THESIS

THE EFFECTS OF CLIMATE ON ENGELMANN SPRUCE REGENERATION AND VIGOR

Submitted by

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ABSTRACT

THE EFFECTS OF CLIMATE ON ENGELMANN SPRUCE REGENERATION AND VIGOR

Recent climate modeling suggests that drought will become more frequent in the southern Rocky Mountains over the next century. Understanding how tree species will respond and adapt to this changing climate is vital to guide future management decisions by land managers. Future increases in drought frequency and severity will likely have an impact on the composition of forests. Modeling studies have been used to predict the effect that increasing drought will have on Engelmann spruce in southwest Colorado, but little field data has been gathered to validate this modeling. This study uses empirical data to test whether drought conditions are related to decreases in seedling establishment and tree vigor. Annual regeneration data from 1990 to 2009 was collected from 24 sites with 30-year PRISM precipitation normals ranging from 531 mm to 924 mm to determine if dry and wet sites respond differently to drought. Elevations of our study sites ranged from 3100 m to 3500 m above sea level. Among these 24 sites, we found the number of seedlings per hectare varied between 1804 and 18975. We used a mixed effects model to identify climate variables important to annual seedling establishment density. A separate provenance study on the White River National Forest was analyzed to identify drought effects on tree vigor. Engelmann spruce bareroot seedlings from twenty sources ranging from British Columbia to New Mexico were planted in 1970 at an elevation of 2930 m north of Vail, Colorado. Annual precipitation normals of the 20 seed sources ranged from 423 – 1918 mm. We collected increment cores from six to eight trees from each of the 20 seed sources in 2016, and standardized the chronology of each tree using standard dendrochronological techniques.

We then analyzed the annual radial growth response of each provenance to a period of severe drought from 2000-2004 using both RWI and a resistance/resilience framework. For both parts of our study, we found weather variability and drought did not impact regeneration or vigor as much as hypothesized, suggesting regeneration and vigor of spruce in these high elevation forests are not reduced by contemporary levels of drought.

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I'd like to personally thank my parents, Mike and Laura Prolic, for their continued support throughout graduate school. My brothers, Ross and Harrison, for their encouragement and for being available to talk at any time. I would also like to mention my friends who provided a break from the grind of graduate school. This includes, but is not limited to, Ryan Davy, David Francis, Kyle O'Neill, Michael Clausen, and Sam Peters.

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CHAPTER 1: INTRODUCTION

Climate change is expected to impact subalpine forests in the western United States in multiple ways. Longer growing seasons, variable precipitation, and more frequent drought events are predicted to lead to shifts in high elevation species' ranges (Rehfeldt et al. 2006, Seager et al. 2007, Hu et al. 2010). Successful range shifts are dependent on species being able to migrate along with climate conditions conducive to survival and growth.

Recent bioclimate modeling suggests that a warmer, drier climate will alter the range of Engelmann spruce in central and southwest Colorado by the year 2060 (Rehfeldt et al. 2015). Anticipated warming and drying will result in climatic conditions in the driest locations that currently support Engelmann spruce-dominated forests becoming warmer and drier than conditions currently associated with the species. Cases of increased mortality due to drought and heat have already been documented in multiple forest types (Allen and Breshears 1998, Allen et al. 2010), and Engelmann spruce dominated forests are expected to respond similarly (Rehfeldt et al. 2006). While several mechanisms may determine the future range of Engelmann spruce, drought-related seedling mortality and reduced vigor of mature trees is likely to be critically important (Noble and Alexander 1977, Alexander 1987, Bentz et al. 2010). To guide management decisions in the future, we must improve our understanding of the effects of drought on regeneration and vigor of this high elevation tree species.

We look at both regeneration and vigor of Engelmann spruce using two separate study designs. With respect to regeneration, we wanted to know whether interannual weather variation

influenced annual seedling establishment. We hypothesized that warmer, drier years would decrease the amount of regeneration success. To test this hypothesis, we sampled stands on the Gunnison National Forest to find annual seedling establishment for each year from 1990 to 2009 in most stands. This period included a wide variety of weather conditions, including severe drought years. To relate yearly seedling establishment density to interannual weather variability, we used mixed effects models to find significant relationships between weather variables and our response variable. This approach helped identify weather variables that were important for spruce regeneration in our stands.

With respect to tree vigor, we wanted to know if seed from various genetic and environmental backgrounds would respond differently to drought in a common planting location. We hypothesized trees from warmer, drier provenances would see less of a decrease in vigor due to drought conditions. We collected increment cores from all provenances to analyze average annual ring width indices (RWI) in relation to 5 year periods during and after drought. We used this standardized ring width index as a proxy for vigor (Dobbertin 2005) and calculated a resistance-resilience framework similar to that of D'Amato et al. (2013) in order to quantify differences between provenances in response to our periods of interest. Mixed effects models and means comparisons were used to find significant differences in resistance and resilience for each provenance.

CHAPTER 2: ANNUAL CLIMATE EFFECTS ON ENGELMANN SPRUCE
REGENERATION IN SOUTHWEST COLORADO

2.1 Introduction

Climate change models suggest that drought events are likely to become more frequent in Colorado's high elevation forests over the next century (Seager et al. 2007). Seager et al. (2007) predicts that the aridity of the 1950's and recent early 2000's drought will be the new climatology of the southwestern United States within the 21st century. Increasing drought has the potential to cause the range of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) to contract substantially throughout the western US (Rehfeldt et al. 2006). To guide management decisions in the future, we must improve our understanding of the effects of drought on regeneration of this high elevation tree species.

