

THESIS

CONIFER REGENERATION AND FUELS TREATMENT LONGEVITY IN DRY MIXED-
CONIFER FORESTS OF THE COLORADO FRONT RANGE

Submitted by

Katie Fialko

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Fall 2018

Master's Committee:

Advisor: Seth Ex

Paula Fornwalt
Chad Hoffman
Monique Rocca

Copyright by Katie Fialko 2018

All Rights Reserved

ABSTRACT

CONIFER REGENERATION AND FUELS TREATMENT LONGEVITY IN DRY MIXED- CONIFER FORESTS OF THE COLORADO FRONT RANGE

Throughout much of the western United States, wildfires have been increasing in size and severity. To prevent negative impacts to communities and ecosystems, costly fuels reduction treatments are being applied to dry, mixed-conifer forests in Colorado and throughout the southern Rockies. The objective of this project was to make inferences about treatment longevity by determining how site, treatment, and vegetation characteristics of treated areas influence the abundance and composition of conifer regeneration, which can serve as fuels to initiate a high severity wildfire. Thinning and mastication treatments ranging in age from 5-14 years old on north and south aspects were examined. Time since treatment and residual overstory density and composition, along with aspect, had the greatest influence on the abundance of Douglas-fir and ponderosa pine regeneration in fuels treatments. Conifer regeneration did not vary by mastication vs thinning treatment type. Although Douglas-fir advance regeneration abundance decreased over time since treatment, it comprised 50% of all regeneration observed. This is a concern because advance regeneration will reduce treatment longevity more than the gradual accumulation of post treatment seedlings, and because it has the potential to release. Post treatment Douglas-fir regeneration was positively related to Douglas-fir residual overstory density but had no relationship with time since treatment. Post treatment ponderosa pine regeneration, however, increased with time since treatment and was negatively related to total residual overstory density. These findings indicate that while Douglas-fir regeneration may be

limited by the lack of residual Douglas-fir in the overstory to provide a seed source, treatments are effectively acting as shelterwood regeneration treatments to increase the abundance of ponderosa pine. Lastly, average abundance of all conifer regeneration was five times greater on north aspects than on south aspects. Forest managers implementing future fuels reduction treatments, or planning the re-treatment of existing units, should monitor advance regeneration for potential release, anticipate a greater post treatment regeneration response on north aspects, and possibly expect a shift in future stand composition towards ponderosa pine.

ACKNOWLEDGEMENTS

I have many people to thank without whom I would not have been able to complete this research project. These include my advisor, Seth Ex, and my thesis committee members, Paula Fornwalt, Chad Hoffman, and Monique Rocca, for all their guidance and support during the research process. I also owe everyone at the Colorado Forest Restoration Institute (staff and field/lab technicians) a big thank-you for their help every step of the way, from planning my sampling design to collecting and analyzing the data: I've really enjoyed working with you all. For their assistance with access to data and sites to sample, I'd also like to thank Christina Burri of Denver Water, Kris Heiny and Kevin Zimlinghaus of the U.S. Forest Service, and Kristin Garrison and Collin Wassink of the Colorado State Forest Service. Ann Hess and Julia Sharp from Statistical Consulting at CSU were also very helpful and patient during my analysis. Lastly, I would like to acknowledge that my family and my partner Spencer have been extremely supportive and have made accomplishing all this work so much easier.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS	iv
CHAPTER 1: CONIFER REGENERATION AND FUELS TREATMENT LONGEVITY IN DRY MIXED-CONIFER FORESTS OF THE COLORADO FRONT RANGE	1
1.1 Introduction.....	1
1.1.1 Wildfire Fuels Reduction Treatments and Conifer Regeneration	2
1.1.2 Site Characteristics and Conifer Regeneration	6
1.1.3 Treatment Characteristics and Conifer Regeneration	7
1.1.4 Vegetation Characteristics and Conifer Regeneration	8
1.1.5 Research Objectives	8
1.2 Methods.....	9
1.2.1 Study Area	9
1.2.2 Treatment Unit Selection and Plot Distribution.....	11
1.2.3 Understory Conifer Regeneration & Sapling Sampling.....	12
1.2.5 Overstory Sampling	15
1.2.6 Conifer Regeneration Age Determination	15
1.2.7 Statistical Analysis.....	15
1.3 Results.....	17
1.3.1 Treatment Type.....	20
1.3.2 Site Characteristics.....	20
1.3.3 Treatment Characteristics	23
1.3.4 Vegetation Characteristics	26
1.4 Discussion.....	26
1.4.1 Treatment Type and Conifer Regeneration.....	28
1.4.1 Site Characteristics and Conifer Regeneration	28
1.4.2 Treatment Characteristics and Conifer Regeneration	29
1.5 Conclusions.....	32
WORKS CITED	34

CHAPTER 1: CONIFER REGENERATION AND FUELS TREATMENT LONGEVITY IN DRY MIXED-CONIFER FORESTS OF THE COLORADO FRONT RANGE

1.1 Introduction

Wildfire is a very important disturbance in Rocky Mountain forests (Peet, 1981). Modern wildfires are burning larger areas at higher severity than they did historically throughout the Southern Rockies (Litschert, Brown, & Theobald, 2012), including in Colorado dry, mixed-conifer forests on the Front Range (Sherriff et al., 2014). These forests exhibit a mixed-severity fire regime, which has been moved outside its historic range of variability in many areas due to past grazing and logging activities and to 20th century fire suppression, (Veblen & Donnegan, 2005) and by climate change (Westerling et al., 2006). In 2002, the Hayman Fire burned over 52,000 hectares in the Upper South Platte watershed (Graham, 2003), and many other such large, high severity fires have occurred along the Front Range since.

Wildfires of such size and severity are costly to communities and have lasting impacts on forest ecosystems. In addition to directly destroying homes and other structures in the Wildland Urban Interface (Cohen, 2008), fires increase soil erosion, especially in areas with steep topography and a coarse, gravely substrate (a common condition along the Front Range) (Graham, 2003; Moody & Martin, 2001). Erosion causes costly damage to water storage and processing facilities (Graham, 2003) in watersheds that provide for the populations of cities downstream, for example, to 1.4 million people in Denver, CO alone (Denver Water, 2018). There is also evidence that some high severity burn patches are so large that conifer forests cannot regenerate adequately within them: Chambers et al. (2016) found that 70% of the high severity burn area in

the Hayman Fire (over 22,500 hectares) exceeds the maximum seed dispersal distance for ponderosa pine (*Pinus ponderosa*), implying that these areas may not be forested again for centuries.

Management activities in dry, fire-adapted forests often aim to simultaneously restore historic forest structure and composition while reducing fuel loads that contribute to high severity wildfire hazard (Addington et al., 2018; Reynolds et al., 2013). Forests today have a higher capacity to support destructive crown fire because they are denser and more continuous than they were historically (Battaglia et al., 2018; Brown et al., 2015; Kaufmann et al., 2001). Treatments, consisting mainly of thinning or mastication, with some limited prescribed burning, have been applied throughout the western U.S. with the goal of reducing high severity fire and protecting resources (Litschert et al., 2012; North et al., 2009; Reynolds et al., 2013; Schwilk et al., 2009; Stephens et al., 2012; Westerling et al., 2006). Since 2010, Denver Water and the U.S. Forest Service made two \$33 million agreements to implement 88,000 acres of fuels reduction treatments in Denver's watershed under the Forests to Faucets partnership (Denver Water, 2018). Nearly 300,000 acres of forests along the Front Range received fuels treatments between 2004 and 2012 as a part of the Front Range Fuels Treatment Partnership (FRFTP, 2012) and treatments continue today (CO DNR, 2016).

1.1.1 Wildfire Fuels Reduction Treatments and Conifer Regeneration

Fuels reduction treatments act in multiple ways to decrease the likelihood of high severity wildfire in dry forests. First, reducing surface fuels also reduces surface fire intensity, which makes it more difficult for fire to transfer into the canopy (torching). Similarly, increasing the

height of live crowns means that longer flames are necessary to begin torching. Ladder fuels (such as understory trees or other vegetation) can facilitate torching by closing the space between surface and canopy fuels in a forest (known as the fuels stratum gap). Third, fuels treatments aim to decrease crown density by thinning overstory trees to reduce the potential for the tree-to-tree transfer of fire (crowning). Lastly, in ecosystems dominated by fire-resistant species, large trees are typically retained in fuels treatments to reduce overstory mortality and to help restore historic forest structure (Agee & Skinner, 2005). However, this last goal is less applicable in mixed-conifer forests that include less fire-resistant species (Hoffman, Collins, & Battaglia, 2018) such as Douglas-fir (*Pseudotsuga menziesii*).

As pre-existing treatments age and new areas are treated, knowing what to expect for the longevity of these treatments is vital. It has been well-demonstrated that fuels treatments are effective in the short term (within 1-2 years) i.e. (Safford et al., 2012; Stephens & Moghaddas, 2005) but less is known about long-term effectiveness as surface and canopy fuels re-accumulate (Fulé et al., 2012; Hudak et al., 2011). Fuels treatments have been shown to remain effective for up to 15 years in more productive Sierra Nevada mixed-conifer forests (Chiono et al., 2012; Stephens et al., 2012) and for about 10 years on average for California forests (Vaillant et al., 2013). Treatments as old as 15 years altered fire behavior during the Hayman Fire (Graham, 2003). Synthesis of research on treatment longevity suggests that conifer regeneration may diminish treatment effectiveness over time (Hoffman, Collins, & Battaglia, 2018; Jain et al., 2012).

Conifer regeneration can reduce treatment longevity because it increases the likelihood of torching (Agee & Skinner, 2005; Keeley, Fotheringham, & Moritz, 2004) by increasing the intensity of surface fire behavior itself, and by serving as ladder fuels. Dry, mixed-conifer forests along the Colorado Front Range are composed mainly of ponderosa pine and Douglas-fir, but Douglas-fir generally has a greater influence on treatment effectiveness over time. This is because it has longer crowns (Hermann & Lavender, 1990) that connect the surface and the canopy fuels in a stand (Keeley et al., 2004), meaning that shorter flames lengths are needed to initiate torching (Agee & Skinner, 2005). The tendency of Douglas-fir to facilitate torching means that it will also experience higher mortality during a fire than ponderosa pine, which has been shown to be remarkably resistant to low intensity surface fire even when small (Battaglia, Smith, & Shepperd, 2008).

