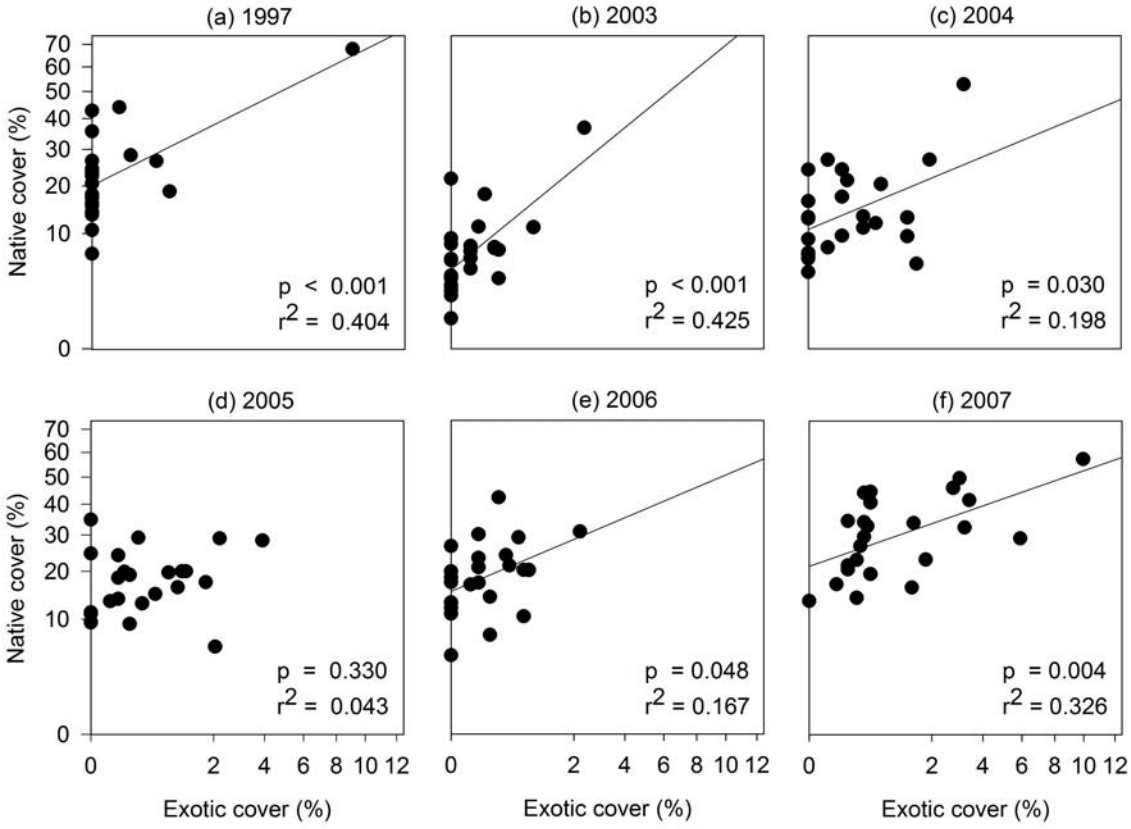


Figure 4.4. Scatterplots depicting the relationship between native and exotic understory plant cover, by year. The axes are on a square root scale so that the untransformed cover values could be presented. The data are combined across all fire severities because the interaction terms total exotic richness * fire severity and total exotic richness * year * fire severity were not significant in the model.



CHAPTER 5: POSTFIRE ESTABLISHMENT MECHANISMS OF UNDERSTORY PLANT SPECIES IN MONTANE FRONT RANGE FORESTS

ABSTRACT

The assemblage of understory plants that arises after fire is greatly influenced by the life history traits of species growing in and around the burn. In this chapter, I review the published literature to examine the mechanisms through which 230 Colorado Front Range understory plant species establish after fire *(i.e.*, does the species survive fire, germinate from onsite seed stored in the soil, and/or germinate from offsite seed dispersed into the burn?). I found that postfire establishment mechanisms for many of these species are poorly understood. Only 21 of the 230 species had published information detailing their ability to establish after fire through each of the three establishment mechanisms. In contrast, establishment mechanisms for 110 species were totally unknown, the majority of which were long-lived forbs. Despite the dearth of information, some broad patterns emerged. Short-lived forbs in this ecosystem appear to establish after fire primarily through seed stored in the soil seedbank, while sprouting is the most common establishment mechanism for long-lived forbs, graminoids, and woody plants. Many species have more than one known postfire establishment mechanism, which helps to ensure their continued presence after fire.

INTRODUCTION

The assemblage of understory plants that arises shortly after fire is greatly influenced by many factors, including the life history traits of individual species growing in and around the burned area (Lyon and Stickney 1976; Miller 2000; Rowe 1983). For many understory species, their presence in early postfire communities is primarily due to their ability to survive fire (Laughlin and Fulé 2008; Lyon and Stickney 1976; Stickney and Campbell 2000; Turner *et al.* 1997). These species are typically top-killed by fire but subsequently sprout from roots, root crowns, rhizomes, or other organs that were insulated from the heat of the burn (Rowe 1983). Understory species also establish immediately after fire from offsite or onsite seed sources (Laughlin and Fulé 2008; Lyon and Stickney 1976; Stickney and Campbell 2000; Turner *et al.* 1997). Offsite colonizers originate from the seeds of plants surviving in unburned areas within or immediately outside the fire perimeter (Stickney 1986). Typically, species that colonize burns from offsite seed sources have seeds with traits that facilitate long distance dispersal through mechanisms such as wind, water, and animals (*e.g.*, small size, aerodynamic shape, fleshy pericarps, or barbs or plumes on the seed surface; Myers *et al*. 2004; Tackenberg *et al.* 2003, 2006). In contrast, onsite colonizers originate after fire from seed present in the soil seedbank at the time of burning; indeed, fire cues such as heat or smoke are needed to trigger germination for some species (Abella *et al.* 2007; Clark 1991; Keeley *et al.* 1985).

In June 2002, the Hayman Fire burned 55,800 ha of *Pinus ponderosa* – *Pseudotsuga menziesii* (ponderosa pine – Douglas-fir) forest in the Colorado Front Range (Graham 2003). Also burned in the fire were pre-existing 1000-m^2 plots that had been

surveyed for understory plant species composition in 1997 (Fornwalt *et al*. 2003, 2009; Kaufmann *et al*. 2000; Chapter 2). Twenty-four of these plots were subsequently surveyed annually from 2003 to 2007 to assess the impact of the Hayman Fire on plant community development (Chapters 3, 4). Results revealed that the abundance of many of the common species found in the surveys was unimpacted by, or even stimulated by, the Hayman Fire, while only a few common species declined in abundance after the fire (Chapters 3, 4).

What mechanism or mechanisms enabled so many of these species to quickly establish after fire? In this chapter, I review the published literature to identify which species are known to survive fire, and which are known to quickly establish after fire from onsite or offsite seed sources, or both. I then discuss what insight the published postfire establishment information provides for interpreting the observed post-Hayman responses.

METHODS

For 230 of the 247 understory plant species identified in the pre- and post-Hayman surveys, I examined the published literature to determine whether or not they are known to survive fire and/or establish after fire from offsite or onsite seeds. The 17 species that were excluded from the literature review were those that had been identified only to genus and occurred infrequently in the dataset. Sources used for the literature review included peer-reviewed journal articles, government publications, books, theses/dissertations, and the internet.

An understory species was considered to survive fire if it sprouts from roots, root crowns, rhizomes, or other organs after fire. For a species to be classified as a survivor, it only had to be capable of surviving low severity fire. This criterion was used because a considerable portion of the available information comes solely from studies of low severity prescribed burns. I assumed that annual species could not survive fire. Species that were reported to have survived some low severity fires but not others were recorded as variable.

I categorized a species as establishing from offsite seed sources after fire if its seeds are known to be dispersed long distances by wind, water, or wildlife. For many species, the best available information on seed dispersal was qualitative rather than quantitative. For species with quantified seed dispersal distances, they were classified as offsite colonizers if their seeds have been observed to disperse 100 m or more from the parent plant (Cain *et al.* 2000). Species with conflicting responses in the literature were categorized as variable.

A species was considered an onsite colonizer after fire if it forms a persistent seedbank in the soil — that is, its seeds remain viable in the soil for at least one year (Thompson and Grime 1979). Fire-induced seed mortality in the seedbank was not considered in the assessment of onsite colonization ability because seed mortality due to fire is poorly researched, and varies greatly with factors such as fire severity, seed depth in soil, and soil moisture (Clark and Wilson 1994; Morgan and Neuenshwander 1988). Species with seeds that formed persistent seedbanks according to some sources but transient seedbanks (*i.e.*, seeds remain viable for less than one year) according to others were recorded as variable.