Trees are slow growing organisms that may find it difficult to migrate along with their desired climatic conditions if climate change occurs as quickly as it is projected to (Williams and Dumroese 2013). In general, it is predicted that plant species will move upward in latitude and altitude in response to a warmer climate (Iverson and Prasad 1998). In one study, an upward shift in elevation has already been observed at the ecotone between a Piñon-juniper woodland and a Ponderosa pine forest (Allen and Breshears 1998).

Recent bioclimate modeling suggests that a warmer, drier climate will alter the range of Engelmann spruce in central and southwest Colorado by the year 2060 and reduce the range of spruce in the Western United States 72% by 2090 (Rehfeldt et al. 2006, 2015). Anticipated

warming and drying will result in climatic conditions in the driest locations that currently support Engelmann spruce-dominated forests becoming warmer and drier than conditions currently associated with the species. Precipitation and water balance has been demonstrated as a good predictor of where species can survive (Stephenson 1990) and we'd expect Engelmann spruce to be no different. Cases of increased mortality due to drought and heat have already been documented in multiple forest types (Allen et al. 2010), and Engelmann spruce dominated forests are predicted to respond similarly (Rehfeldt et al. 2006, 2015).

Every species has a regeneration niche, defined as the environmental conditions required for establishment of new trees (Grubb 1977, Dobrowski et al. 2015). This set of conditions varies for each species, but typically juvenile trees can survive a narrower range of environmental conditions than adults of the same species (Dobrowski et al. 2015, Urza and Sibold 2017). In Colorado, spruce occurs in areas with average annual temperatures of -1 – 2°C and 610 – 1400 mm of average annual precipitation with up to 75% of it occurring as snow (Alexander 1987). These are environmental conditions where mature spruce exist, and we expect the current range of spruce reflects the more restrictive requirements for regeneration, rather than the less restrictive requirements for adult survival.

Successful Engelmann spruce establishment is dependent upon seed production, dispersal of seed, successful germination, and seedling survival (Pelz et al. 2016). While these other mechanisms may also determine the future range of Engelmann spruce, drought and heat related seedling mortality is likely to be critically important (Noble and Alexander 1977, Alexander 1987). Spruce seedlings have the highest survival rate when growing season precipitation is over

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1.25 cm a week and when air temperatures are below 25°C (Noble and Alexander 1977). These temperature and precipitation thresholds have been identified in clearcuts on the Fraser Experimental Forest in Colorado, but a partial overstory has been shown to aid in spruce seedling survival by ameliorating unfavorable weather conditions (Roberts and Long 1991). Specifically, a partial overstory provides shade, reducing the vapor pressure deficit for seedlings (Roberts and Long 1991, Pelz et al. 2016). It is common practice in Colorado to partially cut stands to leave residual basal area in the overstory, while also leaving slash on the ground for microsites (Long 1995).

Seed production will also determine how well spruce is able to move along with its required weather conditions. Past studies have found that Engelmann spruce produces seed crops rated "good" to "bumper" every two to five years, some seed every year, but high variation across locations and years (Alexander 1987, Buechling et al. 2016). We'd expect this annual variation in seed production to cause variation in the number of germinants. The high seed years were correlated with years with high summer temperatures, although a potential threshold temperature of 1.2 °C was identified as the point where seed production began to decline again (Buechling et al. 2016). Buechling et al. (2016) also found increased seed production in drought years.

Bioclimate modeling correlates climatic and topographic variables with a species' distribution to predict future range shifts under a changing climate (Rehfeldt et al. 2015). It is important to understand bioclimate models do not account for all the factors associated with the distribution of tree species, and empirical evidence can help to test these models (Heikkinen et al. 2006). Species have fundamental and realized niches. It's the realized niches that actually determine

where the species is able to thrive (Pearman et al. 2008). Fundamental niches don't consider biological interactions like competition or herbivory.

This study attempts to provide empirical evidence of the actual effect annual fluctuations in precipitation and temperature had on regeneration success in partially cut Engelmann spruce stands. A recent severe drought event in Colorado from 2000-2004 (Fig 1.) provided us with insight as to how high elevation spruce stands responded to high temperatures and lower precipitation. This drought is estimated to be among the most severe of the last 500 years (Andreadis et al. 2005). In this study, we address the following question regarding our objective: Was there a significant effect of interannual weather variation on yearly seedling establishment? We hypothesize that Engelmann spruce will see a decrease in seedling establishment density during hotter, drier years. We also examined stand level variables, such as 30-year precipitation normals, site index, basal area, and heat load index in our analysis to account for any effect these may have on regeneration. We hypothesize that higher site qualities and higher basal areas will lead to an increase in average annual regeneration.
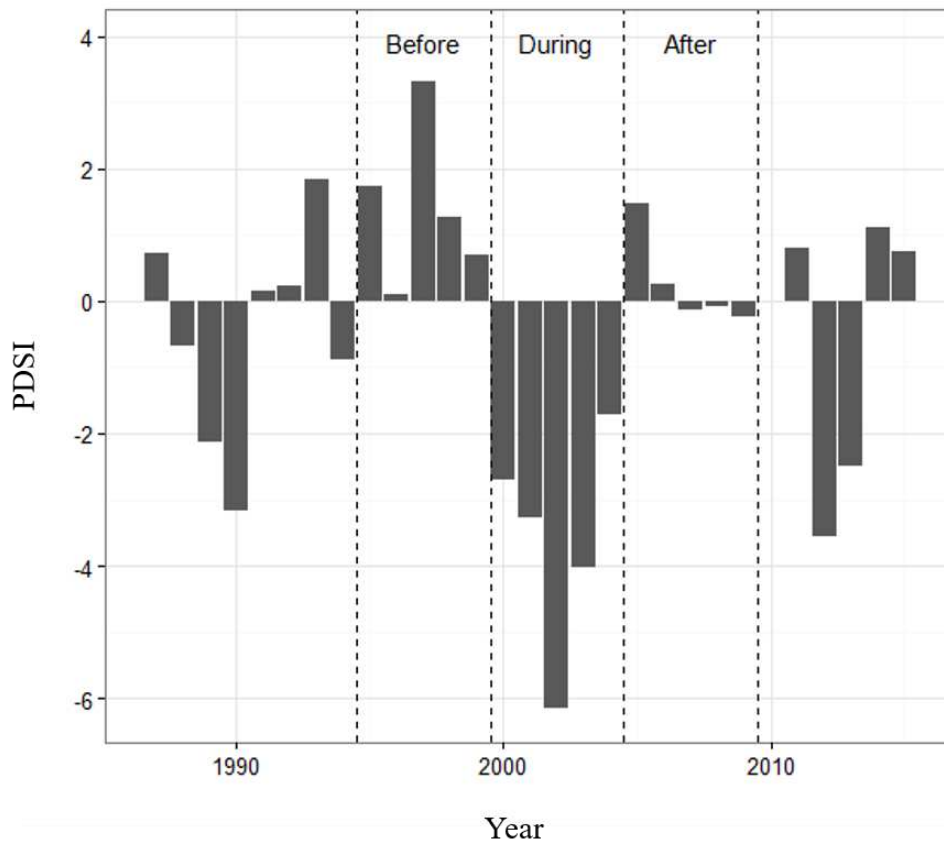
Figure 1: PDSI in the Western Colorado Climate Division for the period of 1987 to 2015, covering our period of interest in this study. Dashed lines indicate time before, during, and after drought. Negative PDSI values indicate drier than average years. PDSI values less than -2 indicate moderate drought, while severe and extreme droughts are those with values less than -3 and -4 respectively (Palmer 1965). PDSI data acquired from National Climatic Data Center (NCDC).