In addition to species composition, the abundance and timing of conifer regeneration are important to potential fire behavior and therefore influence the reduction in treatment effectiveness over time. Previous modeling research by Tinkham et al. (2016) has suggested that longevity in terms of return to pre-treatment wind speeds needed to initiate (torching) and transfer (crowning) crown fire can be reduced by up to 5 years for every 550 and 150 seedlings per hectare, respectively. Regeneration rates for Douglas-fir and ponderosa pine in fuels treatments vary throughout the western United States. Ponderosa pine regeneration varies from just 14-75 trees ha⁻¹ five years post treatment in northern Arizona (Bailey & Covington, 2002), to several thousand trees ha⁻¹ 5-10 years following treatment in the Black Hills of South Dakota (Battaglia et al., 2008). In western Montana ten years post treatment, Fajardo et al. (2007) observed ponderosa pine densities ranging from 33 to 86 trees ha⁻¹ and Douglas-fir densities

ranging from 8 to 156 trees ha⁻¹. Observations of ponderosa pine and Douglas-fir together by Francis, Ex, & Hoffman (2018) in Front Range treated stands were somewhat higher, averaging greater than 500 trees ha⁻¹ by 10 years after treatment. With regards to timing, Tinkham et al. (2016) also reported that a single pulse of regeneration reduced treatment effectiveness more than the gradual accumulation of seedlings over time. Retaining large quantities of advance regeneration in a treatment would have a similar effect on treatment longevity because these trees are typically taller and therefore more likely to close the fuels stratum gap between the ground surface and the forest canopy than seedlings that germinate post treatment. Advance regeneration may also release as a result of reducing overstory density in treatments (Ruel et al., 2000), thereby quickening the return to a forest structure with high torching potential.

It is important, therefore, to know what influences the abundance, timing, and species composition of conifer regeneration in fuels treatments because it reduces treatment effectiveness over time. Conifer regeneration varies by site characteristics including aspect, elevation, and slope. Treatment types can have different impacts on conifer regeneration, as can the residual overstory density and species composition of treated areas. There is also potential for conifer regeneration in fuels treatments to vary by vegetation indicators of either site quality or of competition/facilitation. The goal of this observational study was to determine whether and how these site, treatment, and vegetation characteristics of fuels treatments influence conifer regeneration to make inferences about treatment longevity.

1.1.2 Site Characteristics and Conifer Regeneration

Regeneration abundance of conifers is ultimately determined by seed availability and the suitability of the climate for establishment, which both vary temporally (Brown & Wu, 2005; Shepperd, Edminster, & Mata, 2006). Successful regeneration events occur episodically and are influenced by both the quantity (Shepperd et al., 2006) and seasonality (League, 2004) of annual precipitation, and by patterns of disturbance (Brown & Wu, 2005) that allow for adequate cone production and favorable establishment conditions. These top-down controls on conifer regeneration further interact with stand characteristics related to site quality, effects of the fuels treatments themselves, and the influence of understory vegetation. Site quality is dictated by characteristics like aspect, elevation, and slope. Higher ponderosa pine regeneration after fires has been observed on cooler north facing slopes, which receive less solar radiation and therefore have lower rates of evapotranspiration and less evaporative drying than south and west facing slopes (Rother & Veblen, 2016). Several studies have found lower regeneration densities in ponderosa pine forests at lower elevations (Chambers et al., 2016; Dodson & Root, 2013; Rother & Veblen, 2016), where temperatures are higher and precipitation lower (Peet, 1981). Elevation, aspect, and shading by overstory trees all interact with the slope of a site to further impact the light and temperature conditions of the regeneration environment (Marquis, 1965; Prévost & Raymond, 2012). Steeper slopes, especially those with loose, gravelly soil like those in the South Platte watershed (Graham, 2003), are also vulnerable to erosion. Erosion can decrease seedling survival through direct damage by debris flow, or by washing away nutrients in upper soil layers (Cleary, Greaves, & Hermann, 1978). Aspect, elevation, and slope have a strong influence on the temperature and moisture conditions for conifer germination and growth at the scale of a treatment unit.

1.1.3 Treatment Characteristics and Conifer Regeneration

Treatments themselves can also alter the regeneration environment. Different treatment types leave behind varying amounts of surface fuels (Stephens & Moghaddas, 2005), which can protect seedlings from desiccation (Fajardo et al., 2007). Treatments also typically aim to reduce overstory tree density to limit the potential for the tree-to-tree spread of canopy fire (crowning) (Agee & Skinner, 2005). Thinning and mastication are both common fuels treatments in Colorado (Addington et al., 2018) that differ in how they affect surface fuels. When a treatment area is thinned, the trees and slash may be removed entirely or left in place in varying amounts and in pieces of different sizes. In a mastication treatment, trees are shredded in place using bladed machinery that redistributes the fuel load to the surface in relatively uniformly sized pieces (Stephens & Moghaddas, 2005). The reduction in overstory density from either kind of treatment can influence conifer regeneration by increasing light availability, which benefits shade intolerant species like ponderosa pine (Boyden, Binkley, & Shepperd, 2005; Chen, 1997; Francis et al., 2018). Ponderosa pine regeneration densities have previously been shown to increase over time since treatment (Francis et al., 2018), likely due to this effect. Reducing overstory density may also promote the release of advance regeneration present in treatments (Ruel et al., 2000). Additionally, the species composition of the residual overstory following treatment can affect the availability of seed for regeneration. Fuels treatments along the Colorado Front Range often aim to reduce the proportion of Douglas-fir in stands to satisfy restoration objectives (Addington et al., 2018; Briggs et al., 2017; Brown et al., 2015). Douglas-fir is also a target for reduction in fuels treatments because of its long crowns that are conducive to torching and because it is relatively shade tolerant and therefore reproduces abundantly in the understories of undisturbed stands. Even though Douglas-fir has relatively light seed that can disperse longer

distances (Chambers et al., 2016; Donato et al., 2009) than ponderosa pine (Bonnet, Schoettle, & Shepperd, 2005; Chambers et al., 2016), some research has indicated that preferentially removing Douglas-fir can limit its regeneration (Francis et al., 2018).

1.1.4 Vegetation Characteristics and Conifer Regeneration

Lastly, vegetation can serve as a useful indicator of sites with high conifer regeneration abundance. The maximum height of trees and shrub or herbaceous cover may reflect site quality for conifer regeneration because they incorporate into a single indicator the temperature and moisture conditions dictated by aspect, elevation, and slope that affect plant growth (Carmean, 1975; Daubenmire, 1976). Understory vegetation cover may also directly influence both ponderosa pine (Bonnet et al., 2005) and Douglas-fir (Chambers et al., 2016) regeneration via competition (Pearson, 1942; Peet, 1981) or facilitation (i.e. Puhlick, Laughlin, & Moore, 2012). Previous research has identified a positive relationship between Douglas-fir regeneration and understory vegetation cover in high severity wildfire burns in Colorado under very open growing conditions (Chambers et al., 2016), but it remains to be seen whether a similar relationship exists in fuels treatments where the overstory has not been reduced so dramatically.

1.1.5 Research Objectives

In plots within masticated and thinned treatment units distributed by aspect and elevation, we counted understory trees by species and collected them for age determination to categorize them as either advance or post treatment regeneration relative to the year of treatment. Using multiple regression and mixed models, our objectives were to determine whether and how Douglas-fir and ponderosa pine advance and post treatment regeneration groups vary in abundance 1) by

treatment type: mastication vs thinning, 2) by site characteristics: aspect, elevation, and slope, 3) over time and by residual overstory density and composition, and 4) by vegetation indicators: maximum tree height, and the percent cover of shrubs and herbaceous vegetation in the whole plot vs the regeneration plot.

1.2 Methods

1.2.1 Study Area

Plots were sampled in treatment units in the South Platte and Boulder areas of the Pike-San Isabel and Arapaho-Roosevelt National Forests, respectively (Fig. 1). Forests at lower elevations (from about 1850 to 2200 meters) in the study area consist mainly of denser, mixed ponderosa pine and Douglas-fir on north aspects, and more open ponderosa pine on south aspects. With increasing elevation (up to about 2900 meters), lodgepole pine (*Pinus contorta* subsp. *latifolia*), becomes a more important stand component. Other tree species include Rocky Mountain juniper (*Juniperus scopulorum*), quaking aspen (*Populus tremuloides*), and limber pine (*Pinus flexilis*) (Peet, 1981). In the South Platte, soils are derived from weathered granite of the Pikes Peak formation and are especially coarse-grained (Graham, 2003). In the Boulder area on the northern Front Range, soils are more variable but still generally rocky, coarse in texture, and shallow (Peet, 1981). Vegetation in the understory and forest openings includes bunchgrasses such as Arizona fescue (*Festuca arizonica*) and mountain muhly (*Muhlenbergia montana*) in the South Platte, as well as spike fescue (*Leucopoa kingii*) in the mixed-conifer understory in the Boulder