To aid in the interpretation and presentation of literature review results, species were classified into one of four functional groups based on life history and growth form characteristics; these functional groups included short-lived forbs, long-lived forbs, graminoids, and woody plants. Classifications were made based on the USDA Plants Database (2008) and local botanical keys (Harrington 1964; Weber and Wittmann 2001). Short-lived forbs included annuals and biennials, as well as annuals/biennials, annuals/perennials, and biennials/perennials. Long-lived forbs included perennials only. Graminoids were not separated according to life span because short-lived species were uncommon.

RESULTS AND DISCUSSION

Short-lived forbs

Results of the literature review suggest that many of the short-lived forb species found within the Hayman Fire plots can establish from onsite seed sources after fire — of the 55 species found, 16 are known to form persistent soil seedbanks, while only three are known to form transient seedbanks (Table 5.1). Indeed, four of the known seedbanking species, *Conyza canadensis*, *Corydalis aurea*, *Lactuca serriola*, and *Verbascum thapsus*, increased in abundance in upland portions of the Hayman Fire (Chapter 3), suggesting that viable seeds of these species may have been plentiful in the soil prior to the fire.

Offsite seed sources may also play a role in the postfire establishment of short-lived forbs in the Colorado Front Range, as the seeds of five species are known to disperse long distances by wind (Table 5.1). Three of these species, *Conyza canadensis*, *Lactuca serriola*, and *Tragopogon dubius*, increased in abundance in upland areas burned

by the Hayman Fire, with *C. canadensis* and *L. serriola* also increasing in riparian areas (Chapter 3). Although both offsite and onsite seed sources may be playing a role in the postfire establishment of *C. canadensis* and *L. serriola* (see above), offsite seed dispersal is likely to be particularly important for the postfire establishment of *T. dubius*, as this exotic species probably cannot sprout after fire and its seeds are transient in the soil (Chepil 1946).

The only short-lived forbs that have been observed to sprout after fire from surviving underground parts are *Corydalis aurea* and *Ipomopsis aggregata* (Table 5.1). In contrast, 20 species are annuals assumed to be incapable of sprouting. Given the paucity of sprouting short-lived forbs, it is unlikely that this postfire establishment mechanism played a significant role in short-lived forb establishment after the Hayman.

Postfire establishment mechanisms for 19 of the 55 short-lived forb species are totally unknown (Table 5.1). This includes three short-lived forbs that increased dramatically in abundance in upland portions of the Hayman Fire (*Bahia dissecta*, *Machaeranthera bigelovii*, and *Phacelia heterophylla*; Chapter 3).

Long-lived forbs

In contrast to short-lived forbs, long-lived forbs in montane Colorado Front Range forests appear to establish after fire primarily by sprouting from surviving underground parts. Literature review results show that 21 of the 115 long-lived forbs are documented postfire sprouters; in contrast, only one species, *Pyrola chlorantha*, is consistently killed by low severity fire, although its relative rarity prohibited us from determining whether or not this pattern held after the Hayman (Table 5.1). Many species, such as *Achillea millefolium*, *Apocynum androsaemifolium*, *Astragalus miser*, *Clematis columbiana*, and

Maianthemum stellatum, have been observed to sprout even after high severity fire (Lyon and Stickney 1976; McLean 1969; Stickney 1986). Other common Front Range species whose abundances were unchanged by the Hayman Fire, such as *Geranium caespitosum*, *Heterotheca villosa*, and *Packera fendleri*, may also be strong postfire sprouters, although their sprouting abilities have not been studied (Chapter 3). Six long-lived forbs appear to be variable postfire sprouters, such as *Fragaria* spp. (Table 5.1); these species survived fire in some studies and died after fire in others. I found that the abundance of *Fragaria* spp. was unchanged after the Hayman Fire in both upland and riparian areas, and so it may be a reliable sprouter in Front Range forests (Chapter 3).

Although sprouting was the most commonly documented postfire establishment strategy among long-lived forbs, it is likely that many species also establish from offsite seed sources after fire. Indeed, 14 long-lived forb species have seeds capable of long distance dispersal (Table 5.1). Long distance seed dispersal has been repeatedly documented for *Chamerion angustifolium* and *Cirsium arvense*, for example. Seeds of other long-lived forbs, including *Antennaria* spp., *Heterotheca villosa*, *Packera fendleri*, and *Symphyotrichum porteri*, also may disperse into burned areas from offsite sources, though this has not yet been documented in the literature. These members of the Asteraceae family have a well-developed pappus that facilitates wind dispersal (Harrington 1964; USDA 2008).

The seeds of seven long-lived forbs have been observed to persist in the soil seedbank, including the common species *Artemisia frigida* and *Taraxacum officinale* (Table 5.1). In contrast, three species, *Apocynum androsaemifolium*, *Galium boreale*, and *Linnaea borealis*, are known to form only transient seedbanks (Table 5.1).

Astonishingly, 74 of the 115 species have no available postfire establishment information (Table 5.1). Many of these species are extremely common in Front Range forests and warrant further study.

Graminoids

Sprouting also appears to be a common method of postfire regeneration among graminoids, with 21 of the 39 species found in the Hayman plots known to regenerate from surviving underground parts (Table 5.1). Species that are well-documented postfire sprouters include *Bouteloua gracilis*, *Koeleria macrantha*, *Poa fendleriana*, and *Schizachyrium scoparium*, all of which were unchanged in abundance in upland areas burned by the Hayman Fire (Chapter 3). Indeed, none of the perennial graminoid species are known to be consistently killed by low severity fire (Table 5.1). I assumed that the two annual graminoids were incapable of sprouting after fire (Table 5.1).

Only seven graminoid species are known to have seeds that can disperse long distances, while four are known to have seeds that disperse only in the vicinity of the parent plant (or seeds are sterile, in the case of ×*Triticosecale rimpaui*, which was used in postfire rehabilitation activities; Table 5.1). Offsite colonizers include the exotic species *Bromus tectorum*, which was not found in the Hayman Fire plots before the fire, but was found after (Chapter 4). While this species may have dispersed into the Hayman by wind or wildlife (Hulbert 1955), it is also possible that it was introduced by humans as a contaminant of postfire rehabilitation materials (Chong *et al.* 2003).

Postfire establishment from onsite seed sources is also possible for eight of the graminoids (Table 5.1). Onsite colonizers include *Calamagrostis canadensis*, *Carex* spp., *Elymus trachycaulus*, and *Phleum pratense*. Seeds of four graminoids, *Bromus*

inermis, *Koeleria macrantha*, *Pseudoroegneria spicata*, and ×*Triticosecale rimpaui*, are known to be only transient in the seedbank.

In general, postfire establishment mechanisms of graminoids are better understood than the establishment mechanisms of short- and long-lived forbs. This may be because many of the graminoids are important forage species for cattle and wildlife, and the use of fire as a management tool for improving range conditions has been widely researched (Dwyer and Pieper 1967; Wright 1974). Also, many of the graminoids are broadly distributed throughout the western United States, and so their response to fire is of interest to a large group of researchers and land managers, while many of the forbs are restricted in their range and therefore are less apt to be studied (USDA 2008). That being said, I still found that 10 of the 39 graminoids have no available postfire establishment information (Table 5.1). This includes *Bromus ciliatus* and *Festuca saximontana*, two species that are very common in montane Front Range forests.

Woody plants

Many woody understory plant species found in the Hayman plots can reestablish after fire by sprouting. Indeed, this has been documented in the literature for 13 of the 21 species (Table 5.1). Species such as *Cercocarpus montanus*, *Ribes cereum*, *Rosa* spp., and *Symphoricarpos albus* are widely known to sprout postfire, and all were unchanged by the Hayman Fire in upland and/or riparian areas (Chapter 3). In contrast, only one species, *Juniperus communis*, is known to be consistently killed by low severity fire (Table 5.1), and indeed it declined in abundance after the Hayman Fire in uplands, although not in riparian zones where fire behavior was more spotty (Chapter 3).

Six woody species potentially establish from offsite seed sources after fire (Table 5.1). These include *Rosa* spp., *Rubus idaeus*, and *Symphoricarpos albus*. For the remainder of the species, their potential to reestablish after fire from offsite seed sources was variable or unknown.