2.2 Methods

2.2.1 Study Design

The experimental unit for our study was the site. We designed our study to find sites partially-cut in the late 1980's to mid-1990's and containing spruce as the dominant part of the overstory. We also identified sites across a gradient of precipitation to attempt to obtain a sample spanning

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the range of spruce habitat. We put 20 plots in each site in a systematic grid derived from a random starting point. At each plot, we measured seedling heights and later aged the seedlings to give us a year of establishment for each seedling. The number of seedlings that established in each year became our final response variable, which we compared to a subset of weather variables to determine how weather variability impacted annual seedling establishment. Because we retroactively sampled throughout a range of years on each site, we used a repeated measures structure for our mixed effects modeling.

2.2.2 Study Area

We located sites on the Gunnison National Forest in southwest Colorado to be sampled (Fig. 2). We used both ArcGIS 10.3 and the Forest Service Activity Tracking System (FACTS) database to identify stands that had been partially cut in the late 1980's or 1990's that had a spruce seed source and available growing space for seedlings from the 1990's to present day. We looked for these criteria to be certain that our findings weren't altered by a lack of a suitable regeneration environment during our period of interest. Partial cutting allows for regeneration to occur in spruce dominated forests. We also used a vegetation layer showing dominant overstory tree species to identify areas where Engelmann spruce was a prominant part of the overstory. In addition, we stratified sampling across a precipitation gradient using interpolated PRISM 30-year precipitation normals at a resolution of 800 m^2 (PRISM Climate Group 2016). Potential sites were then ground-truthed to be sure that a spruce overstory was present and no confounding factors, such as planting or recent severe disturbances, were preventing natural regeneration from occurring.

2.2.3 Sampling design

We selected 24 sites that were subsequently sampled with a systematic grid of nested plots built around a randomly placed starting point. Spacing between plots was determined by calculating the square spacing needed to place 30 plots within the boundaries of the site, leaving us with more plots than needed. We established plots until 20 plots had been measured in each site, skipping over any plots that were deemed unfit for regeneration to occur, such as plots that fell on rocky outcroppings or roads. Slope, aspect, and basal area of all living and dead trees were collected at each plot. Elevation was determined later in Google Earth from a point selected near the middle of the range of elevations spanned by each site (Google 2017).

Seedlings were sampled using a 28 m^2 fixed radius plot where each tree less than 130 cm in height was sampled. Species was recorded and height on each seedling was measured to the nearest centimeter. Size classes were classified into 5 cm intervals up to 130 cm, at which point trees became part of the overstory plots. Each seedling was then cut at ground level, labeled, and taken to be aged later. When more than three trees of one species were present within a 5-cm height class in each plot, we cut the first three seedlings of each species that fell within the size class, while only measuring heights of subsequent seedlings. We used either a 4.6 m^2 hectare^{-1} or 2.3 m^2 hectare^{-1} basal area factor prism to estimate overstory basal area at each plot.

At every other plot, we collected an increment core to be aged in order to calculate site index (Clendenen 1977). We collected cores until we hit the pith of the tree. The tallest, free-growing Engelmann spruce tree on every other plot was selected to be the site tree. Trees that appeared to

have their growth suppressed at on any point were not used. We determined suppression by

looking for obvious growth releases in the cores we collected. If no suitable site tree was present