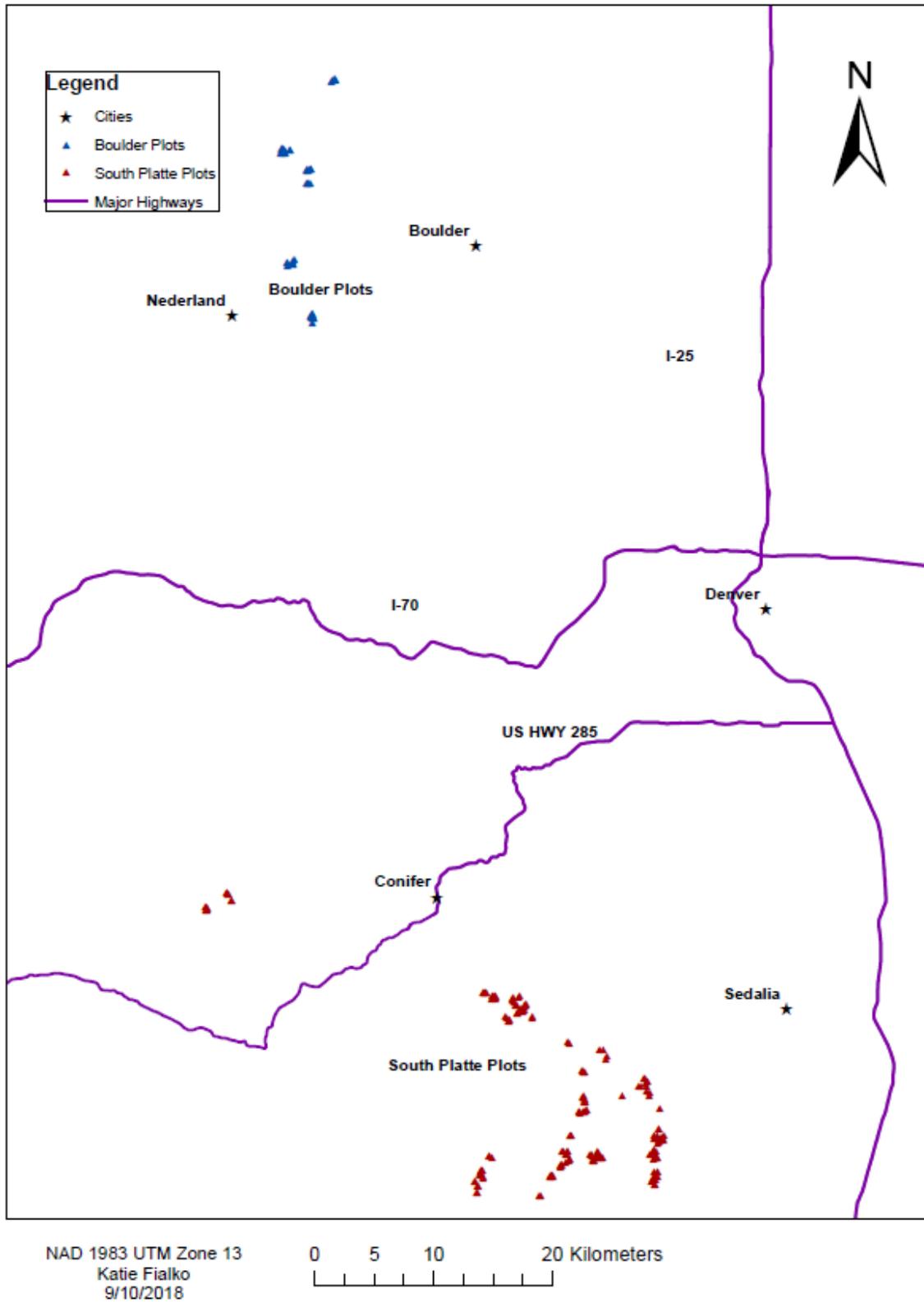


Figure 1: Plot locations in the South Platte and Boulder treated areas.

area. Shrub species throughout the both areas include mountain mahogany (*Cercocarpus montanus*), kinnikinnick (*Arctostaphylos uva-ursi*), and common juniper (*Juniperus communis*). Total annual precipitation and mean annual temperature range from about 457 mm and 8.2° C at lower elevations (near Twin Cedars, CO at 1890 meters) to 546 mm and 4.8° C at higher elevations (near Nederland, CO at 2500 meters) (PRISM, 2017).

1.2.2 Treatment Unit Selection and Plot Distribution

Fifty-two individual fuels treatment units were identified for sampling using the U.S. Forest Service Activity Tracking database (USFS, 2016) and data provided by Denver Water (personal communication). They ranged in age from 5 to 14 years old (completed in 2003 to 2012).

Treatments in the South Platte area were either masticated or thinned. Material from the thinning treatments was removed as product, lopped and scattered, piled (and sometimes burned), or some combination of these three. In the Boulder area, there were no mastication treatments comparable to the South Platte, and slash from thinning treatments was piled and burned. We used the plot as our unit of observation rather than the treatment unit to better characterize variation in conifer regeneration abundance at sub-unit scales. 229 total plots were completed, 181 of which were in the South Platte (Fig. 1). Plots were randomly placed but distributed as evenly as possible across elevation (approximately 1880-2870 meters), and aspect (within 45° of North or South), and by treatment type in the South Platte (Table 1). Percent slope was recorded at each plot.

Table 1: Sample size of plots by treatment type (mastication or thinning), aspect (north or south), and time since treatment (TST) in years.

TST (years)		TST (years)	
# Plots		# Plots	
Mastication	106	Thinning	121
North	53	North	59
5	2	5	16
6	1	6	7
7	0	7	5
8	17	8	11
9	13	9	6
10	3	10	2
11	6	11	0
12	5	12	10
13	2	13	0
14	4	14	2
South	53	South	62
5	6	5	12
6	1	6	9
7	1	7	18
8	18	8	9
9	8	9	6
10	2	10	0
11	2	11	4
12	10	12	3
13	4	13	0
14	1	14	1

1.2.3 Understory Conifer Regeneration & Sapling Sampling

Conifer regeneration was sampled in fixed 3.59-meter radius plots (Fig.2), where the species and height of all regeneration was recorded before collecting basal cross sections for age determination. Regeneration was considered any understory tree less than 1.37 meters tall. In plots where more than approximately 30 conifer seedlings were collected from the first quarter or

half of a regeneration plot (7 plots total), regeneration in the remaining $\frac{3}{4}$ or half were not collected for aging but were counted by species and their heights measured. We did not attempt to sample first-year germinant seedlings (with succulent stems that had not yet hardened) because although they are very numerous, they have a low probability of survival (Shepperd et al., 2006). Conifer saplings (trees taller than 1.37 meters but less than 12.7 cm in DBH) were also recorded by species and live or dead status in the fixed-radius plots.

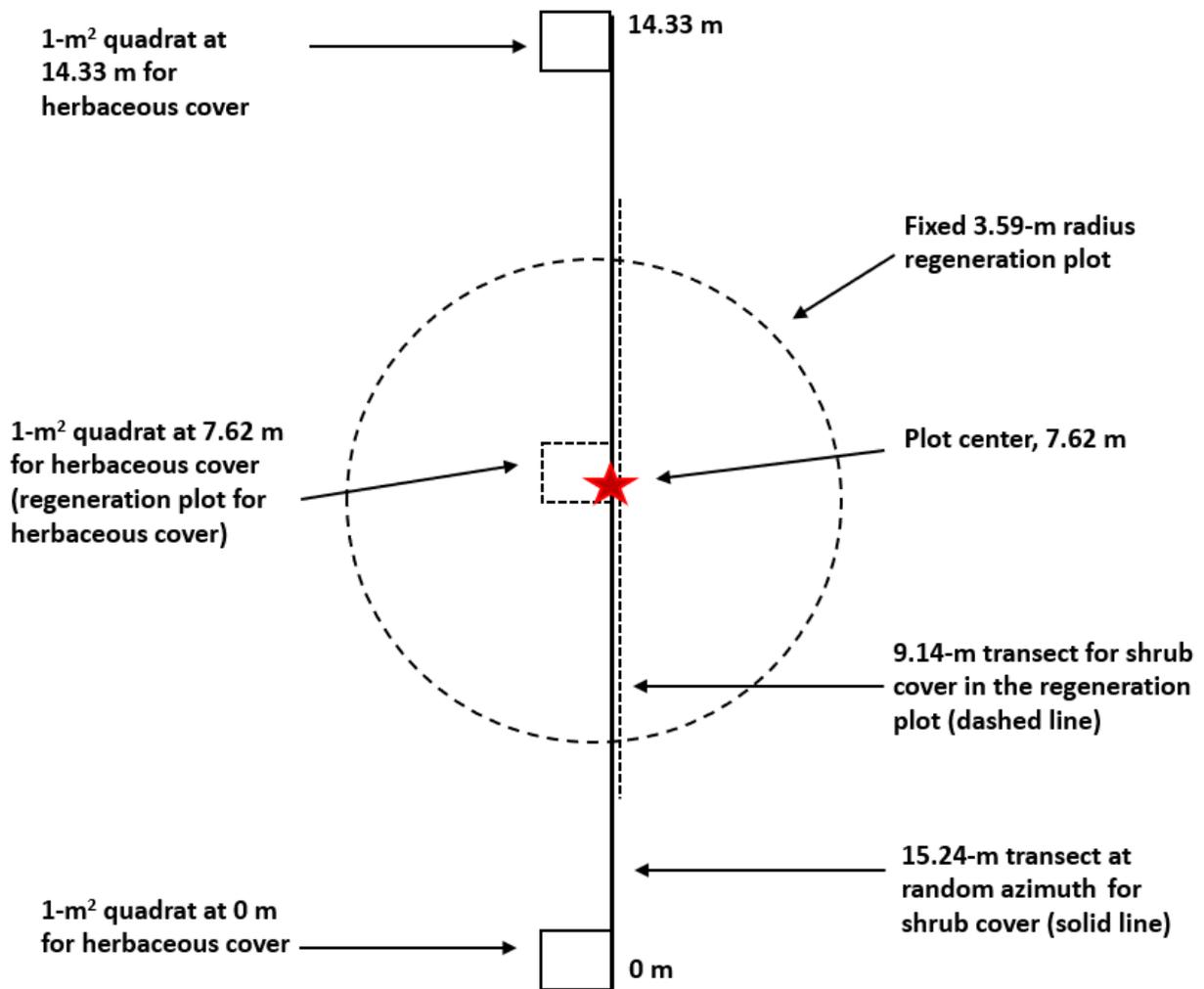


Figure 2: Diagram of plot design with 15.24-m shrub cover transect, fixed radius regeneration plot, and three 1-m² herbaceous cover quadrats. (scale approximate)

1.2.4 Understory Vegetation Sampling

Understory vegetation cover data were collected using ocular cover estimates in quadrats for herbaceous plants and line-intercept transects for shrubs (Fig. 2). The total percent cover of shrubs was estimated using the line-intercept method along a 15.24-meter transect (at a randomly selected azimuth) with plot center at 7.62 meters (Colorado Forest Restoration Institute, 2016). Gaps were recorded where there was 15.24 cm or more of the transect without shrub cover. The percent cover of shrubs for the whole plot (*% shrub cover/plot*) was taken to be the cover along the entire transect (solid line in Fig. 2) and is included as a potential indicator of site quality in the analysis. To account for potential competitive or facilitative effects of shrubs on conifer regeneration, the percent cover of only the shrubs along the portion of the transect within the fixed 3.59-m radius regeneration plot was determined separately from the plot total. A 0.9-meter buffer was added to each end of the transect outside of the regeneration plot to account for any potential influence of nearby taller shrubs on the growing environment (i.e. shading). Therefore, the percent cover of shrubs within and around the regeneration plot (*% shrub cover/regeneration plot*) was estimated from 3.05-12.19 meters along the 15.24-meter transect through plot center (dashed line in Fig.2).