Literature review results show that five of the woody understory species documented here store seeds in the soil seedbank, while two do not (Table 5.1). Examples of seedbanking species include *Rubus idaeus*, whose seeds can remain viable in the soil for decades (Brinkman 1974; Whitney 1986). In contrast, seeds of *Salix* spp. only remain viable for a few months at most (Densmore and Zasada 1983; Moss 1938).

Postfire establishment mechanisms for woody plants are nearly as well researched as graminoids, and likely for the same reasons. Yet some knowledge voids still remain — seven of the 21 woody species lack any postfire establishment information, including *Jamesia americana*, *Ribes inerme*, and *Rubus deliciosus*, all of which are widespread in the Front Range.

SUMMARY AND CONCLUSIONS

Postfire regeneration strategies for many of the Colorado Front Range plant species studied here are poorly understood. Only 21 of the 230 species had published information detailing their ability to establish after fire through each of three mechanisms — sprouting from surviving organs at or near the soil surface, establishing from offsite seed sources, and establishing from seed stored in the soil seedbank. In contrast, establishment mechanisms for 110 species were totally unknown. Postfire establishment

mechanisms of long-lived forbs were considerably less well-understood than those of short-lived forbs, graminoids and woody plants, and clearly warrant future research.

Despite the dearth of information, some patterns nonetheless emerged. Seedbanking was the most commonly documented postfire establishment mechanism for short-lived forbs, while sprouting was the most commonly documented mechanism for long-lived forbs, graminoids, and woody plants. Many species had more than one known mechanism for establishing after fire, which helps to ensure their persistence in burned areas.

Fire-related factors such as severity, extent, and seasonality clearly impact plant establishment after fire (Lee 2004; Turner *et al.* 1997; Wang and Kemball 2005). Unfortunately, these factors could not be incorporated here due to the limited availability of postfire establishment information. Because *Pinus ponderosa – Pseudotsuga menziesii* forests in the Colorado Front Range typically burn with a mixed severity fire regime (Brown *et al*. 1999; Veblen *et al*. 2000), future work on postfire plant establishment should incorporate factors such as fire severity if it is to provide the clearest insight into how Front Range plant communities recover after fire.

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Table 5.1. Documented postfire establishment mechanisms for 230 Colorado Front Range plant species. Documented postfire establishment mechanisms include: survive (*i.e.*, the species is capable of surviving fire by sprouting from surviving organs at or near the soil surface after fire); offsite seed (*i.e.*, the species can quickly establish burned areas from offsite seed sources); and onsite seed (*i.e.*, the species can quickly establish burned areas from seed stored in the soil seedbank).

Species	Survive	Offsite seed	Onsite seed	Comments	References
Short-lived forbs					
Aliciella pinnatifida, sticky gilia	unknown	unknown	unknown		
Amaranthus retroflexus, redroot amaranth	no	variable	yes	I assumed annuals could not survive fire; seeds typically fall <2 m from the parent plant; seeds may possibly be dispersed long distances by wildlife and water; seeds can remain viable in the soil for decades	Burnside *et al*. 1981; Chepil 1946; Costea 2004; Kivilaan and Bandurski 1981; Thompson *et al*. 1997; Toole and Brown 1946; USDA Forest Service 2008
Androsace septentrionalis, pygmyflower rockjasmine	unknown	unknown	yes	Seed longevity in the seedbank is 2-5 y	Chambers 1995; Thompson *et al*. 1997
Arabis glabra, tower rockcress	unknown	unknown	unknown	seeds possibly persist in the soil seedbank	Clark 1991
Arabis hirsuta, hairy rockcress	unknown	unknown	variable	Seeds are transient or short-term persistent in the soil seedbank	Thompson *et al*. 1997
Artemisia campestris, field sagewort	unknown	unknown	no		Thompson *et al*. 1997

Species	Survive	Offsite seed	Onsite seed	Comments	References
Axyris amaranthoides, Russian pigweed[a]	no	unknown	variable	I assumed annuals could not survive fire	Chepil 1946; Toole and Brown 1946
Bahia dissecta, ragleaf bahia	unknown	unknown	unknown		
Bassia scoparia, burningbush[a]	no	yes	variable	I assumed annuals could not survive fire; can colonize sites via its "tumbleweed" dispersal mechanism; seeds are typically transient or short-term persistent in the soil	Becker 1978; Burnside *et al*. 1981; Chepil 1946; Iverson and Wali 1981; Thompson *et al*. 1997; USDA Forest Service 2008; Zorner *et al*. 1984
Camelina microcarpa, littlepod falseflax[a]	unknown	unknown	no		Chepil 1946
Carduus nutans, nodding plumeless thistle[a]	unknown	variable	yes	Possibly sprouts from the root crown after fire; seeds mainly fall near the parent plant, with <1% moving 100 m under windy conditions; seed can remain viable in the soil seedbank for 10 y or more; can increase dramatically after fire	Burnside *et al*. 1981; Desrochers *et al*. 1988; Floyd-Hanna *et al*. 1993; Popay and Medd 1990; Smith and Kok 1984; Thompson *et al*. 1997; USDA Forest Service 2008
Chaenactis douglasii, Douglas' dustymaiden	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Chamaesyce maculata, spotted sandmat	no	no	unknown	I assumed annuals could not survive fire	Ohnishi *et al*. 2008
Chenopodium capitatum, blite goosefoot	no	unknown	unknown	I assumed annuals could not survive fire; seeds possibly persist in the seedbank	Clark 1991
Chenopodium graveolens, fetid goosefoot	no	unknown	unknown	I assumed annuals could not survive fire	
Chenopodium, goosefoot	no	unknown	unknown	Species are mostly *C. fremontii* and *C. leptophyllum*, and possibly *C. album*; I assumed annuals could not survive fire; can increase dramatically after fire	Laughlin *et al*. 2004; Poreda 1994
Cirsium canescens, prairie thistle	unknown	unknown	unknown	Seeds possibly do not disperse far from the parent plant	Lamp and McCarty 1981
Cirsium undulatum, wavyleaf thistle	unknown	unknown	unknown		
Collomia linearis, narrowleaf mountain trumpet	no	unknown	yes	I assumed annuals could not survive fire; can increase in abundance after fire	Hauser 2008; Stickney and Campbell 2000

Species	Survive	Offsite seed	Onsite seed	Comments	References
Conyza canadensis, Canadian horseweed	unknown	yes	yes	Seeds can disperse >100 m from the parent plant; seeds are typically short-term persistent in the soil seedbank, but can remain viable for >10 y; can increase dramatically after fire	Crawford *et al.* 2001; Dauer *et al.* 2007; Regehr and Bazzaz 1979; Stickney 1986; Thompson *et al*. 1997; Weaver 2001
Corydalis aurea, scrambledeggs	yes	no	yes	Seeds are long-lived in the soil seedbank and seed germination is probably stimulated by fire; often increases dramatically during the first or second postfire year	Anderson and Romme 1991; Catling *et al*. 2001, 2002; Crane *et al*. 1983; Hanzawa *et al*. 1985; USDA Forest Service 2008; Wang and Kemball 2005
Cryptantha virgata, miner's candle	unknown	unknown	unknown		
Descurainia incana, mountain tansymustard	unknown	unknown	unknown		
Descurainia sophia, herb sophia[a]	unknown	unknown	yes	Seeds are possibly dispersed long distances by wildlife; seeds can remain viable in the soil seedbank for at least 2 y, and up to 10 y	Best 1977; Conn and Deck 1995; Thompson *et al*. 1997; USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Dracocephalum parviflorum, American dragonhead	unknown	unknown	yes	Seeds can remain viable for >10 y in the soil seedbank; often increases dramatically during the first or second postfire year	Anderson and Romme 1991; Catling *et al.* 2001, 2002; Conn and Deck 1995; Stickney and Campbell 2000; USDA Forest Service 2008
Epilobium brachycarpum, autumn willowweed	no	unknown	unknown	I assumed annuals could not survive fire; establishes from seed after fire, although seed origin is unknown	Metlen *et al.* 2006
Erigeron divergens, spreading fleabane	unknown	unknown	unknown		
Erigeron flagellaris, trailing fleabane	unknown	unknown	unknown		
Erysimum capitatum, sanddune wallflower	unknown	unknown	unknown		
Gayophytum diffusum, spreading groundsmoke	no	unknown	unknown	I assumed annuals could not survive fire; can increase dramatically after fire	Laughlin *et al.* 2004
Gentianella amarella, autumn dwarfgentian	unknown	unknown	unknown	Seeds are possibly stored in the soil seedbank	Stickney and Campbell 2000