at a plot, a site tree core was collected at the next plot.
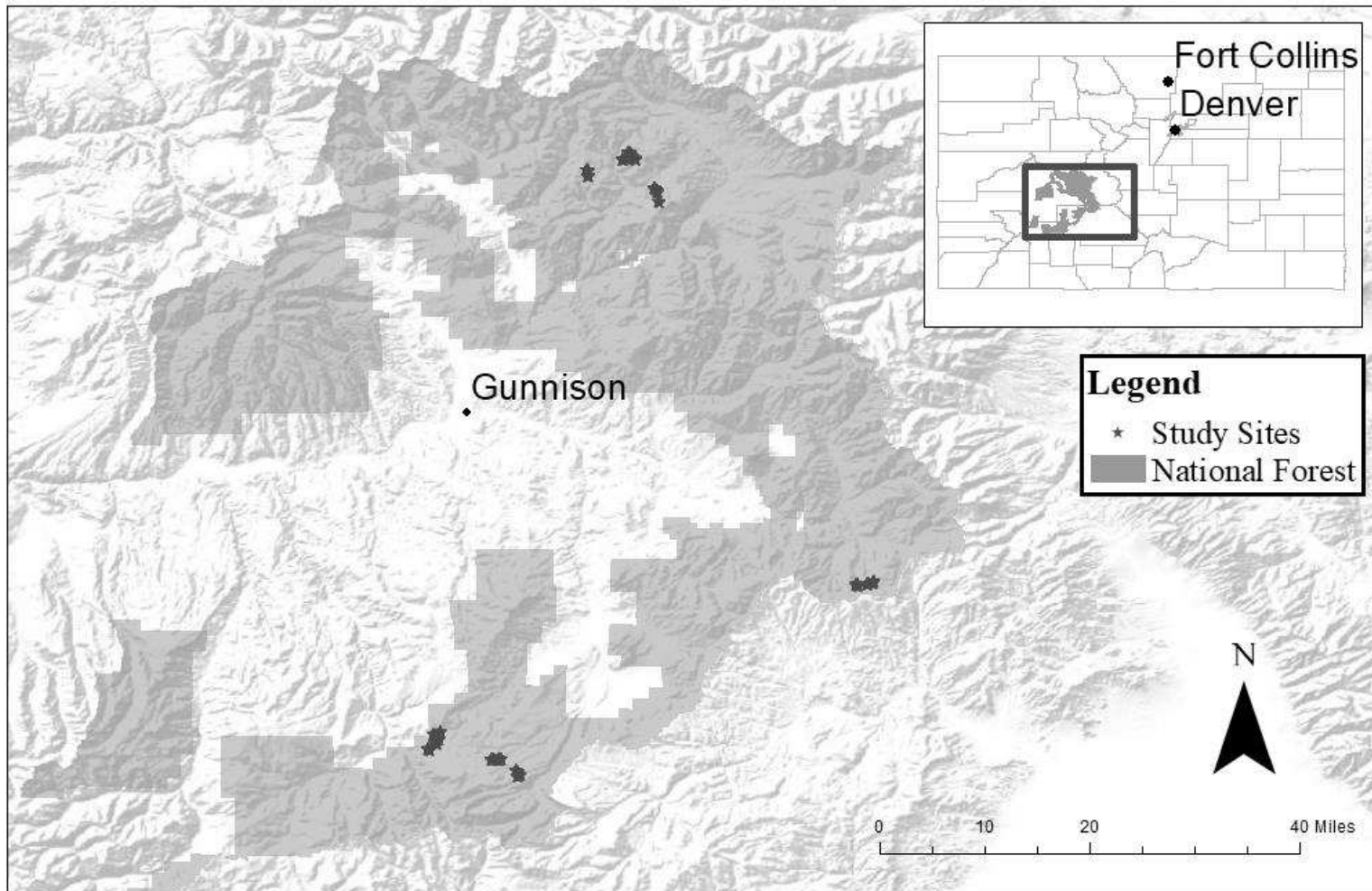
Figure 2: Map of 24 study site locations on the Gunnison National Forest in Southwest Colorado. Annual seedling establishment density was measured within each site retroactively from the year after treatment to 2009 and then related to annual and monthly weather variables.

2.2.4 Lab analysis

Seedling and overstory samples were taken back to the lab to be processed. Site tree cores were mounted and sanded using progressively finer grit sand paper. Site trees were aged by counting the rings to pith. Seedling cross-sections were sanded and then aged by counting rings under a microscope to determine the year in which each seedling established.

2.2.5 Statistical Analysis

Linear regression models were used to predict missing seedling ages due to subsampling. We used backwards stepwise selection starting with predictor variables of height, overstory basal area, elevation, site index, slope, aspect, and interactions between these variables. We used AIC values to compare models until we found the model with the lowest AIC value.

We conducted an exploratory analysis to identify any obvious strong relationships between weather variables and yearly seedling establishment density. All weather data was obtained from ClimateNA which downscales other interpolated climate models to determine climate conditions for specified points based on latitude, longitude, and elevation (Wang et al. 2016). For the United States, ClimateNA downscales 800 x 800 m data from PRISM to a single point located at the coordinates we provided (Wang et al. 2016, PRISM Climate Group 2016). This resolution gave us unique weather variable values for each site as ClimateNA interpolates variables based on a single point and the elevation at that point. Yearly seedling establishment density was our response variable, and weather variables were used as predictors. We considered weather variables that were relevant to the ecology of the species, such as annual and monthly

precipitation, annual and monthly temperature, the length of the growing season, and so on. For each variable, we also considered previous and future years' effects on establishment. Obvious, linear relationships were looked for between annual seedling establishment density and weather variables.

To analyze the effects of weather on seedling establishment, we used a mixed effects repeated measures analysis of variance with site as a random effect. The analysis was carried out using the nlme package in R which builds linear and nonlinear mixed effects models (Pinheiro et al. 2016). Multiple ecological studies have used this method to quantify tree population level responses to climate, fire, or management (D'Amato et al. 2013, Curzon et al. 2016, Scherer et al. 2016). Repeated measures analysis accounts for a lack of independence between measurements taken from the same experimental unit, in our case the site (Sullivan 2008). Because yearly seedling establishment density was reconstructed using tree rings in each site, we ended up with measurements for each year in our period of interest. We cannot assume independence between our measurements, because the amount of regeneration in one year depends on the amount of regeneration in other years. To account for this correlation, we used a covariance structure called "autoregressive of order 1" or AR(1) (Sullivan 2008). This covariance structure assumes that adjacent years are more highly correlated than years further apart and fits our data structure of continuous, equally spaced measurements through time.