Percent cover of all herbaceous vegetation (graminoids and forbs) was estimated to the nearest percent in three 1-m² quadrats at 0, 7.62, and 14.33 meters along the left side of the 15.24-meter transect through plot center. To determine total percent cover of all herbaceous vegetation at the plot level as a potential indicator of site quality (*% herbaceous cover/plot*), cover was averaged among the three quadrats (solid line box in Fig. 2). To describe herbaceous cover within just the regeneration plot as an indicator of potential competitive or facilitative effects (*% herbaceous*

cover/regeneration plot), only data from the quadrat at plot center (7.62 meters) was used (dashed line box in Fig. 2).

1.2.5 Overstory Sampling

Live overstory trees and snags greater than 1.37 meters tall and 12.7 cm in diameter at breast height (DBH) were sampled in a variable radius plot using a 2.296 m² ha⁻¹ (10 ft² ac⁻¹) basal area factor prism. The species, DBH (cm), height (meters), and live or dead status of each tree was recorded. Trees per hectare, basal area (m² ha⁻¹), and stand density index (SDI, a measure of residual overstory density) (Reineke, 1933) of each species and as a total for each plot were calculated using this data.

1.2.6 Conifer Regeneration Age Determination

Basal cross-sections of all collected conifer regeneration were sanded and polished, and then the annual rings were counted under a microscope to ascertain the trees' establishment years. These years were then compared to treatment years for each plot to determine if the tree was advance regeneration or if it germinated post treatment.

1.2.7 Statistical Analysis

Using generalized linear mixed models with a negative binomial distribution, we first tested whether conifer regeneration varied by treatment type using plots from just the South Platte, as this area contained both thinning and mastication treatment types. Separate models were developed for advance and post treatment regeneration of Douglas-fir and ponderosa pine groups. Once it was established that conifer regeneration in each of these groups did not vary by

treatment type, plots from both the South Platte and Boulder areas were used to test for variation by the site, treatment, and vegetation characteristics listed in Table 2. Analysis was performed in R (R Development Core Team, 2013) using the Glmmadmb package (Bolker et al., 2012) to include treatment unit as a random effect in generalized linear mixed models.

Table 2: Potential predictors for conifer regeneration. All variables except aspect are continuous.

<u>Site</u>
Slope (%)
Aspect (North or South)
Elevation (meters)
Slope:Aspect (Interaction)
Aspect:Elevation (Interaction)
<u>Treatment</u>
Time Since Treatment (5-14 years)
<u>Residual Overstory Density and Composition:</u>
Basal Area (BA), all species (m ² ha ⁻¹)
Trees ha ⁻¹ (TPH), all species
Stand Density Index (SDI), all species
Basal Area (BA), response species (m ² ha ⁻¹)
Trees ha ⁻¹ (TPH), response species
Stand Density Index (SDI), response species
<u>Vegetation</u>
Maximum Tree Height (meters)
% Shrub cover/plot
% Herbaceous cover/plot
% Shrub cover/regeneration plot
% Herbaceous cover/regeneration plot

The distribution of each full model containing all potential predictors was chosen using corrected Akaike information criterion (AICc) (Burnham & Anderson, 2003). Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial distributions were considered as options for modeling our count data, and the negative binomial distribution was deemed

appropriate in every case because the data was both overdispersed and included zeros (Zuur et al., 2009). Backwards stepwise selection also based on AICc was used to choose a final model for each response. The results of model selection with and without potential outliers (plots with high regeneration counts relative to the other observations) were compared, and the model without the outliers was chosen when including them changed which predictors were selected. Four and two outliers were removed from the ponderosa pine advance and the Douglas-fir post treatment regeneration models, respectively. Time since treatment was included in every model because treatment age is a key, inherent difference between the treatment units to account for. If a predictor was not selected, the plots with missing values for it were added back in to the dataset to re-run model selection. Raw parameter estimates were exponentiated for interpretation as incidence rate ratios. Emtrends from the Emmeans package (Lenth, 2018) was used to evaluate significant interactions. All lower order terms in significant interactions were kept. Statistical significance was evaluated at the $\alpha = 0.05$ level.

1.3 Results

Mean conifer regeneration in fuels treatments from the 227 plots analyzed in this study was 7.5 trees per 3.59-meter radius plot, or 1846 trees ha⁻¹. However, this mean encompasses wide variability in regeneration abundance at the plot-level: 37% percent of 227 plots analyzed had no understory conifers and another 41% had 10 or less, while 4% of the plots contained 30 or more, including one plot with 181 seedlings. Most conifer regeneration encountered was Douglas-fir and ponderosa pine, and overall, Douglas-fir was much more abundant (Table 3): 1316 total Douglas-fir seedlings were observed compared to only 325 ponderosa pines (71% Douglas-fir). Lodgepole pine, Engelmann spruce (*Picea engelmannii*), limber pine, and Rocky Mountain

juniper regeneration were also observed in lesser abundance than Douglas-fir and ponderosa pine. Almost 2/3 of the trees were advance regeneration, and half was Douglas-fir advance regeneration.

Table 3: Total observed conifer regeneration counts by species, advance vs post treatment regeneration status, treatment type, & aspect from 229 plots. Other conifer species include lodgepole pine, Rocky Mountain juniper, limber pine, and Engelmann spruce.

	Mastication	Thinning	North	South	Total
Douglas-fir	696	620	1165	151	1316
<u>Advance Regeneration</u>	450	466	795	121	916
<u>Post Treatment Regeneration</u>	184	105	259	30	289
<u>Not aged</u>	62	49	111	0	111
Ponderosa pine					
	206	119	171	154	325
<u>Advance Regeneration</u>	58	75	53	80	133
<u>Post Treatment Regeneration</u>	125	42	109	58	167
<u>Not aged</u>	23	2	9	16	25
Other conifers					
	21	179	188	12	200
<u>Advance Regeneration</u>	8	83	81	10	91
<u>Post Treatment Regeneration</u>	13	96	107	2	109
<u>Not aged</u>	0	0	0	0	0
Totals					
	923	918	1524	317	1841
Totals					
<u>Advance Regeneration</u>	1140				
<u>Post Treatment Regeneration</u>	565				
<u>Not aged</u>	136				

Eighty-three percent of regeneration was found on north aspects, but there were many plots on both aspects with no regeneration. Mean total conifer regeneration density ranged from 2.8 trees/plot or 681.2 trees ha⁻¹ on south aspects to 13.6 trees/plot or 3362.4 trees ha⁻¹ on north aspects. Over time since treatment, the mean total conifer regeneration densities we observed ranged from 556 trees ha⁻¹ in 11-year-old treatments to 3329 trees ha⁻¹ in 5-year-old treatments.

There were 136 total seedlings that were counted but not collected and therefore not aged (Table 3) according to the sampling method described in section 1.2.3. Additionally, data from two plots with very high regeneration density that were sampled this way was excluded from the analysis because their seedlings counts per plot were unreliable, but their total regeneration counts are still included in Table 3.

Mean residual overstory density ranged from 139.7 trees ha⁻¹ or 12.5 m²ha⁻¹ in basal area in mastication treatments on south aspects, to 326.6 trees ha⁻¹ or 16.4 m²ha⁻¹ in basal area in thinning treatments on north aspects (Table 4). Douglas-fir was more restricted to north aspects, while ponderosa pine dominated south aspects. Overstory conifer species other than Douglas-fir and ponderosa pine, including lodgepole pine, limber pine, Engelmann spruce, and Rocky Mountain juniper, were observed in some plots, but they were considerably less abundant. Mean percent shrub and herbaceous cover and mean maximum tree height all tended to be greater in masticated than in thinned plots.

Table 4: Mean post treatment conditions (standard deviations in parentheses) where conifer regeneration abundance and composition were characterized, by treatment type and north or south aspect.

	Mastication			Thinning		
	Total	North	South	Total	North	South
# Plots	106	53	53	121	59	62
Basal Area (m ² ha ⁻¹)	14.0 (7.3)	15.6 (7.2)	12.5 (7.2)	14.2 (7.1)	16.4 (6.7)	12.1 (6.8)
Trees ha ⁻¹	173.4 (139.5)	207.1 (147.1)	139.7 (123.8)	239.5 (232.7)	326.6 (279.6)	156.7 (133.7)
Douglas-fir Basal Area (%)	42.7 (39.6)	61.4 (36.4)	23.9 (33.6)	23.6 (31.2)	38.3 (35.0)	9.7 (18.7)
Ponderosa pine Basal Area (%)	54.1 (40.0)	33.5 (33.9)	74.6 (34.9)	64.4 (36.4)	43.3 (35.2)	84.5 (24.3)
% Shrub cover/plot	19.4 (20.5)	17.1 (17.5)	21.7 (23.0)	13.7 (19.0)	15.8 (20.0)	11.8 (18.0)
% Shrub cover/ regeneration plot	20.4 (23.5)	17.1 (19.0)	23.7 (27.0)	13.8 (20.1)	15.5 (20.7)	12.2 (19.5)
% Herbaceous cover/plot	12.7 (9.8)	11.6 (10.4)	13.9 (9.1)	8.2 (6.1)	7.0 (5.5)	9.3 (6.5)
% Herbaceous cover/ regeneration plot	12.5 (14.2)	13.5 (17.2)	11.5 (10.4)	8.2 (7.3)	6.6 (6.2)	9.6 (8.1)
Maximum Tree Height (m)	18.4 (2.9)	18.4 (3.5)	18.4 (3.2)	16.3 (3.4)	16.0 (3.1)	16.2 (3.2)

1.3.1 Treatment Type

In the South Platte area, conifer regeneration did not vary by treatment type: this predictor was not selected using backwards stepwise model selection based on AICc for any of the models for Douglas-fir or ponderosa pine advance or post treatment regeneration response groups.

Therefore, results reported in Table 5 for each group reflect model selection using plots from the entire sample including the Boulder area, without consideration of treatment type as a potential predictor.