Species	Survive	Offsite seed	Onsite seed	Comments	References
Hackelia floribunda, manyflower stickseed	unknown	unknown	unknown	Seeds are possibly stored in the soil seedbank	Clark 1991
Ipomopsis aggregata, skyrocket gilia	yes	unknown	unknown	Sprouts from the root crown after fire; seeds possibly persist in the soil seedbank	Paige 1992
Lactuca serriola, prickly lettuce[a]	unknown	yes	yes	Seeds are typically viable in the seedbank for 3-5 y; seeds are primarily wind dispersed, but dispersal by water may also be important; can increase dramatically after fire	Chepil 1946; Crane *et al*. 1983; Lyon 1971; Marks and Prince 1982; Stickney and Campbell 2000; Thompson *et al*. 1997; Toole and Brown 1946; Weaver and Downs 2003
Laennecia schiedeana, pineland marshtail	no	unknown	unknown	I assumed annuals could not survive fire; possibly establishes from the soil seedbank	Abella *et al*. 2007
Lappula occidentalis, stickseed	unknown	unknown	unknown		
Machaeranthera bigelovii, Bigelow's tansyaster	unknown	unknown	unknown		
Matricaria discoidea, disc mayweed	no	unknown	yes	I assumed annuals could not survive fire; seeds can remain viable in the soil for >5 y	Conn and Deck 1995; Roberts and Neilson 1981; Thompson *et al*. 1997

Species	Survive	Offsite seed	Onsite seed	Comments	References
Oenothera villosa, hairy evening primrose	unknown	unknown	yes	Seeds can remain viable in the soil for >3 y	Chepil 1946
Orthocarpus luteus, yellow owlclover	no	unknown	unknown	I assumed annuals could not survive fire	
Phacelia alba, white phacelia	no	unknown	unknown	I assumed annuals could not survive fire	
Phacelia bakeri, Baker's scorpionweed	unknown	unknown	unknown		
Phacelia heterophylla, varileaf phacelia	unknown	unknown	unknown		
Polygonum convolvulus, black bindweed[a]	no	unknown	yes	I assumed annuals could not survive fire; seeds are possibly dispersed long distances by water; seeds can remain viable in the soil for >5 y, but tend to germinate as soon as conditions are favorable	Chepil 1946; Conn and Deck 1995; Hume *et al*. 1983
Polygonum douglasii, Douglas' knotweed	no	unknown	yes	I assumed annuals could not survive fire; can increase dramatically after fire	Laughlin *et al*. 2004; Stickney and Campbell 2000

Species	Survive	Offsite seed	Onsite seed	Comments	References
Potentilla norvegica, Norwegian cinquefoil	unknown	yes	yes	Seeds are capable of long-distance dispersal, although most fall close to the parent plant; seeds can remain viable in the soil for decades	Conn and Deck 1995; Stickney and Campbell 2000; Thompson *et al*. 1997; Toole and Brown 1946; Werner and Soule 1976
Pseudognaphalium macounii, Macoun's cudweed	unknown	unknown	unknown		
Rorippa sphaerocarpa, roundfruit yellowcress	no	unknown	unknown	I assumed annuals could not survive fire	
Rudbeckia hirta, blackeyed Susan	unknown	unknown	yes	Possibly sprouts from the root crown after fire; seeds can remain viable for >30 y in the soil seedbank	Toole and Brown 1946; USDA Forest Service 2008
Silene antirrhina, sleepy silene	no	unknown	unknown	I assumed annuals could not survive fire	
Solanum triflorum, cutleaf nightshade	no	unknown	unknown	I assumed annuals could not survive fire	
Sonchus asper, spiny sowthistle[a]	no	unknown	variable	I assumed annuals could not survive fire; seeds are possibly dispersed long distances by wind; seeds can be transient or persistent in the seedbank	Hutchinson *et al*. 1984; Roberts and Neilson 1981; Thompson *et al*. 1997

Species	Survive	Offsite seed	Onsite seed	Comments	References
Townsendia grandiflora, largeflower townsend daisy	unknown	unknown	unknown		
Tragopogon dubius, yellow salsify[a]	unknown	yes	no	Wind gusts can transport seeds >250 m, although most seeds fall within 5 m of parent plants; can increase dramatically after fire	Chepil 1946; Clements *et al*. 1999; Gross 1980; Lyon 1971; Stickney and Campbell 2000; Thompson *et al*. 1997
Verbascum thapsus, common mullein[a]	unknown	no	yes	Seeds typically fall close to the parent plant; seeds can remain viable in the seedbank for decades; can increase dramatically after fire	Gross 1980; Gross and Werner 1978; Kivilaan and Bandurski 1981; Lyon 1971; Stickney and Campbell 2000; Thompson *et al*. 1997; Toole and Brown 1946; USDA Forest Service 2008
Long-lived forbs					
Achillea millefolium, common yarrow	yes	yes	variable	Sprouts from extensive rhizomes after fire; seeds can be transient or short-term persistent in the soil seedbank	Anderson and Romme 1991; Kannangara and Field 1985; Lyon and Stickney 1976; McLean 1969; Stickney and Campbell 2000; Thompson *et al*. 1997; USDA Forest Service 2008; Wang and Campbell 2005

Species	Survive	Offsite seed	Onsite seed	Comments	References
Agoseris aurantiaca, orange agoseris	unknown	unknown	unknown		
Allium cernuum, nodding onion	yes	unknown	unknown	Sprouts from a deeply buried bulb	Stickney and Campbell 2000
Anemone canadensis, Canadian anemone	yes	unknown	unknown		Wang and Kemball 2005
Anemone cylindrica, candle anemone	unknown	unknown	unknown		
Antennaria neglecta, field pussytoes	variable	unknown	unknown	Can be harmed or killed by low severity fire, seeds are possibly dispersed long distances by wind	Hauser 2008; Stickney 1986
Antennaria parvifolia, smallleaf pussytoes	unknown	unknown	unknown	The light seeds are possibly dispersed by wind; seeds are possibly transient in the soil seedbank	USDA Forest Service 2008
Apocynum androsaemifolium, spreading dogbane	yes	yes	no	Sprouts from deeply buried rhizomes	Ahlgren 1960; Lyon and Stickney 1976; Steele and Geier-Hayes 1995; USDA Forest Service 2008
Aquilegia coerulea, Colorado blue columbine	unknown	unknown	unknown	Possibly sprouts after fire	Bartos and Mueggler 1981
Arabis fendleri, Fendler's rockcress	unknown	variable	unknown		Stickney and Campbell 2000