We used the dredge function from the R package "MuMIn" to find the model with the lowest AIC value (Barton 2016). We compared AIC values using $\Delta_i = AIC_i - AIC_{min}$, where models with $\Delta_i < 2$ were considered to have substantial support (Burnham and Anderson 2002). When

building our models, we used the "Maximum Likelihood" method which allows mixed models

with different fixed effects to be compared (Ann Hess, pers. comm.). Because the restricted

maximum likelihood method estimates random-effect parameters averaged over the values of the

fixed-effect parameters, it doesn't allow for the direct comparison of models with different fixed

effects (Bolker et al. 2009). The number of seedlings per hectare per year after treatment up to

2009 were used for analysis. We cut off our data at the year 2009 to give us 20 years of

measurements in most stands (1990-2009) and to remove recent years with many young

germinants that may still experience high rates of mortality. Also, ten of our stands experienced

high levels of spruce bark beetle (*Dendroctonus rufipennis* Kirby) mortality among overstory

trees from 2009 onwards, altering the regeneration environment in those areas.

2.3 Results

2.3.1 Stand Characteristics

Stand elevations ranged from 3136 to 3500 m above sea level. In all 24 stands, spruce was the

dominant species in the overstory. Subalpine fir (*Abies lasiocarpa*) and quaking aspen (*Populus*

tremuloides) were the most common associates with lodgepole pine (*Pinus* contorta) occurring

infrequently. Site indices (base age 100) were calculated using the methods described in

Clendenen 1977 (Table 1). 30 year PRISM climate normals ranged from 531 to 924 mm of

precipitation annually (PRISM Climate Group). The average of our PRISM normals was 721

mm of annual precipitation (Fig. 3). The mean size of our stands was 16.1 hectares with a

minimum and maximum size of 2.5 hectares and 42.5 hectares. Spruce regenerated at an average

rate of 78.6 seedlings per hectare per year in our stands between the years 1990 and 2009. This

number would be higher if we included trees less than five years old, but the future survival rate

of those young trees is unknown.

Table 1: Summary statistics for stand characteristics of all 24 sites.

	Mean	Minimum	Maximum
SI_{100} (m)	13.7	9.2	18.1
Basal Area (m^2 hectare^{-1}) *	25.3	13.8	33.9
% Spruce Mortality (Basal Area) *	43.1	4.3	92.2
% Spruce (Basal Area) *	82	61	100
Trees per hectare **	1570	684	3709
Elevation (m)	3347	3136	3505
Spruce Seedlings per Hectare	3513	672	13316

* Only trees > 1.3 m in height

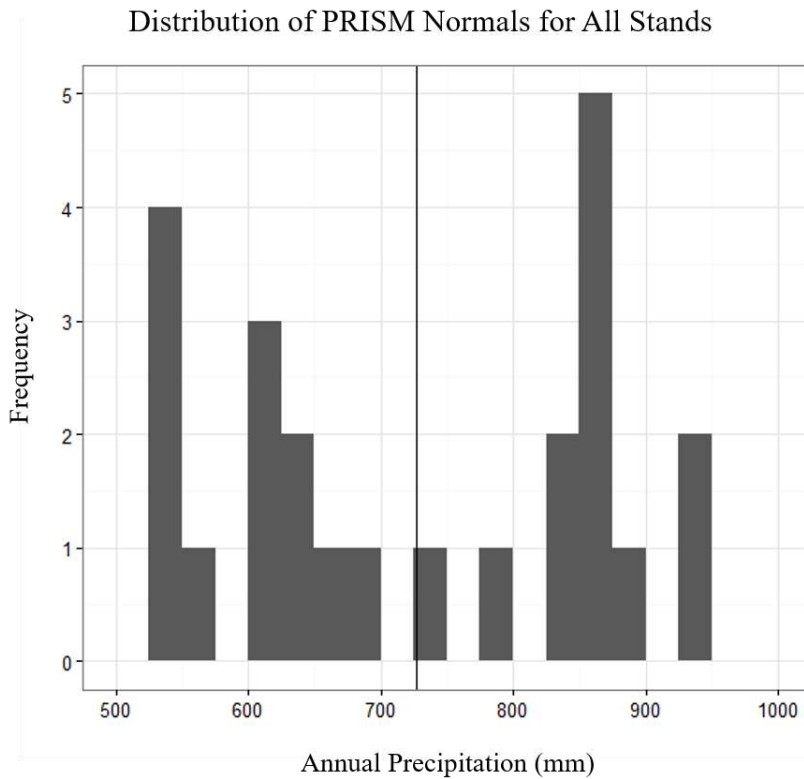** Only trees greater than 1" in diameter at breast height

Figure 3: Distribution of 30-year PRISM precipitation normals for all 24 sampled sites at a resolution of 800 m^2. Vertical line indicates the mean for sites sampled of 727 mm of precipitation per year.

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In the context of the recent bioclimate modeling done in southwest Colorado, our stands fell into the "threatened" or "persistent" categories established by Rehfeldt et al. (2015). These categories correspond to where spruce is expected to be able to survive in the year 2060 based on the climate envelope the species currently occupies. Our "persistent" stands, therefore, are predicted with a high degree of confidence to still be within the climatic envelope of spruce in 2060. Our threatened stands are in areas where Rehfeldt's model had a low degree of confidence in whether spruce would be lost or persistent in those areas. We were unable to sample any stands that were in the "lost" category, as they correspond with lower elevations and south aspects which are not as prevalent or partially cut as often on the Gunnison National Forest.