1.3.2 Site Characteristics

For Douglas-fir advance regeneration, the simple relationship with aspect was not significant (Fig. 3A), but there was a significant interaction between slope and aspect (Table 5). However, the trends for slope on both aspects were not significantly different from zero (Emtrends slope

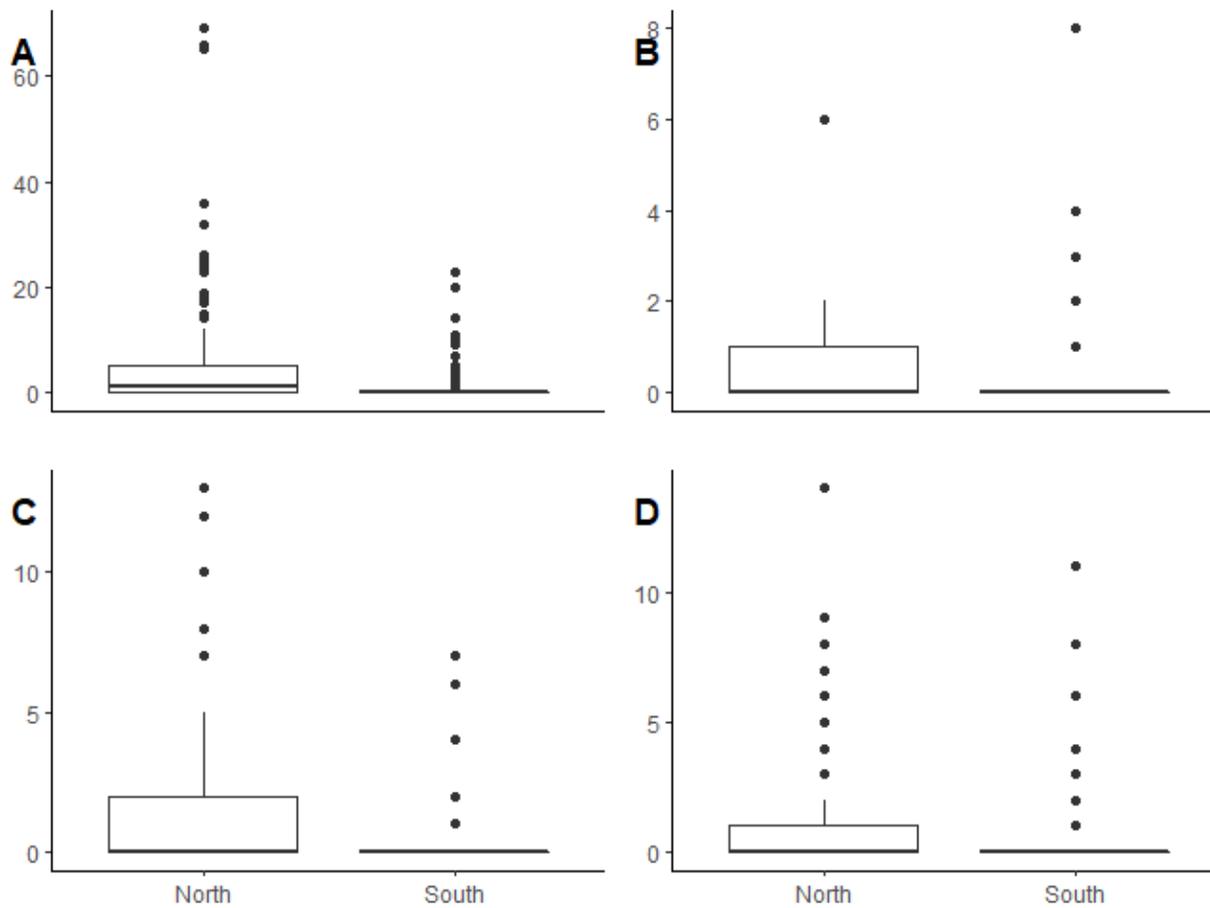


Figure 3: Observed regeneration counts per plot by aspect for: A) Douglas-fir advance regeneration (relationship not significant), B) ponderosa pine advance regeneration, C) post treatment Douglas-fir, D) post treatment ponderosa pine.

Table 5: Conifer regeneration response by species and advance or post treatment status with n = the number of observations, and the parameter estimates with 95% confidence intervals for each significant predictor included in the selected model, and their significance codes: 0.001 ‘***’, 0.01 ‘**’, 0.05 ‘*’. Parameter estimates are interpreted as incidence rate ratios, such that values greater than 1 represent a percent increase in the response for every one-unit increase in the parameter, while values less than one represent a percent decrease in the response for every one-unit increase. TST was included in each model even when it was not significant (NS). “Interaction” denotes that a term was involved in a significant interaction (Interaction*), which is examined further in the results.

<u>Predictors</u>	<u>Advance Regeneration Douglas-fir</u>	<u>Advance Regeneration Ponderosa pine</u>	<u>Post Treatment Douglas-fir</u>	<u>Post Treatment Ponderosa pine</u>
	n = 225	n = 224	n = 223	n = 227
Slope	Interaction	.	0.97* (0.941-1.000)	.
Aspect (with respect to South)	Interaction	0.459* (0.231-0.910)	0.202*** (0.089-0.458)	0.273** (0.113-0.659)
Elevation
Slope:Aspect Interaction	Interaction*	.	.	.
Aspect:Elevation Interaction
Time Since Treatment (TST)	0.685*** (0.572-0.820)	NS	NS	1.405** (1.131-1.745)
Basal Area (BA)	.	0.921** (0.870-0.974)	.	.
Trees per hectare (TPH)	.	.	.	0.992** (0.987-0.998)
Stand Density Index (SDI)
Response Species BA
Response Species TPH	.	.	.	1.007* (1.001-1.013)
Response Species SDI	1.104*** (1.041-1.171)	.	1.183*** (1.108-1.263)	.
Maximum Tree Height
% Shrub/whole plot
% Herbaceous/whole plot
% Shrub/regeneration plot
% Herbaceous/regeneration plot

trends = -0.012 for south and -0.001 for north, confidence level 0.95). There was 49% as much ponderosa pine advance regeneration on south aspects as on north aspects (Fig. 3B). Post treatment Douglas-fir regeneration decreased by about 3% for every 1% increase in slope (Table 5). There was also 20% as much post treatment Douglas-fir and 27% as much post treatment ponderosa pine regeneration on south aspects as on north aspects (Fig. 3C & 3D).

1.3.3 Treatment Characteristics

Douglas-fir advance regeneration decreased by about 30% for every year after treatment (Fig. 4) and increased by 10-14% for every one unit increase in Douglas-fir SDI (Table 5).

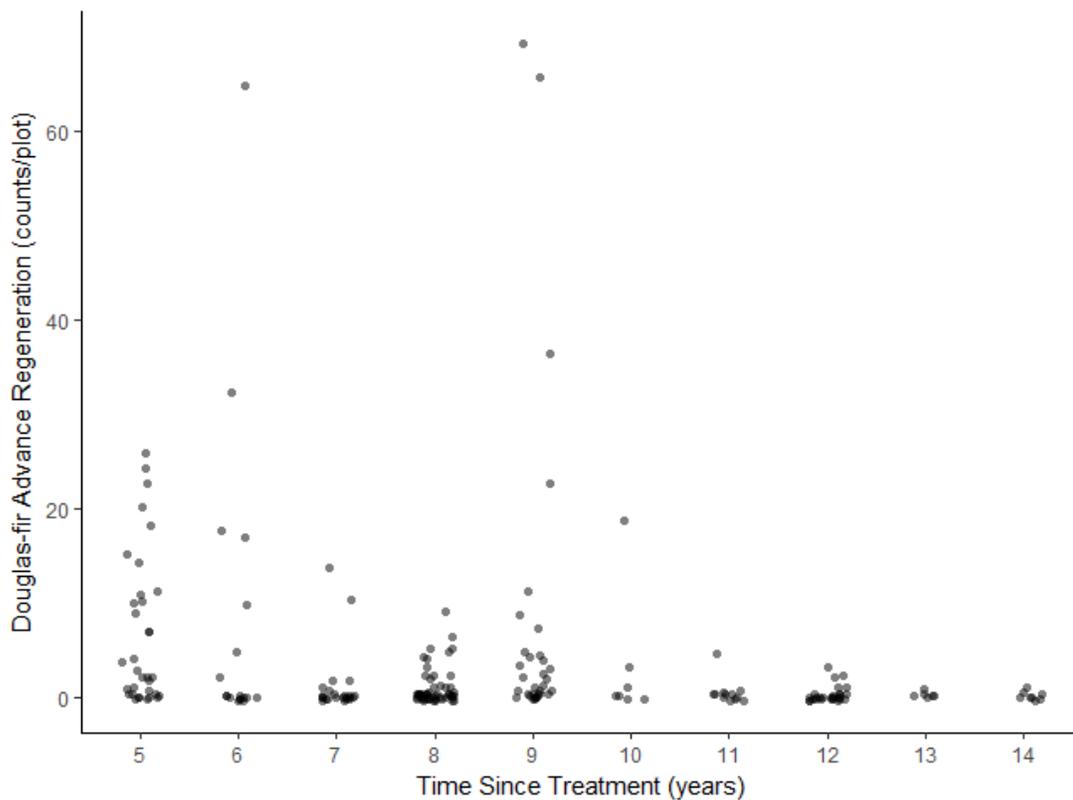


Figure 4: Observed Douglas-fir advance regeneration (counts/per) over time since treatment in years. One outlier (with 126 adv. regen. trees 5 years since treatment), was removed from this plot but was included in the model.

Ponderosa pine advance regeneration did not vary over time since treatment but decreased by about 6% with every 1 m² increase in total overstory basal area (Table 5).