Species	Survive	Offsite seed	Onsite seed	Comments	References
Arenaria hookeri, Hooker's sandwort	unknown	unknown	unknown		
Artemisia frigida, fringed sagewort	unknown	unknown	yes	Buried seeds can remain viable for >5 y in the soil, but tend to geminate whenever conditions are favorable	Bai and Romo 1994; USDA Forest Service 2008
Artemisia ludoviciana, louisiana sagewort	unknown	unknown	unknown	May sprout from rhizomes; can increase in cover after fire	Forde *et al*. 1984; USDA Forest Service 2008
Astragalus alpinus, alpine milkvetch	unknown	unknown	unknown	Possibly establishes from soil-stored seed after fire; seed germination can be enhanced by heat treatments	Clark 1991
Astragalus miser, weedy milkvetch	yes	unknown	unknown	Sprouts from buds along the taproot; sprouts even after severe fire; possibly regenerates from soil-stored seed	Anderson and Romme 1991; Fischer and Clayton 1983; McLean 1969; Steele and Geier-Hayes 1995
Astragalus parryi, Parry's milkvetch	unknown	unknown	unknown		
Besseya plantaginea, white river coraldrops	unknown	unknown	unknown		
Brickellia eupatorioides, false boneset	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Brickellia grandiflora, tasselflower brickellbush	unknown	unknown	unknown		
Campanula rotundifolia, bluebell bellflower	yes	unknown	variable	Sprouts from rhizomes after fire; possibly establishes from offsite sources; seeds can be transient or persistent in the soil seedbank	Bakker *et al*. 1996; Hobbs *et al*. 1984; Stickney 1986; Thompson and Grime 1979; Thompson *et al*. 1997
Castilleja integra, wholeleaf Indian paintbrush	unknown	unknown	unknown		
Castilleja miniata, scarlet Indian paintbrush	yes	yes	unknown	Sprouts from the caudex or from the taproot after fire	McLean 1969; Stickney 1986; Stickney and Campbell 2000
Cerastium arvense, field chickweed	unknown	unknown	variable	Seeds are transient or short-term persistent in the soil seedbank	Thompson *et al*. 1997
Chamerion angustifolium, fireweed	yes	yes	variable	Sprouts from rhizomes after fire; the light, plumed seeds can be dispersed long distances by wind; seeds are typically transient or short-term persistent in the soil; can increase dramatically after fire	Ahlgren 1960; Dale 1989; Haeussler *et al*. 1990; Lyon and Stickney 1976; McLean 1969; Myerscough 1980; Stickney and Campbell 2000; Thompson and Grime 1979; Thompson *et al*. 1997; USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Cirsium arvense, Canadian thistle[a]	yes	yes	yes	Sprouts from surviving rhizomes and roots, even after severe fire; seeds can be carried by wind for kilometers; seed longevity in the soil is highly variable, ranging from 2 to >20 y	Chepil 1946; Moore 1975; Stickney 1986; Stickney and Campbell 2000; Thompson *et al*. 1997; Toole and Brown 1946; USDA Forest Service 2008; Wood and del Moral 2000
Clematis columbiana, rock clematis	yes	unknown	unknown	Sprouts from the root crown	Bradley *et al*. 1992a; Lyon and Stickney 1976
Cystopteris fragilis, brittle bladderfern	unknown	unknown	unknown	Spores are not tolerant of heat	Strickler and Edgerton 1976
Dodecatheon pulchellum, darkthroat shootingstar	yes	unknown	unknown	Can establish from seed after fire, although seed origin is unknown	Metlen *et al*. 2006
Epilobium ciliatum, hairy willowherb	unknown	yes	yes	Can increase dramatically following fire	Lyon 1971; Thompson *et al*. 1997; Wang and Kemball 2005
Equisetum arvense, field horsetail	yes	yes	unknown	Sprouts from deeply buried rhizomes	Bradley *et al*. 1992a; Stickney 1986; USDA Forest Service 2008
Erigeron compositus, cutleaf daisy	unknown	unknown	unknown		
Erigeron pumilus, shaggy fleabane	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Erigeron subtrinervis, threenerve fleabane	unknown	unknown	unknown		
Erigeron vetensis, early bluetop fleabane	unknown	unknown	unknown		
Eriogonum alatum, winged buckwheat	unknown	unknown	unknown		
Eriogonum umbellatum, sulphur wildbuckwheat	yes	unknown	unknown		Rau *et al*. 2008
Euphorbia brachycera, horned spurge	unknown	unknown	unknown		
Fragaria, strawberry	variable	yes	variable	Species are *F. vesca* and *F. virginiana; Fragaria* spp. can be severely harmed or killed by low severity fire; *F. vesca* seed germination can be enhanced by heat treatments; seeds can be transient or persistent in the soil seedbank	Ahlgren 1960; Fischer and Clayton 1983; McLean 1969; Steele and Geier-Hayes 1995; Stickney 1986; Stickney and Campbell 2000; Strickler and Edgerton 1976; Thompson *et al*. 1997; USDA Forest Service 2008
Gaillardia aristata, common gaillardia	unknown	unknown	yes		Bruce Beyers unpublished data
Galium boreale, northern bedstraw	yes	unknown	no	Sprouts from rhizomes	Thompson *et al*. 1997; USDA Forest Service 2008; Wang and Kemball 2005

Species	Survive	Offsite seed	Onsite seed	Comments	References
Galium triflorum, fragrant bedstraw	variable	unknown	yes	Sprouts from shallow, fine rhizomes; typically a poor sprouter after fire; seeds are possibly dispersed by wildlife	Crane *et al*. 1983; Stickney 1986; Stickney and Campbell 2000; USDA Forest Service 2008; Wang and Kemball 2005
Geranium caespitosum, pineywoods geranium	unknown	unknown	unknown	Smoke and heat do not promote seed germination	Abella *et al*. 2007
Geranium richardsonii, Richardson's geranium	unknown	unknown	unknown	May sprout from rhizomes or the caudex; seeds may not remain viable for >1y	Green 1978; USDA Forest Service 2008; Van Cott 1969
Geum aleppicum, yellow avens	unknown	unknown	unknown		
Gutierrezia sarothrae, broom snakeweed	variable	variable	variable	Plants are usually severely harmed or killed by fire; most seeds fall close to the parent plant; can increase dramatically after fire	McDaniel 1979; McDaniel *et al*. 1997; Osman and Pieper 1988; Osman *et al*. 1987; Parmenter 2008; Thacker *et al*. 2008; USDA Forest Service 2008; Wood 1997; Wright *et al*. 1979
Helianthella parryi, Parry's dwarfsunflower	unknown	unknown	unknown		
Helianthus pumilus, little sunflower	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Heracleum maximum, common cowparsnip	unknown	yes	unknown		USDA Forest Service 2008; Wang and Kemball 2005
Heterotheca villosa, hairy goldenaster	unknown	unknown	unknown		
Heuchera parvifolia, littleleaf alumroot	unknown	unknown	unknown		
Hieracium fendleri, yellow hawkweed	unknown	unknown	unknown		
Hydrophyllum fendleri, Fendler's waterleaf	unknown	unknown	unknown		
Iris missouriensis, Rocky Mountain iris	unknown	unknown	unknown		
Leucocrinum montanum, common starlily	unknown	unknown	unknown		
Liatris punctata, dotted gayfeather	unknown	unknown	unknown	Possibly sprouts after fire; seeds are possibly dispersed long distances by wind	Menhusen 1973; USDA Forest Service 2008
Linaria vulgaris, butter and eggs[a]	yes	no	variable	The winged seeds typically do not disperse long distances; seeds can be transient or persistent in the soil	Nadeau and King 1991; Saner *et al*. 1994; Thompson *et al*. 1997; USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Linnaea borealis, twinflower	variable	unknown	no	Sprouts from rhizomes that are buried in the duff layer; susceptible to fire kill even after low severity fire; seeds typically do not persist in the soil seedbank for more than 1 y	Ahlgren 1960; Crane *et al*. 1983; McLean 1969; Noste and Bushey 1987; Thompson *et al*. 1997; USDA Forest Service 2008
Lithospermum multiflorum, manyflowered gromwell	unknown	unknown	unknown		
Lupinus argenteus, silvery lupine	yes	unknown	unknown	Sprouts from the caudex; can sprout even after high severity fire	Anderson and Romme 1991; Lyon and Stickney 1976; Stickney 1986; Stickney and Campbell 2000
Maianthemum stellatum, starry false lily of the valley	yes	unknown	unknown	Sprouts from creeping rhizomes; can sprout even after severe fire	Lyon and Stickney 1976; Stickney 1986; Stickney and Campbell 2000; USDA Forest Service 2008
Mentha arvensis, wild mint	unknown	yes	variable	Seed longevity in the soil is highly variable, ranging from 1 y to >30y	Thompson *et al*. 1997; Wang and Kemball 2005
Mentzelia speciosa, jeweled blazingstar	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Mertensia ciliata, mountain bluebells	unknown	unknown	unknown	Possibly sprouts from rhizomes that can extend 50 cm into the soil; seeds are inherently dormant and possibly persist in the soil	Pelton 1961
Mertensia lanceolata, lanceleaf bluebells	unknown	unknown	unknown	Often found in disturbed areas	Beidleman *et al*. 2000
Mirabilis hirsuta, hairy four o'clock	unknown	no	unknown	Seeds typically do not fall far from the parent plant	Platt 1976
Mirabilis linearis, narrowleaf four o'clock	unknown	unknown	unknown		
Moehringia lateriflora, bluntleaf sandwort	unknown	unknown	unknown		
Moehringia macrophylla, largeleaf sandwort	variable	unknown	unknown	Can be harmed or killed by low severity fire; possibly establishes from offsite seed sources	Hauser 2008; Stickney and Campbell 2000
Monarda fistulosa, wildbergamot beebalm	unknown	unknown	unknown		
Noccaea montana, alpine pennycress	unknown	unknown	unknown		
Oenothera caespitosa, tufted evening-primrose	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Oenothera coronopifolia, crownleaf evening primrose	unknown	unknown	unknown		
Oreochrysum parryi, Parry's goldenrod	unknown	unknown	unknown		
Oxalis dillenii, Dillen's oxalis	unknown	unknown	unknown	Seeds possibly disperse only short distances from the parent plant	Doust *et al*. 1985
Oxytropis lambertii, Lambert's crazyweed	unknown	unknown	unknown		
Oxytropis multiceps, southwestern locoweed	unknown	unknown	unknown		
Packera cana, woolly groundsel	unknown	unknown	unknown		
Packera fendleri, Fendler's ragwort	unknown	unknown	unknown		
Packera werneriifolia, hoary groundsel	unknown	unknown	unknown		
Paronychia jamesii, James' nailwort	unknown	unknown	unknown		
Pediocactus simpsonii, Simpson hedgehog cactus	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Penstemon glaber, sawsepal penstemon	unknown	unknown	unknown	Germination of *Penstemon* seeds is often enhanced by smoke	Abella *et al*. 2007; Keeley and Fotheringham 1998
Penstemon secundiflorus, sidebells penstemon	unknown	unknown	unknown	Germination of *Penstemon* seeds is often enhanced by smoke	Abella *et al*. 2007; Keeley and Fotheringham 1998
Penstemon virens, Front Range beardtongue	unknown	unknown	unknown	Germination of *Penstemon* is often enhanced by smoke	Abella *et al*. 2007; Keeley and Fotheringham 1998
Pericome caudata, mountain leaftail	unknown	unknown	unknown		
Phemeranthus parviflorus, sunbright	unknown	unknown	unknown		
Physaria vitulifera, roundtip twinpod	unknown	unknown	unknown		
Potentilla concinna, elegant cinquefoil	unknown	unknown	unknown		
Potentilla fissa, bigflower cinquefoil	unknown	unknown	unknown		
Potentilla hippiana, woolly cinquefoil	unknown	unknown	unknown	Possibly sprouts from a woody caudex after fire	USDA Forest Service 2008
Potentilla pulcherrima, beautiful cinquefoil	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Pseudocymopterus montanus, alpine false springparsley	unknown	unknown	unknown		
Pulsatilla patens, American pasqueflower	unknown	unknown	unknown	Possibly sprouts from buried dormant buds; seed germination is enhanced by fire if bare soil is exposed	Kalamees *et al*. 2005; Wildeman and Steeves 1982
Pyrola chlorantha, greenflowered wintergreen	no	unknown	unknown		Stickney and Campbell 2000
Rudbeckia laciniata, cutleaf coneflower	unknown	unknown	unknown		
Saxifraga bronchialis, yellowdot saxifrage	unknown	unknown	unknown		
Scutellaria brittonii, Britton's skullcap	unknown	unknown	unknown		
Sedum lanceolatum, spearleaf stonecrop	unknown	unknown	unknown		
Senecio eremophilus, desert groundsel	unknown	yes	unknown		Wang and Kemball 2005
Senecio spartioides, broom groundsel	unknown	unknown	unknown		
Silene scouleri, Scouler's campion	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Sisyrinchium montanum, mountain blueeyed grass	unknown	unknown	unknown		
Solidago, goldenrod	unknown	unknown	unknown	Species are *S. simplex*, and possibly also *S. missouriensis*, *S. velutina* and *S. nana*; *S. missouriensis* regenerates from rhizomes; *S. missouriensis* seeds are probably short-lived	Rabinowitz 1981; Stickney and Campbell 2000; USDA Forest Service 2008
Stachys palustris, marsh hedgenettle	unknown	unknown	variable		Thompson *et al*. 1997
Symphyotrichum laeve, smooth blue aster	unknown	yes	unknown	Possibly sprouts from rhizomes after fire	Stickney 1986; Stickney and Campbell 2000; USDA Forest Service 2008
Symphyotrichum porteri, smooth white aster	unknown	unknown	unknown		
Symphyotrichum spathulatum, western mountain aster	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Taraxacum officinale, common dandelion[a]	unknown	yes	yes	Possibly sprouts from a deep taproot; prolific producer of wind dispersed seed; seeds can persist in the soil for years, although they usually germinate as soon as conditions are favorable	Chepil 1946; Roberts and Neilson 1981; Stickney 1986; Stickney and Campbell 2000; Stewart-Wade *et al*. 2002; Thompson *et al*. 1997; USDA Forest Service 2008
Thalictrum fendleri, Fendler's meadowrue	unknown	unknown	unknown	Smoke and heat do not promote seed germination	Abella *et al*. 2007
Urtica dioica, stinging nettle	yes	variable	yes	Sprouts from rhizomes and from the caudex; seeds can remain viable in the soil seedbank for 5 y or more	Bassett *et al*. 1977; Crane *et al*. 1983; Stickney and Campbell 2000; Thompson *et al*. 1997; USDA Forest Service 2008; Wang and Kemball 2005
Veronica americana, American speedwell	unknown	unknown	unknown		
Viola adunca, hookedspur violet	yes	unknown	unknown	Sprouts from rhizomes after fire; may not sprout after high severity fires; possibly establishes from the soil seedbank	Clark 1991; Lyon and Stickney 1976; Stickney and Campbell 2000