2.3.2 Spruce Seedling Age Prediction Model

Overall, we measured ages on 2776 spruce seedlings, compared to 4730 that we sampled heights on. Therefore, we only needed to predict ages on 41.4% of our sampled spruce seedlings. Our final predictor variables included seedling height on the log scale, plot basal area of live and dead trees, and an interaction term between the two variables. We also log transformed the response variable, age. We ended up with a model with a R^2 of 0.8039 with all variables being highly significant. We then used this model to fill in the missing ages and ages were back-transformed from the log scale. After back-transforming the predicted ages, we corrected for transformation bias (Sprugel 1983). Diagnostic plots were examined to determine the goodness of fit for our model (Fig. 4). The coarse diagonal lines in Fig. 3 are the result of the log scale in the model. We found a model with equal variance across the range of values, with slight

overprediction bias occurring with trees over 15 years old. We were not concerned with this

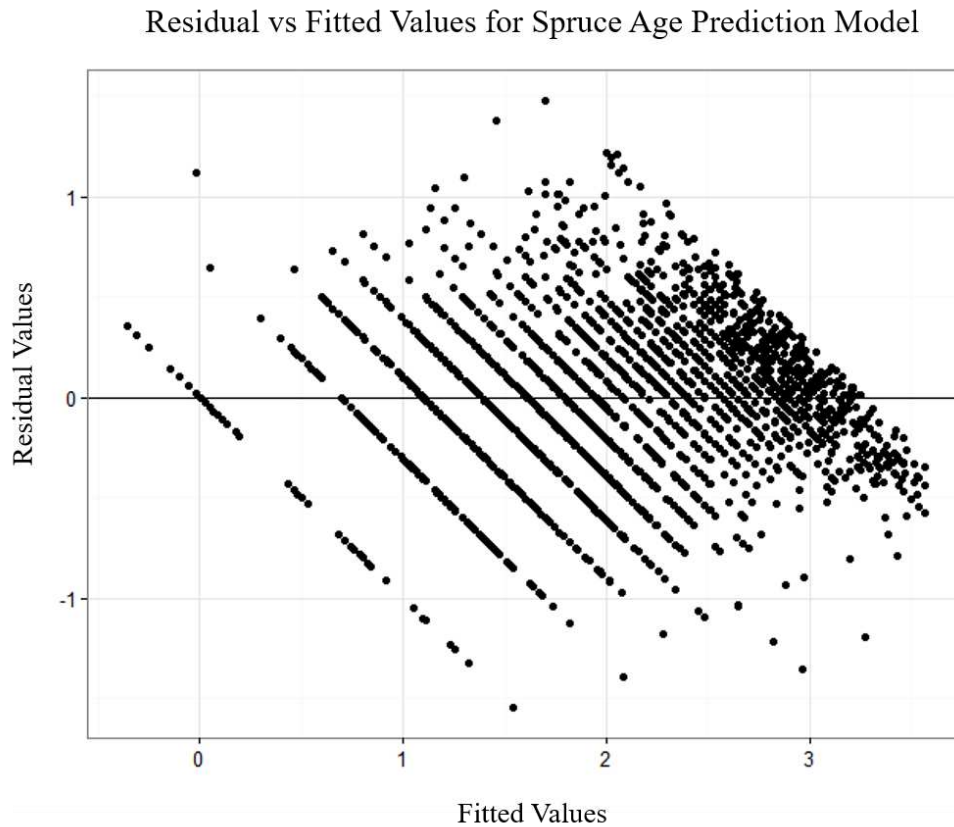bias, however, as our model predicted only 3.7% of our missing ages to be greater than 20 years.

Residual vs Fitted Values for Spruce Age Prediction Model

Figure 4: Plot of model residual values vs. fitted values used to check the goodness of fit for our spruce seedling age prediction model.

2.3.3 Mixed Effects Modeling with Repeated Measures

Mixed effect modeling showed that few weather variables and stand-level variables showed any

relationship with annual seedling establishment density. The model with the lowest AIC value

included year, mean annual temperature (MAT), annual precipitation (AP), an interaction term

between MAT and AP, and June precipitation (PPT06) of the year of establishment as predictor

variables with annual seedling establishment density as the response. All three predictors were

significant in the model (Table 2), but relationships appeared very weak when examined

graphically (Figs. 5 – 7).

The relationship between mean annual temperature and seedling density was the strongest we

found (Fig. 5). June precipitation was also highly significant, but had a slightly negative

relationship with seedling establishment (Fig. 6). The interaction term between MAT and AP

showed at lower levels of precipitation the relationship between MAT and seedling

establishment is positive, but at higher levels of precipitation the same relationship flattens out

(Fig. 7).   There was no significant relationship between annual precipitation and seedling

density but, it was included in the final model due to its interaction with MAT.

Table 2: Summary of final mixed effects model parameters and p-values at a significance level of $\alpha = 0.05$.

	Slope	Std Err	p-value
MAT	3.803	3.80	0.0013
AP	0.002	0.00	0.3679
PPT06	-0.072	0.02	0.0036
MAT:AP	-0.004	0.00	0.0134

Other models considered included one with year and MAT as predictor variables, and another

model with year, MAT, and PPT06 as predictors. However, with Δ_i values of 5.97 and 2.6

respectively, these models were deemed to not have enough support. We also included

Rehfeldt's bioclimate modeling classifications in our models, but it was not found to be

significant.