Post treatment Douglas-fir regeneration did not vary over time since treatment. Mean (per plot) annual establishment was greatest in earlier years post treatment and declined over time (Fig. 5).¹ Post treatment Douglas-fir regeneration also increased by 18% for every one unit increase in Douglas-fir SDI.¹

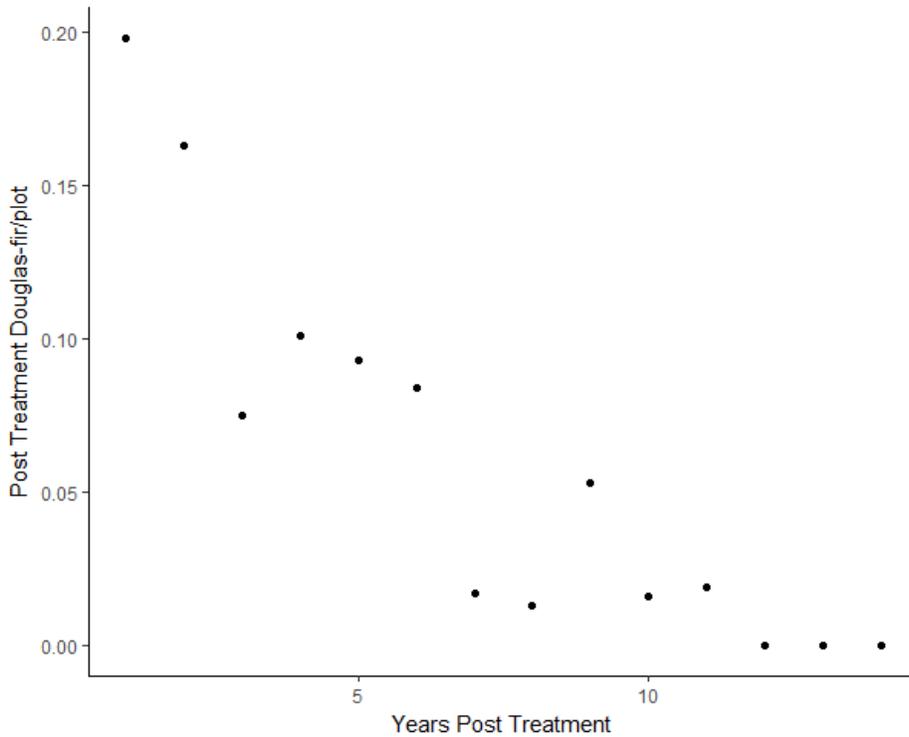


Figure 5: Mean annual establishment of post treatment Douglas-fir regeneration per plot.

Post treatment ponderosa pine increased by about 40% for every one year after treatment (Fig. 6). Mean (per plot) annual establishment (Fig. 7). showed no obvious trend for 5-9 years post treatment and no establishment 10-14 years post treatment. It also increased slightly (<1%) with increasing ponderosa pine trees per hectare in the overstory and decreased (by 1%) with increasing trees per hectare of all overstory species (Table 5).

¹Years post treatment represents sequential years over the treatment lifetime rather than calendar years reflected in time since treatment. For example, establishment 5 years post treatment would be from the year 2015 in a treatment performed in 2010, but from the year 2010 in a treatment performed in 2005.

1.3.4 Vegetation Characteristics

Douglas-fir or ponderosa pine, advance or post treatment regeneration did not vary by maximum tree height, or by the percent cover of shrubs or herbaceous vegetation in the whole plot (solid lines in Fig. 2) or in the regeneration plot (dashed lines in Fig. 2).

1.4 Discussion

Conifer regeneration in fuels treatments was most influenced by aspect, time since treatment, and residual overstory density and species composition. No relationships were observed between Douglas-fir or ponderosa pine advance or post treatment regeneration and treatment type, or with any of the vegetation characteristics listed in Table 2.

Conifer regeneration was highly variable at the plot-level in the fuels treatments analyzed in this study: while a large portion of the sample contained little to no regeneration, abundance was very high under some conditions. This was especially true of north aspects, which had very high abundance of Douglas-fir and advance regeneration. These proportions are significant because Tinkham et al. (2016) suggest retaining large quantities of advance regeneration, akin to a single pulse of regeneration establishing following treatment, can impact treatment longevity more than the gradual establishment of post treatment seedlings. Douglas-fir is also of particular concern because it is less fire resistant than ponderosa pine and more likely to serve as ladder fuels (Hermann & Lavender, 1990; Keeley et al., 2004).

Mean total conifer regeneration density per plot ranged from hundreds to thousands of trees ha⁻¹. Briggs, Fornwalt, & Feinstein (2017) used a plot-level sampling design like ours to investigate

conifer regeneration densities (including both seedlings and saplings taller than 1.37 meters) in untreated areas and in treated areas pre- and one year post-treatment. The mean density they report for all plots and years combined is 3939 trees ha⁻¹, a value comparable to ours that also encompasses wide variability (42% of their plots contained no regeneration). Although our values also appear comparable to the densities in excess of a thousand trees ha⁻¹ reported 10 years post treatment by Battaglia et al. (2008) in the Black Hills of South Dakota, densities from this region are consistently higher and less variable than the values we report here. The regeneration abundance we observed also appears much higher than the ranges reported ten years post treatment by Fajardo et al. (2007) in western Montana: 33 to 86 trees ha⁻¹ for ponderosa pine or 8 to 156 trees ha⁻¹ of Douglas-fir; or five years post treatment by Bailey and Covington (2002) or Fulé, Laughlin, & Covington (2005) in northern Arizona at 14-75 trees ha⁻¹. The actual regeneration rates in these regions may actually be more similar to ours than these reported values might indicate, however, because Fajardo et al. (2007) did not include advance regeneration and Bailey and Covington (2002) only sampled regeneration greater than 20 cm in height. At the plot level, our minimum regeneration density per hectare appears very low (0 trees ha⁻¹), and our maximum density appears very high (44,691 trees ha⁻¹). But because 37% of our plots contained no regeneration, this indicates that treatment effectiveness is deteriorating rapidly only in the portion of our sample with a very high regeneration density. Using the plot as our unit of observation, we can also make inferences about site, treatment, and vegetation conditions that vary at sub-stand scales and influence regeneration density, and estimate how common these conditions are across the landscape.

1.4.1 Treatment Type and Conifer Regeneration

Our results indicate that treatment type does not influence the abundance or composition of conifer regeneration in fuels treatments. Other research has also noted that mastication has variable effects on conifer regeneration abundance (Battaglia et al., 2009) and growth (Roberts, Harrington, & Terry, 2005; Zabowski et al., 2000), and therefore on future stand development and fire potential (Reinhardt, Holsinger, & Keane, 2010). This may simply be because conifer regeneration rates naturally vary due to annual variation in seed production and the climatic conditions for establishment (Brown & Wu, 2005; Savage, Brown, & Feddema, 1996; Shepperd et al., 2006) or because of variability in the microsite conditions for regeneration created by mastication. In our study, the mastication treatments did not necessarily have higher surface fuels than the thinning treatments, because these encompassed several different management actions and slash treatment methods (unpublished data). For example, in some less accessible treatment areas logs were felled and left in place rather than removed. In some plots, slash was lopped and scattered but piled and burned in others. This is pertinent because woody surface fuels affect the regeneration environment, for example by providing shade that helps prevent regeneration from desiccating (Fajardo et al., 2007). Mastication treatments simply may not alter microsite conditions sufficiently or consistently enough to have a strong positive or negative impact on conifer regeneration relative to other treatment types.

1.4.1 Site Characteristics and Conifer Regeneration

There was less conifer regeneration of both species and advance or post treatment groups on south than on north aspects. In mountainous regions of the western U.S., aspect has a strong impact on treatment-scale climate. Regeneration can be limited by high temperatures and low moisture in dry, mixed-conifer forests (Petrie et al., 2016). Both this study and previous research

(Ertl, 2015; Francis et al., 2018; Larson & Franklin, 2005; Rother & Veblen, 2016) have shown that the cooler, wetter conditions on north aspects favor greater conifer regeneration abundance. This is especially true of shade tolerant species: here, 87% of all Douglas-fir regeneration, but only 52% of all ponderosa pine regeneration, was found on north aspects. The natural variation in regeneration rates by aspect suggests there is the potential for fuels treatments to work with or against such natural biogeographical patterns. Leveraging these patterns to increase the combined effectiveness of treatments at the landscape level has been previously proposed by North, Collins, & Stephens (2012) and North et al. (2009). The regeneration patterns observed here indicate that managers should anticipate shorter treatment longevity on north aspects, especially because of the greater presence of Douglas-fir advance regeneration there relative to south aspects. However, trends in conifer regeneration over time since treatment and according to residual overstory density and composition must be considered along with the influence of aspect.

1.4.2 Treatment Characteristics and Conifer Regeneration

Douglas-fir advance regeneration decreases over time since treatment. It is likely that this is partially due to mortality. Although little dead regeneration was observed in our plots, these trees are small and would not be expected to persist in a recognizable form for long after they died. It is also possible that some of this advance regeneration is releasing, or growing faster in response to overstory disturbance that redistributes light and other resources (Lorimer & Frelich, 1989). Release has been observed in Douglas-fir in response to overstory disturbance (i.e. Arabas et al., 2008). Only 18 total live or dead Douglas-fir saplings were observed in all the plots, which suggests that most advance regeneration of this species has not yet released enough post-treatment to grow into the overstory. However, Douglas-fir advance regeneration may have

grown taller, just not tall enough to be considered saplings, meaning that these trees are still closing the gap between surface and canopy fuels, which reduces treatment effectiveness. Alternatively, release may have been delayed (Kneeshaw et al., 2002), and could still occur. Whether release is occurring could be determined by monitoring the height growth of advance regeneration remaining in fuels treatments. Comparing the annual ring widths from sampled understory trees would also reveal if the growth of advance regeneration did indeed increase post treatment, just not enough for them to grow into saplings. It would be beneficial to know if release is occurring or will occur in Colorado's forests or in other dry, mixed-conifer forests throughout the western U.S. to plan future treatments and to schedule maintenance of treated stands.

The relationship between time since treatment and post treatment regeneration varied by species. An increase in post treatment ponderosa pine regeneration over time since treatment was observable in this study, even given expected background variation in regeneration rates due to annual variability in seed production and suitable climatic conditions for subsequent establishment (Brown & Wu, 2005; Savage et al., 1996; Shepperd et al., 2006). However, there was no relationship between time since treatment and post treatment Douglas-fir. Plots of post treatment regeneration of each species by years post treatment indicate that most Douglas-fir establishes early in the treatment lifetime (Fig.5), while ponderosa pine establishes more evenly throughout years post treatment (Fig.7), such that only ponderosa pine accumulates over time since treatment. These trends in post treatment regeneration with respect to time since treatment likely reflect the relative shade tolerance of each species, as well as the relationships between these regeneration groups and the residual overstory density and composition of treated areas.