Species	Survive	Offsite seed	Onsite seed	Comments	References
Viola canadensis, Canadian white violet	unknown	yes	unknown		Wang and Kemball 2005
Yucca glauca, small soapweed	yes	unknown	unknown	Sprouts from rhizomes and the caudex; seeds are large and probably do not disperse far from the parent plant; possibly establishes from the seedbank; seeds are moderately tolerant of high temperatures	Keeley and Meyers 1985; Masters *et al*. 1988; Parmenter 2008; USDA Forest Service 2008
Zigadenus elegans, mountain deathcamas	yes	unknown	unknown	Sprouts from a deeply buried bulb	Fischer and Clayton 1983
Graminoids					
Achnatherum hymenoides, Indian ricegrass	yes	unknown	unknown	Sprouts from the root crown; seeds are inherently dormant and therefore possibly persist in the soil; seeds can remain viable for 20 y in storage	Hull 1973; USDA Forest Service 2008; Wright *et al*. 1979; Zemetra 1983
Achnatherum nelsonii, Columbia needlegrass	yes	unknown	unknown		USDA Forest Service 2008; Wright *et al.* 1979
Achnatherum scribneri, Scribner needlegrass	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Agropyron cristatum, crested wheatgrass[a]	yes	unknown	unknown		Bradley *et al*. 1992a; Lodge 1960; USDA Forest Service 2008; Wright *et al*. 1979
Agrostis scabra, rough bentgrass	yes	unknown	variable	Possibly establishes after fire from wind dispersed seeds; seeds are transient or short-term persistent in the soil seedbank	Abella *et al*. 2007; Metlen *et al*. 2006; Stickney 1986; Thompson *et al*. 1997; USDA Forest Service 2008
Blepharoneuron tricholepis, pine dropseed	unknown	unknown	unknown		
Bouteloua gracilis, blue grama	yes	unknown	unknown		Dwyer and Pieper 1967; Gosz and Gosz 1996; Parmenter 2008; USDA Forest Service 2008
Bromus ciliatus, fringed brome	unknown	unknown	unknown	Possibly sprouts after low and moderate severity fire	Bartos and Mueggler 1981; USDA Forest Service 2008
Bromus inermis, smooth brome[a]	yes	no	no	Sprouts after fire from rhizomes; seeds typically do not disperse more than a few meters from the parent plant	Blankespoor 1987; Blankespoor and May 1996; Otfinowski *et al*. 2007; Steele and Geier-Hayes 1995; Thompson *et al*. 1997; USDA Forest Service 2008; Willson and Stubbendieck 1997