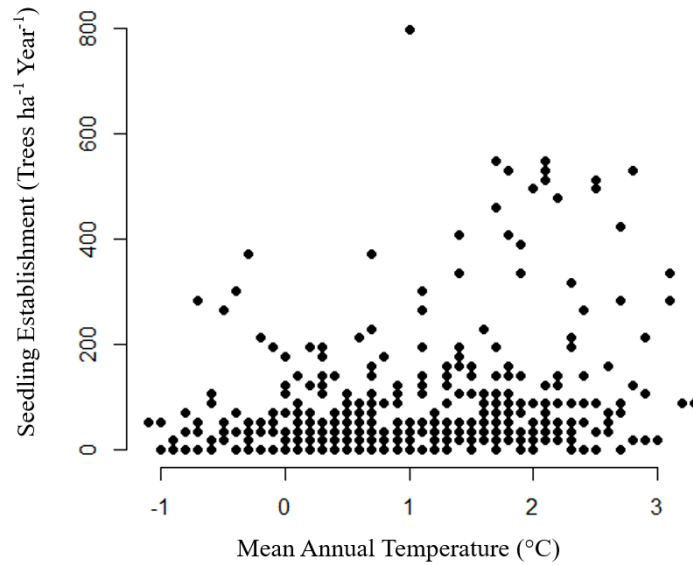**Annual Seedling Establishment vs Mean Annual Temperature**

Figure 5: Relationship between annual seedling establishment density and mean annual temperature across all 24 sites sampled on the Gunnison National Forest. Each point represents a single annual seedling density value within a site.

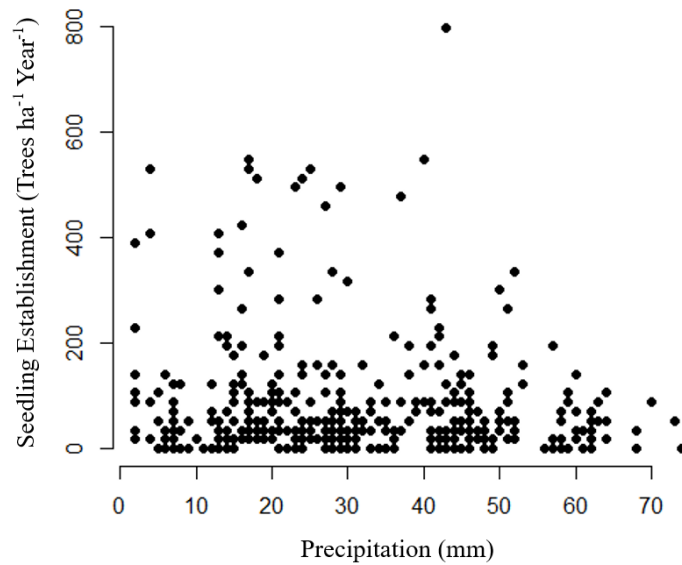**Annual Seedling Establishment vs June Precipitation**

Figure 6: Relationship between annual seedling establishment and June precipitation in the year of establishment across all 24 sites samples on the Gunnison National Forest. Each point represents a single annual seedling density value within a site.
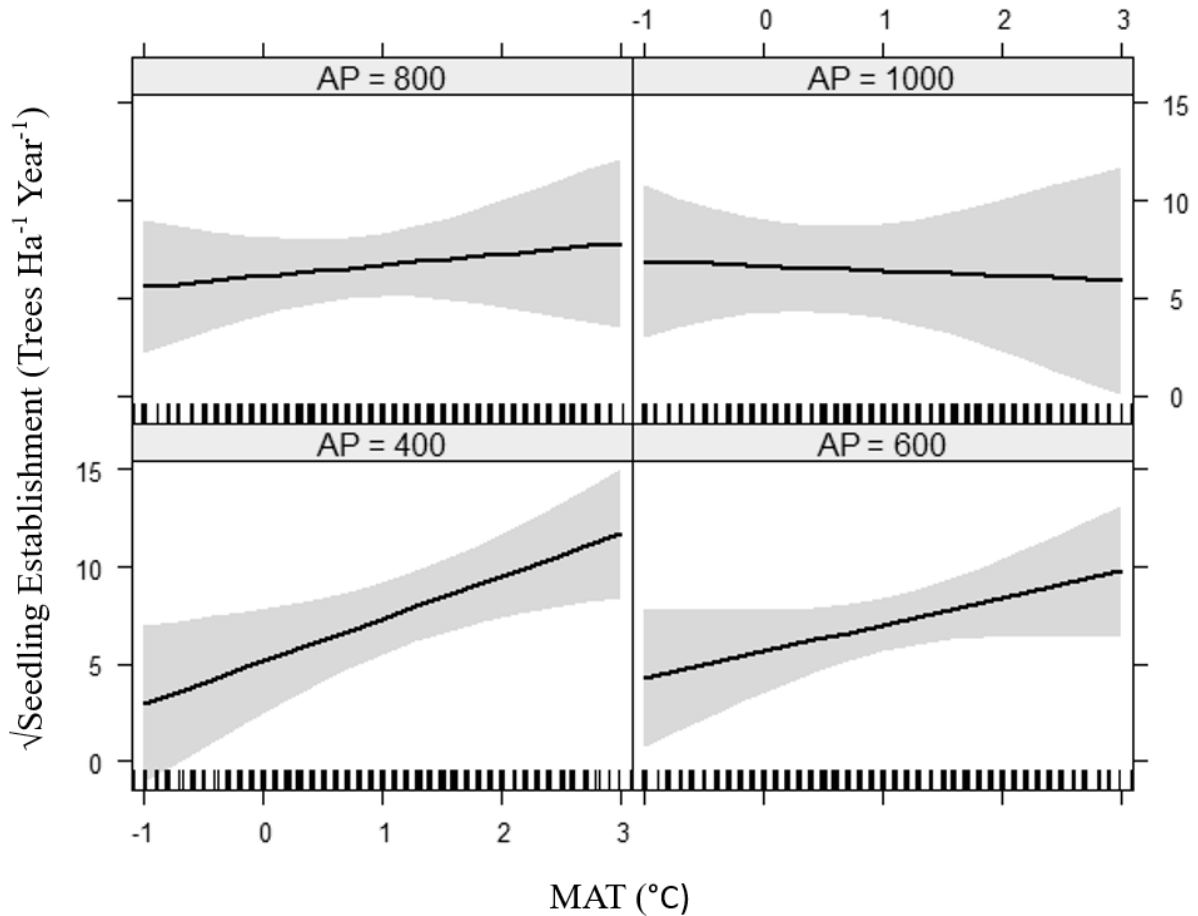
Interaction Plots for MAT and AP