Ponderosa pine is more shade intolerant than Douglas-fir, so it should benefit more from the open canopy conditions created post treatment (Boyden et al., 2005; Chen, 1997), and this advantage may persist years into the treatment lifetime. Both advance and post treatment ponderosa pine regeneration did indeed decrease with increasing overstory density (basal area or trees per hectare), a finding which agrees with previous research showing that shade intolerant species regenerate in greater abundance under more open overstory conditions (Ertl, 2015; Francis et al., 2018; Gray et al., 2005; Zald et al., 2008). Conversely, post treatment Douglas-fir regeneration is positively related to Douglas-fir SDI. This is consistent with results from Francis et al. (2018), who also observed that ponderosa pine was well-represented in most all treated stands, while Douglas-fir was more reduced relative to untreated stands. Our study did not examine regeneration from an untreated condition, but the overstory density of Douglas-fir was generally lower than ponderosa pine (Table 4 above). A common goal of fuels treatments is to reduce overstory Douglas-fir relative to ponderosa pine because it is more shade tolerant and therefore establishes in greater abundance in undisturbed stands (Hermann & Lavender, 1990). Therefore, the positive relationship with residual overstory Douglas-fir density observed in our study and by Francis et al. (2018) suggests that post treatment Douglas-fir regeneration may be limited by seed availability in treated areas. Hence, whereas post treatment Douglas-fir regeneration is not increasing over time since treatment due to reduced seed availability, post treatment ponderosa pine regeneration is increasing because the treatments are effectively acting as shelterwood regeneration treatments by making the establishment environment more favorable for this species while continuing to provide a seed source.

1.5 Conclusions

Aspect, time since treatment, and residual overstory density and species composition had the greatest influence on conifer regeneration abundance in 5 to 14 year-old wildfire fuels reduction treatments in dry, mixed-conifer forests along Colorado's Front Range. Conifer regeneration did not vary between mastication and thinning treatment types. Douglas-fir advance regeneration is abundant in treated areas (50% of all observed regeneration). Although it appears to be decreasing over time since treatment, its presence is still concerning with regards to treatment effectiveness for two reasons. First, retaining a large quantity of advance regeneration is more likely to reduce treatment longevity than the gradual establishment of post treatment seedlings (Tinkham et al., 2016). This is especially true of Douglas-fir because it tends to have longer crowns and is therefore is less fire resistant and more likely to serve as ladder fuels than ponderosa pine (Hermann & Lavender, 1990; Keeley et al., 2004). Second, the influence of this species on treatment effectiveness will be exacerbated if it releases post treatment. If this is the case, forest managers should that anticipate that treatments containing lots of advance regeneration will deteriorate at a faster rate. Post treatment Douglas-fir regeneration did not increase over time since treatment, likely because it is limited by the residual density of overstory Douglas-fir to provide a seed source. Post treatment ponderosa pine regeneration, however, is accumulating steadily over time since treatment, which suggests, as has other recent research (Ertl, 2015; Francis et al., 2018), that fuels treatments may be effectively acting as shelterwood regeneration treatments for this species by reducing total overstory density while maintaining a seed source. Lastly, aspect will also influence fuels treatment longevity because less than 1/5 of all conifer regeneration was found on south aspects. However, regeneration on

north aspects is still highly variable, so managers should also consider the influence of residual overstory density and composition in treated areas when estimating treatment longevity.

WORKS CITED

- Addington, R.N., Aplet, G.H., Battaglia, M.A., Briggs, J.S., Brown, P.M., Cheng, A.S., Dickinson, Y., Feinstein, J.A., Pelz, K.A., Regan, C.M. and Thinnies, J. (2018). Principles and practices for the restoration of ponderosa pine and dry mixed-conifer forests of the Colorado Front Range. RMRS-GTR-373. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 121 p., 373.
- Acker, S. A., Greene, S. E., & Keyes, C. R. (2001). Overstory and shrub influences on seedling recruitment patterns in an old-growth ponderosa pine stand. *Northwest Science*, 75(3), 204-210
- Agee, J. K., & Skinner, C. N. (2005). Basic principles of forest fuel reduction treatments. *Forest Ecology and Management*, 211(1-2), 83-96.
- Anning, A. K., & McCarthy, B. C. (2013). Competition, size and age affect tree growth response to fuel reduction treatments in mixed-oak forests of Ohio. *Forest Ecology and Management*, 307, 74-83.
- Arabas, K. B., Black, B., Lentile, L., Speer, J., & Sparks, J. (2008). Disturbance history of a mixed conifer stand in central Idaho, USA. *Tree-Ring Research*, 64(2), 67-80.
- Bailey, J. D., & Covington, W. W. (2002). Evaluating ponderosa pine regeneration rates following ecological restoration treatments in northern Arizona, USA. *Forest Ecology and Management*, 155(1-3), 271-278.
- Battaglia, M. A., Smith, F. W., & Shepperd, W. D. (2008). Can prescribed fire be used to maintain fuel treatment effectiveness over time in Black Hills ponderosa pine forests? *Forest Ecology and Management*, 256(12), 2029-2038.
- Battaglia, M., Rhoades, C., Rocca, M. E., & Ryan, M. G. (2009). A regional assessment of the ecological effects of chipping and mastication fuels reduction and forest restoration treatments. Joint Fire Science Program Final Report. Project ID: 06-3-2-26
- Battaglia, M. A., Gannon, B., Brown, P. M., Fornwalt, P. J., Cheng, A. S., & Huckaby, L. S. (2018). Changes in forest structure since 1860 in ponderosa pine dominated forests in the Colorado and Wyoming Front Range, USA. *Forest Ecology and Management*, 422, 147-160.
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9(5), 191-193.
- Bolker, B., Skaug, H., Magnusson, A., & Nielsen, A. (2012). Getting started with the glmmADMB package. Available at: [glmmadmb.r-forge r-project.org/glmmADMB.pdf](http://glmmadmb.r-forge.r-project.org/glmmADMB.pdf).
- Bonnet, V. H., Schoettle, A. W., & Shepperd, W. D. (2005). Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. *Canadian Journal of Forest Research*, 35(1), 37-47.

- Boyden, S., Binkley, D., & Shepperd, W. (2005). Spatial and temporal patterns in structure, regeneration, and mortality of an old-growth ponderosa pine forest in the Colorado Front Range. *Forest Ecology and Management*, 219(1), 43-55.
- Briggs, J. S., Fornwalt, P. J., & Feinstein, J. A. (2017). Short-term ecological consequences of collaborative restoration treatments in ponderosa pine forests of Colorado. *Forest Ecology and Management*, 395, 69-80.
- Brown, P. M., Battaglia, M. A., Fornwalt, P. J., Gannon, B., Huckaby, L. S., Julian, C., & Cheng, A. S. (2015). Historical (1860) forest structure in ponderosa pine forests of the northern Front Range, Colorado. *Canadian Journal of Forest Research*, 45(11), 1462-1473.
- Brown, P. M., & Wu, R. (2005). Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology*, 86(11), 3030-3038.
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.
- Callaway, R. M., DeLucia, E. H., Moore, D., Nowak, R., & Schlesinger, W. H. (1996). Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. *Ecology*, 77(7), 2130-2141.
- Carmean, W. H. (1975). Forest site quality evaluation in the United States. In *Advances in Agronomy* (Vol. 27, pp. 209-269). Academic Press.
- Chambers, M. E., Fornwalt, P. J., Malone, S. L., & Battaglia, M. A. (2016). Patterns of conifer regeneration following high severity wildfire in ponderosa pine-dominated forests of the Colorado Front Range. *Forest Ecology and Management*, 378, 57-67.
- Chen, H. Y. (1997). Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. *Canadian Journal of Forest Research*, 27(9), 1383-1393.
- Chiono, L. A., O'hara, K. L., De Lasaux, M. J., Nader, G. A., & Stephens, S. L. (2012). Development of vegetation and surface fuels following fire hazard reduction treatment. *Forests*, 3(3), 700-722.
- Cleary, B. D., Greaves, R. D., & Hermann, R. K. (1978). *Regenerating Oregon's forests: a guide for the regeneration forester*.
- Cohen, J. (2008). The wildland-urban interface fire problem: A consequence of the fire exclusion paradigm. *Forest History Today*. Fall: 20-26., 20-26.
- Colorado Department of Natural Resources (CO DNR). 2016. Wildfire Risk Reduction Grant Program. [Online]. Last accessed 8 May 2018 from: <https://cdnr.us/#/programs>.
- Colorado Forest Restoration Institute. (2016). *Field Data Collection Protocol for Evaluating Fire Mitigation Effectiveness with The Fuel and Fire Tools Software System*. Fort Collins, CO: Colorado State University
- Daubenmire, R. F. (1976). The use of vegetation in assessing the productivity of forest lands. *The Botanical Review*, 42(2), 115-143.

- Denver Water, 2018. Watershed Protection & Management. Retrieved from <https://www.denverwater.org/your-water/water-supply-and-planning/watershed-protection-and-management>
- Dodson, E. K., & Root, H. T. (2013). Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA. *Forest Ecology and Management*, 302, 163-170.
- Donato, D. C., Fontaine, J. B., Campbell, J. L., Robinson, W. D., Kauffman, J. B., & Law, B. E. (2009). Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath–Siskiyou Mountains. *Canadian Journal of Forest Research*, 39(4), 823-838.
- Dunne, J. A., & Parker, V. T. (1999). Species-mediated soil moisture availability and patchy establishment of *Pseudotsuga menziesii* in chaparral. *Oecologia*, 119(1), 36-45.
- Ertl, E. (2015). Restoration impacts on understory plant species in a Colorado Front Range ponderosa pine and Douglas-fir forest (Master's Thesis, Colorado State University Libraries).
- Fajardo, A., Graham, J. M., Goodburn, J. M., & Fiedler, C. E. (2007). Ten-year responses of ponderosa pine growth, vigor, and recruitment to restoration treatments in the Bitterroot Mountains, Montana, USA. *Forest Ecology and Management*, 243(1), 50-60.
- Francis, D., Ex, S., & Hoffman, C. (2018). Stand composition and aspect are related to conifer regeneration densities following hazardous fuels treatments in Colorado, USA. *Forest Ecology and Management*, 409, 417-424.
- Front Range Fuels Treatment Partnership (FRFTP). 2012. 2012 Annual Report. 8 p.
- Fulé, P. Z., Laughlin, D. C., & Covington, W. W. (2005). Pine-oak forest dynamics five years after ecological restoration treatments, Arizona, USA. *Forest Ecology and Management*, 218(1-3), 129-145.
- Fulé, P. Z., Crouse, J. E., Roccaforte, J. P., & Kalies, E. L. (2012). Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management*, 269, 68-81.
- Graham, R. T. (2003). Hayman fire case study. Gen. Tech. Rep. RMRS-GTR-114. Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 396 p., 114.
- Gray, A. N., Zald, H. S., Kern, R. A., & North, M. (2005). Stand conditions associated with tree regeneration in Sierran mixed-conifer forests. *Forest Science*, 51(3), 198-210.
- Hermann, R. K., & Lavender, D. P. (1990). *Pseudotsuga menziesii* (Mirb.) franco Douglas-fir. *Silvics of North America*, 1, 527-540.
- Hoffman C.M., Collins B., Battaglia M. (2018). Wildland Fuel Treatments. In: Manzello S. (eds) *Encyclopedia of Wildfires and Wildland-Urban Interface (WUI) Fires*. Springer, Cham