Species	Survive	Offsite seed	Onsite seed	Comments	References
Bromus tectorum, cheatgrass[a]	no	unknown	variable	I assumed annuals could not survive fire; seeds are possibly dispersed long distances by wind and wildlife; seeds are transient or short-term persistent in the soil, but typically germinate as soon as conditions are favorable	Burgert *et al.* 1971; Chepil 1946; Floyd *et al*. 2006; Hulbert 1955; Hull and Hansen 1974; Lyon 1971; Stickney and Campbell 2000; Thompson *et al*. 1997; Upadhyaya *et al*. 1986; USDA Forest Service 2008; Wicks *et al*. 1971; Wright *et al.* 1979
Calamagrostis canadensis, bluejoint	yes	yes	yes	Seeds can remain viable in the soil for up to 10 y	Ahlgren 1960; Bradley *et al*. 1992a; Conn and Deck 1995; Lieffers and MacDonald 1993; MacDonald and Lieffers 1991; Smith and James 1978; USDA Forest Service 2008
Calamagrostis purpurascens, purple reedgrass	unknown	unknown	unknown	Possibly sprouts from rhizomes; seeds remained viable after 2 y of cold storage	Chambers 1989; USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Carex, sedge	yes	unknown	yes	Species are mostly *C. rossii*, and possibly others such as *C. occidentalis* and *C. obtusata*; most *C. rossii* seeds fall close to the parent plant; *C. rossii* germination can be enhanced by heat treatments	Bradley *et al.* 1992a; Clark 1991; Fischer and Clayton 1983; Lyon 1971; Steele and Geier-Hayes 1995; Stickney and Campbell 2000; Strickler and Edgerton 1976; USDA Forest Service 2008
Dactylis glomerata, orchardgrass[a]	unknown	yes	variable	Possibly sprouts from the root crown; seeds are transient or short-term persistent in the soil; smoke, charred wood, and nitrogen increase seed germination	Pérez-Fernández and Rodríguez-Echeverría 2003; Stickney and Campbell 2000; Thompson and Grime 1979; Thompson *et al*. 1997; USDA Forest Service 2008
Danthonia spicata, poverty danthonia	yes	no	yes	Seeds usually fall within 1 m of parent plant; seeds can remain dormant in the soil for decades	Darbyshire and Cayouette 1989; Livingston and Allessio 1968; Scheiner and Teeri 1986; USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Elymus elymoides, bottlebrush squirreltail	yes	variable	unknown	Sprouts even after severe fires; smoke and heat do not promote seed germination	Abella *et al*. 2007; Marlette and Anderson 1986; USDA Forest Service 2008; Vose and White 1987, 1991; Wright 1971; Wright and Klemmedson 1965; Wright *et al*. 1979
Elymus lanceolatus, streambank wheatgrass	yes	unknown	yes	Sprouts from rhizomes; seeds can persist for 3-4 y in the seedbank	Blaisdell 1953; USDA Forest Service 2008; Zhang and Maun 1994
Elymus trachycaulus, slender wheatgrass	unknown	unknown	yes	Seeds can remain viable for 3-6 y in the seedbank; can increase after fire	Nimir and Payne 1978; USDA Forest Service 2008
Festuca saximontana, Rocky Mountain fescue	unknown	unknown	unknown		
Hesperostipa comata, needle and thread	variable	unknown	unknown	Extremely susceptible to fire kill	USDA Forest Service 2008; Wright 1971; Wright *et al*. 1979; Wright and Klemmedson 1965

Species	Survive	Offsite seed	Onsite seed	Comments	References
Hordeum jubatum, foxtail barley	unknown	yes	variable	Seeds can be transient or persistent in the soil seedbank	Best *et al*. 1978; Chepil 1946; Conn and Deck 1995; Taylor *et al*. 1958; Thompson *et al*. 1997; USDA Forest Service 2008
Juncus arcticus, arctic rush	unknown	unknown	unknown		
Koeleria macrantha, prairie junegrass	yes	unknown	no	Seeds are typically transient in the soil seedbank; can increase dramatically after fire	Fischer and Clayton 1983; Thompson and Grime 1979; Thompson *et al*. 1997; USDA Forest Service 2008; Wright *et al*. 1979
Leucopoa kingii, spike fescue	yes	yes	unknown		Bradley *et al*. 1992a; USDA Forest Service 2008
Muhlenbergia montana, mountain muhly	yes	unknown	unknown	Can be harmed or killed by moderate and high severity fires; possibly establishes from offsite seed sources after fire	USDA Forest Service 2008; Vose and White 1987, 1991
Muhlenbergia racemosa, marsh muhly	unknown	unknown	unknown	Possibly sprouts from rhizomes after fire	USDA Forest Service 2008
Oryzopsis asperifolia, roughleaf ricegrass	yes	unknown	unknown		Chapman and Crow 1981
Pascopyrum smithii, western wheatgrass	unknown	unknown	unknown	Possibly sprouts from rhizomes after fire	USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Phleum pratense, timothy[a]	yes	yes	yes	Sprouts from the root crown; seed longevity in the soil is highly variable	Anderson and Romme 1991; Stickney and Campbell 2000; Thompson *et al*. 1997; Toole and Brown 1946; USDA Forest Service 2008
Piptatherum micranthum, littleseed ricegrass	unknown	unknown	unknown		
Poa annua, annual bluegrass[a]	unknown	no	yes	Most seeds fall <1 m from the parent plant; seeds can remain viable in the soil for 5 y or more; seeds can accumulate in the seedbank in large numbers	Law 1975; Thompson and Grime 1979; Thompson *et al*. 1997; Warwick 1979
Poa fendleriana, muttongrass	yes	unknown	unknown	Possibly establishes from offsite seed sources after fire	USDA Forest Service 2008; Vose and White 1987, 1991
Poa palustris, fowl bluegrass	unknown	yes	variable		Stickney 1986; Stickney and Campbell 2000; Thompson *et al*. 1997
Poa pratensis, Kentucky bluegrass[a]	yes	yes	variable	Can be harmed or killed by early spring burning; seeds longevity in the soil is highly variable, ranging from 1 y to >20 y	Benson and Hartnett 2006; Blankespoor 1987; Engle and Bultsma 1984; Stickney and Campbell 2000; Thompson *et al*. 1997; Toole and Brown 1946; USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Poa reflexa, nodding bluegrass	unknown	unknown	unknown		
Pseudoroegneria spicata, bluebunch wheatgrass	yes	unknown	no	Sprouts from rhizomes and the root crown; can increase dramatically after fire	Blaisdell 1953; Conrad and Poulton 1966; Fischer and Clayton 1983; Steele and Geier-Hayes 1995; Uresk *et al.* 1976; USDA Forest Service 2008; Wright *et al.* 1979
Schizachyrium scoparium, little bluestem	yes	unknown	unknown	Possibly does not establish from offsite seed sources; seeds possibly do not have long-term viability in the soil seedbank	Hopkins *et al*. 1948; Rabinowitz 1981; USDA Forest Service 2008; Wright 1974
Sporobolus cryptandrus, sand dropseed	yes	unknown	yes	Can be severely harmed or killed by fire; sprouts from the root crown; the small seeds are possibly dispersed long distances by wind	Miller 2000; Toole and Brown 1946; USDA Forest Service 2008; Wright 1974

Species	Survive	Offsite seed	Onsite seed	Comments	References
×*Triticosecale rimpaui*, triticale[a]	no	no	no	Sterile hybrid between *Triticum aestivum* and *Secale cereale*; intentionally seeded after the Hayman Fire; I assumed annuals could not survive fire; both *T. aestivum* and *S. cereale* are transient in the soil seedbank	Robichaud *et al*. 2003; Thompson *et al*. 1997; Toole and Brown 1946
Woody plants					
Acer glabrum, Rocky Mountain maple	yes	unknown	no	Sprouts from the root crown, even after severe fire; seeds possibly disperse long distances by wind, although postfire establishment from seed is not common	Bradley *et al*. 1992a; Crane *et al*. 1983; Haeussler *et al.* 1990; Lyon and Stickney 1976; Steele and Geier-Hayes 1995; Stickney 1986; USDA Forest Service 2008
Arctostaphylos uva-ursi, kinnikinnick	yes	unknown	yes	Sprouts after fire from stolons and the root crown; susceptible to fire kill; seeds are possibly dispersed long distances by wildlife; seeds can remain viable in the soil seedbank for years; seeds have moderate heat tolerance	Berg 1974; del Barrio *et al.* 1999; Fischer and Clayton 1983; Granström and Schimmel 1993; McLean 1969; Noste and Bushey 1987; Thompson *et al*. 1997; USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Artemisia filifolia, sand sagebrush	yes	unknown	unknown	Sprouts from the root crown after fire	USDA Forest Service 2008; Vermeire *et al*. 2001
Betula occidentalis, water birch	yes	unknown	unknown	Sprouts from the root crown; the small seeds are possibly dispersed long distances by wind	USDA Forest Service 2008
Cercocarpus montanus, true mountain mahogany	yes	yes	unknown	Sprouts from the root crown and the stem after fire; sprouts even after high severity fire; seeds can remain viable for 10 y or more in warehouse storage, although they possibly do not persist in the soil seedbank	Biswell and Gilman 1961; Bradley *et al*. 1992b; Cook *et al.* 1994; Liang 2005; Stevens *et al.* 1981; USDA Forest Service 2008; Wright *et al*. 1979; Young and Bailey 1975
Clematis ligusticifolia, western white clematis	unknown	unknown	unknown		
Dasiphora fruticosa, shrubby cinquefoil	yes	unknown	unknown	Sprouts from the root crown after fire	Bradley *et al*. 1992a; Nimir and Payne 1978; Redfern 1984; USDA Forest Service 2008

Species	Survive	Offsite seed	Onsite seed	Comments	References
Ericameria nauseosa, rubber rabbitbrush	yes	yes	unknown	Sprouts from the stem and root crown after fire; seeds can remain viable for 10 y in warehouse storage	Bradley *et al*. 1992b; Robertson and Cords 1957; Stevens *et al.* 1981; USDA Forest Service 2008; Wright *et al*. 1979
Ericameria parryi, Parry's rabbitbrush	unknown	unknown	unknown		
Jamesia americana, cliffbush	unknown	unknown	unknown		
Juniperus communis, common juniper	no	variable	variable	Does not sprout after fire; foliage is very resinous and ignites easily; seeds can be dispersed long distances by wildlife; seeds can be transient or persistent in the soil seedbank; seed establishment is rare due to low seed viability	Bradley *et al*. 1992b; Diotte and Bergeron 1989; Edlin 1958; Fischer and Clayton 1983; Hobbs *et al*. 1984; Livingston 1972; Noste and Bushey 1987; Steele and Geier-Hayes 1995; Stickney 1986; Thompson *et al*. 1997; USDA Forest Service 2008
Physocarpus monogynus, mountain ninebark	unknown	unknown	unknown		

Species	Survive	Offsite seed	Onsite seed	Comments	References
Prunus virginiana, common chokecherry	yes	unknown	yes	Sprouts from the root crown and occasionally from rhizomes; seeds are possibly dispersed long distances by wildlife	Fischer and Clayton 1983; Holmgren 1954; Noste and Bushey 1987; Stickney and Campbell 2000; USDA Forest Service 2008
Ribes cereum, wax currant	yes	unknown	yes	Sprouts from the root crown after low severity fires; can be killed by high severity fire; seeds are possibly dispersed long distances by wildlife; seeds can remain viable in storage for >25 y	Bradley *et al*. 1992a; Noste and Bushey 1987; Pfister 1974; USDA Forest Service 2008; Young and Bailey 1975
Ribes inerme, whitestem gooseberry	unknown	unknown	unknown	*Ribes* seeds are possibly dispersed long distances by wildlife; seeds possibly remain viable in the soil for years	Pfister 1974
Ribes leptanthum, trumpet gooseberry	unknown	unknown	unknown	*Ribes* seeds are possibly dispersed long distances by wildlife; seeds possibly remain viable in the soil for years	Pfister 1974

Species	Survive	Offsite seed	Onsite seed	Comments	References
Rosa, rose	yes	yes	yes	Our species are likely *R. woodsii* and *R. acicularis*; *Rosa* spp. sprout from the root crown; seeds can remain viable in the seedbank for >5 y	Ahlgren 1960; Bradley *et al*. 1992a; Gill and Pogge 1974; Haeussler *et al*. 1990; Jorgenson and Stevens 2004; Noste and Bushey 1987; Shaw *et al*. 2004; USDA Forest Service 2008; Vose and White 1991; Wang and Kemball 2005
Rubus deliciosus, delicious raspberry	unknown	unknown	unknown		
Rubus idaeus, American red raspberry	yes	yes	yes	Sprouts from the root crown, roots and rhizomes; seeds are dispersed long distances by wildlife; seeds can remain viable in the soil seedbank for decades; often increases dramatically after fire	Ahlgren 1960; Bock and Bock 1984; Brinkman 1974; Flinn and Wein 1977; Graber and Thompson 1978; Haeussler *et al*. 1990; Johnston and Woodward 1985; Rowe 1983; Stickney 1986; Stickney and Campbell 2000; Thompson *et al*. 1997; Whitney 1986

Species	Survive	Offsite seed	Onsite seed	Comments	References
Salix, willow	yes	yes	no	The small downy seeds of *Salix* are easily dispersed by wind and water; seeds typically remain viable for only a few days or weeks	Densmore and Zasada 1983; Haeussler *et al*. 1990; Moss 1938; Monsen *et al*. 2004; Mueggler 1965; Noste and Bushey 1987; Thompson *et al*. 1997; USDA Forest Service 2008; Wright 1972
Symphoricarpos albus, common snowberry	yes	yes	unknown	Sprouts from rhizomes and basal buds; can sprout even after severe fire; seeds are dispersed long distances by wildlife; possibly establishes from the soil seedbank after fire	Crane *et al*. 1983; Haeussler *et al*. 1990; Lyon and Stickney 1976; McLean 1969; Morgan and Neuenschwander 1988; Noste and Bushey 1987; Rowe 1983; Stickney 1986; Stickney and Campbell 2000; USDA Forest Service 2008; Wright *et al*. 1979

[a] This species is exotic to the continental United States.

CHAPTER 6: CONCLUSIONS

Colorado's forests have been subjected to a wide range of disturbances since they were first settled by European-Americans approximately 150 years ago, including settlement-era logging and domestic grazing, and more recently, wildfire. The four studies I completed for my dissertation improve our understanding of how these past and present disturbances have impacted understory plant communities in *Pinus ponderosa – Pseudotsuga menziesii* forests of the Front Range.

In **Chapter 2**, I investigated the long-term impacts of settlement-era logging and grazing on *P. ponderosa – P. menziesii* understory plant communities by comparing understory composition in a historically logged and grazed area to that of an environmentally similar area that was protected from such activities. I found that total and functional group species richness and cover rarely differed between the two study areas in both upland and riparian forests. In contrast, differences in community composition between the two study areas varied with topography; there was little difference in species composition between upland portions of the study areas, although compositional differences were apparent in riparian zones. My findings led me to conclude that settlement-era logging and grazing have had little to no long-term impacts on understories of upland forests, although they have had some long-term influence on riparian understories, where such activities were likely the most intense.

In **Chapter 3**, I examined the role of prefire community composition, fire severity, and time since fire in shaping postfire understory development after the 2002 Hayman Fire. In upland forests, I found that some declines in species richness and cover occurred immediately following fire, but by postfire year five, they often exceeded prefire conditions, even in severely burned areas. For all fire severities, the fire-induced changes in community composition that were observed were primarily due to the postfire recruitment of new species, particularly short-lived forbs, rather than due to the loss of prefire species. In riparian forests, which burned largely with low severity in the areas studied here, postfire changes in species' abundances, community composition, and plant richness and cover were subtle. I concluded that the Hayman Fire has had largely favorable impacts on understory plant communities in upland plots, regardless of fire severity, but in lightly burned riparian plots, fire effects were neutral.

In **Chapter 4**, I focused my attention on the Hayman's impact on exotic species, and found that exotic richness and cover generally increased as both fire severity and time since fire increased. I also found that the prefire exotic community at both local and landscape scales strongly influenced the composition of the postfire exotic community at a given location. Regardless of fire severity and topographic position, the exotic species that were present in a plot before the fire were also largely present in the plot after the fire; furthermore, most new species in a plot were present elsewhere in the study area before the fire, which likely enabled them to quickly establish in new plots postfire. However, some new exotic species were truly new invaders that were not found in any prefire surveys, the most notable of which was *Bromus tectorum* (cheatgrass). Despite the increase in exotics after the Hayman Fire and the unwelcome arrival of *B. tectorum*,

exotic richness and cover remain low at this point in time. Furthermore, the positive or non-significant correlations observed between native and exotic richness and cover suggest that exotic species have not yet impacted the recovering native plant community, and so I do not consider them to be a major ecological threat at present. Continued monitoring is necessary to evaluate if they will pose a threat in future years.

What life history traits enabled so many native and exotic species to return, and in some cases flourish, after the Hayman Fire? This question was explored in the literature review presented in **Chapter 5.** The most striking result to emerge from the literature review was that the mechanisms through which many of these species reestablish after fire are poorly understood. Despite the dearth of available information, some broad patterns emerged. Short-lived forbs in these forests appear to establish after fire primarily through seed stored in the soil seedbank, while sprouting is the most common establishment mechanism for long-lived forbs, graminoids, and woody plants. Many species have more than one known postfire establishment mechanism, which helps to ensure their continued presence after fire and other disturbances.

Taken as a whole, the findings within this dissertation suggest that Colorado Front Range *P. ponderosa – P. menziesii* understory communities are resilient to a wide range of disturbances over both the short- and the long-term. Looking to the future, however, it is apparent that many important questions remain unanswered. How will these understory communities weather the current onslaught of forest restoration treatments, expanding human development, and mountain pine beetle epidemics? Over longer time frames, what mark might climate change bring to bear? Addressing these questions will

provide further insight into the resilience of Front Range understory plant communities to disturbance.