- Hudak, A. T., Rickert, I., Morgan, P., Strand, E., Lewis, S. A., Robichaud, P., Hoffman, C., and Holden, Z. A. (2011). Review of fuel treatment effectiveness in forests and rangelands and a case study from the 2007 megafires in central Idaho USA.
- Jain, T. B., Battaglia, M. A., Han, H. S., Graham, R. T., Keyes, C. R., Fried, J. S., & Sandquist, J. E. (2012). A comprehensive guide to fuel management practices for dry mixed conifer forests in the northwestern United States. Joint Fire Science Program Synthesis Report. RMRS-GTR-292, USDA Forest Service Rocky Mountain Research Station
- Kaufmann, M. R., Fornwalt, P. J., Huckaby, L. S., & Stoker, J. M. (2001). Cheesman Lake-a historical ponderosa pine landscape guiding restoration in the South Platte watershed of the Colorado Front Range. In: Vance, Regina K.; Edminster, Carleton B.; Covington, W. Wallace; Blake, Julie A., comps. Ponderosa pine ecosystems restoration and conservation: steps toward stewardship; 2000 April 25-27; Flagstaff, AZ. Proceedings RMRS-P-22. Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 9-18., 22, 9-18.
- Keeley, J. E., Fotheringham, C. J., & Moritz, M. A. (2004). Lessons from the October 2003. Wildfires in Southern California. *Journal of Forestry*, 102(7), 26-31.
- Keyes, C. R., & Maguire, D. A. (2005). Postive seedling-shrub relationships in natural regeneration of ponderosa pine. In In: Ritchie, Martin W.; Maguire, Douglas A.; Youngblood, Andrew, tech. coordinators. Proceedings of the Symposium on Ponderosa Pine: Issues, Trends, and Management, 2004 October 18-21, Klamath Falls, OR. Gen. Tech. Rep PSW-GTR-198. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture: 95-107 (Vol. 198).
- Keyes, C. R., & Maguire, D. A. (2008). Some shrub shading effects on the mid-summer microenvironment of Ponderosa pine seedlings in Central Oregon. *Northwest Science*, 82(4), 245-250.
- Kinthead, C. S., Stambaugh, M. C., & Kabrick, J. M. (2017). Mortality, scarring, and growth in an oak woodland following prescribed fire and commercial thinning in the Ozark Highlands. *Forest Ecology and Management*, 403, 12-26.
- Kneeshaw, D. D., Williams, H., Nikinmaa, E., & Messier, C. (2002). Patterns of above-and below-ground response of understory conifer release 6 years after partial cutting. *Canadian Journal of Forest Research*, 32(2), 255-265.
- Larson, A. J., & Franklin, J. F. (2005). Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. *Forest Ecology and Management*, 218(1-3), 25-36.
- League, K. R. (2004). The role of recent climatic variability on episodic *Pinus ponderosa* recruitment patterns along the forest-grassland ecotone of northern Colorado (Doctoral dissertation, University of Colorado).
- Lenth, R., Love, J., & Lenth, M. R. (2018). Package 'lsmeans'. *The American Statistician*, 34(4), 216-221.

- Litschert, S. E., Brown, T. C., & Theobald, D. M. (2012). Historic and future extent of wildfires in the Southern Rockies Ecoregion, USA. *Forest Ecology and Management*, 269, 124-133.
- Lorimer, C. G., & Frelich, L. E. (1989). A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*, 19(5), 651-663.
- Marquis, D. A. (1965). Controlling light in small clearcuttings. Res. Pap. NE-39. Upper Darby, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 16 p., 39.
- Moody, J. A., & Martin, D. A. (2001). Initial hydrologic and geomorphic response following a wildfire in the Colorado Front Range. *Earth Surface Processes and Landforms: The Journal of the British Geomorphological Research Group*, 26(10), 1049-1070.
- North, M., Collins, B. M., & Stephens, S. (2012). Using fire to increase the scale, benefits, and future maintenance of fuels treatments. *Journal of Forestry*, 110(7), 392-401.
- North, M., Stine, P., O'Hara, K., Zielinski, W., & Stephens, S. (2009). An ecosystem management strategy for Sierran mixed-conifer forests. Gen. Tech. Rep. PSW-GTR-220 (Second printing, with addendum). Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station. 49 p, 220.
- Pearson, G. A. (1942). Herbaceous vegetation a factor in natural regeneration of ponderosa pine in the Southwest. *Ecological Monographs*, 12(3), 315-338.
- Peet, R. K. (1981). Forest vegetation of the Colorado front range. *Vegetation*, 45(1), 3-75.
- Petrie, M. D., Wildeman, A. M., Bradford, J. B., Hubbard, R. M., & Lauenroth, W. K. (2016). A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. *Forest Ecology and Management*, 361, 328-338.
- Prévost, M., & Raymond, P. (2012). Effect of gap size, aspect and slope on available light and soil temperature after patch-selection cutting in yellow birch–conifer stands, Quebec, Canada. *Forest Ecology and Management*, 274, 210-221.
- PRISM. (September 4, 2017). PRISM Climate Group at Oregon State University. Retrieved from: <http://prism.oregonstate.edu>
- Puhlick, J. J., Laughlin, D. C., & Moore, M. M. (2012). Factors influencing ponderosa pine regeneration in the southwestern USA. *Forest Ecology and Management*, 264, 10-19.
- Reineke, L. H. (1933). Perfecting a stand-density index for even-aged forests.
- Reinhardt, E. D., Holsinger, L., & Keane, R. (2010). Effects of biomass removal treatments on stand-level fire characteristics in major forest types of the Northern Rocky Mountains. *Western Journal of Applied Forestry*, 25(1), 34-41.
- Reynolds, R. T., Meador, A. J. S., Youtz, J. A., Nicolet, T., Matonis, M. S., Jackson, P. L., DeLorenzo, D.G., & Graves, A. D. (2013). Restoring composition and structure in

- southwestern frequent-fire forests: A science-based framework for improving ecosystem resiliency. USDA Forest Service-General Technical Report RMRS-GTR, (310 RMRS-GTR), 1-76.
- Roberts, S. D., Harrington, C. A., & Terry, T. A. (2005). Harvest residue and competing vegetation affect soil moisture, soil temperature, N availability, and Douglas-fir seedling growth. *Forest Ecology and Management*, 205(1-3), 333-350.
- Rother, M. T., & Veblen, T. T. (2016). Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. *Ecosphere*, 7(12).
- Ruel, J. C., Messier, C., Claveau, Y., Doucet, R., & Comeau, P. (2000). Morphological indicators of growth response of coniferous advance regeneration to overstorey removal in the boreal forest. *The Forestry Chronicle*, 76(4), 633-642.
- Safford, H. D., Stevens, J. T., Merriam, K., Meyer, M. D., & Latimer, A. M. (2012). Fuel treatment effectiveness in California yellow pine and mixed conifer forests. *Forest Ecology and Management*, 274, 17-28.
- Savage, M., Brown, P. M., & Feddema, J. (1996). The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience*, 3(3), 310-318.
- Schwilk, D. W., Keeley, J. E., Knapp, E. E., McIver, J., Bailey, J. D., Fettig, C. J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., & Skinner, C. N. (2009). The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. *Ecological Applications*, 19(2), 285-304.
- Shepperd, W. D., Edminster, C. B., & Mata, S. A. (2006). Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado front range. *Western Journal of Applied Forestry*, 21(1), 19-26.
- Sherriff, R. L., Platt, R. V., Veblen, T. T., Schoennagel, T. L., & Gartner, M. H. (2014). Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. *PloS one*, 9(9), e106971.
- Stephens, S. L., McIver, J. D., Boerner, R. E., Fettig, C. J., Fontaine, J. B., Hartsough, B. R., Kennedy, P.L., & Schwilk, D. W. (2012). The effects of forest fuel-reduction treatments in the United States. *BioScience*, 62(6), 549-560.
- Stephens, S. L., & Moghaddas, J. J. (2005). Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. *Forest Ecology and Management*, 215(1-3), 21-36.
- Team, R. C. (2013). R: A language and environment for statistical computing.
- Tinkham, W. T., Hoffman, C. M., Ex, S. A., Battaglia, M. A., & Saralecos, J. D. (2016). Ponderosa pine forest restoration treatment longevity: implications of regeneration on fire hazard. *Forests*, 7(7), 137.
- United States Forest Service Activity Tracking Database (USFS). 2016. Download National Datasets. [Online]. Last accessed September 2016 from: <https://data.fs.usda.gov/geodata/edw/datasets.php>.

- Vaillant, N. M., Noonan-Wright, E., Dailey, S., Ewell, C., & Reiner, A. (2013). Effectiveness and longevity of fuel treatments in coniferous forests across California. Joint Fire Science Program Final Report. Project ID: 09-1-01-1, USDA Forest Service
- Veblen, T. T., & Donnegan, J. A. (2005). Historical range of variability for forest vegetation of the national forests of the Colorado Front Range. USDA Forest Service, Rocky Mountain Region.
- Westerling, A. L., Hidalgo, H. G., Cayan, D. R., & Swetnam, T. W. (2006). Warming and earlier spring increase western US forest wildfire activity. *Science*, 313(5789), 940-943.
- Zabowski, D., Java, B., Scherer, G., Everett, R. L., & Ottmar, R. (2000). Timber harvesting residue treatment: Part 1. Responses of conifer seedlings, soils and microclimate. *Forest Ecology and Management*, 126(1), 25-34.
- Zald, H. S., Gray, A. N., North, M., & Kern, R. A. (2008). Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. *Forest Ecology and Management*, 256(1-2), 168-179.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). Mixed effects models and extensions in ecology with R. *Statistics for biology and health*.