Figure 7: Interaction plot showing the effect on annual seedling establishment (square root scale) of MAT (°C) at various levels of AP (mm).

2.4 Discussion

Our study attempted to characterize the effect of interannual weather variation on Engelmann spruce seedling establishment in southwest Colorado. We predicted that Engelmann spruce seedling establishment would be lower in warmer, drier years, but we did not find evidence of this effect. Ultimately, we were unable to detect any strong relationships between seedling establishment and annual weather variation. Annual variation in precipitation in these high

elevation stands seems to be of minor importance for seedling establishment, while temperature, not drought, had the strongest relationship with seeding establishment among the weather variables we examined.

Our results weakly suggest that warmer mean annual temperatures may actually benefit Engelmann spruce seedlings in high elevation forests, but it has also been shown in the literature that air temperatures above 25°C during the day are detrimental to seedling survival (Alexander 1984). The weakly positive relationship we found between seedling establishment and mean annual temperature may indicate that daytime air temperatures in these stands are below this threshold. Slash and overstory basal are likely regulating surface temperatures and the vapor pressure deficit felt by seedlings in our sites, although we were unable to test this directly (Roberts and Long 1991, Pelz et al. 2016).

The positive relationship we found between seedling establishment and temperature could be interpreted in two ways. First, a warmer mean annual temperature likely also means a longer growing season, giving seedlings a longer period to establish. Second, with a partial overstory in our stands and cold temperatures frequently occurring during the growing season, seedlings may have experienced conditions that were too cold for growth. Early frosts and snow cover persisting late into the growing season could hinder spruce regeneration by killing or suppressing young germinants. Short growing seasons are detrimental to spruce seedling survival especially in the year of germination as seedlings greater than 12 weeks old by the time of the first frost are more likely to survive (Noble 1973). Thus, a warmer mean annual temperature and longer growing season would be helpful in facilitating establishment.

Seed production variability also needs to be considered. Engelmann spruce seed production is highly variable across time and space, which could make seedling establishment patterns highly variable as well. As Buechling et al. (2016) found warmer, more arid years were associated with higher levels of seed production. This effect could explain the lack of a negative drought response in seedling establishment on our sites. Spruce is also known to produce seed every year, with high seed production every 2 to 5 years (Alexander 1987).

The interaction we found between mean annual temperature and annual precipitation is not interpretable within the confines of what we know about Engelmann spruce regeneration. We expected to see regeneration increase with increasing precipitation and colder average annual temperatures, but we found the opposite. Our results show that at low levels of precipitation, higher mean annual temperatures increase the number of seedlings that establish in each year. However, as precipitation increases, the slope becomes flat. This is contrary to what we would expect to see. It seems logical that at low levels of precipitation, temperature would have a negative effect on seedling establishment as seedlings would be stressed by low moisture. At higher levels of precipitation, temperature would be expected to be less important as seedlings have more water to mitigate for temperature related stress.

A couple of caveats should be considered with our results. First, while we saw an increase in regeneration with increasing temperatures, we did not account for competition with other species in our study. Competition dynamics will likely be highly important in determining the future range of spruce. In addition, our results suggest droughty, warm conditions are not yet detrimental to seedling survival, but a warmer, drier climate is also expected to increase the

frequency of insect outbreaks in these forests (Bentz et al. 2010). These outbreaks may alter the future composition of spruce stands, as past outbreaks have (Cahill 1951).

2.6 Conclusion

Our results did not support our hypothesis of reduced seedling establishment in warmer, drier years. We found the opposite, although the significant relationships we found were weak overall. The relationship with temperature was the strongest climatic relationship we discovered, while precipitation seemed to be of minor importance in the high elevation stands we investigated. It is possible climate-related range shifts in southwest Colorado would be associated with more droughty conditions than those we examined, or other disturbances, such as insect outbreaks, will be the mechanism by which range shifts are initiated. Further research should be done to investigate spruce seedling establishment during drought years at lower elevations where range contractions seem most likely to start.

It is also important to point out the partial overstory in our stands may have ameliorated drought conditions for the seedlings. When comparing the regeneration in our stands to that of other studies, the main difference appears to be an overstory. Another study that looked at spruce regeneration in openings with no overstory found significant climate effects on spruce seedling survival (Alexander 1984). In addition, another study found that spruce seedling survival in patch clearcuts was aided by the presence of coarse woody debris (Ryan Davy, unpublished data). Survival in these studies were very low, while with a partial overstory in our stands, we found regeneration slowly filled in year by year. This suggests managers should avoid removing

the entire overstory in stands where spruce regeneration is desired, and coarse woody debris

should be left to provide microsites for establishing seedlings.

CHAPTER 3: DROUGHT EFFECTS ON ENGELMANN SPRUCE VIGOR IN A SEED
SOURCE STUDY

3.1 Introduction

Climate change is expected to impact subalpine forests in the western United States in multiple

ways. Longer growing seasons, variable precipitation, and more frequent drought events are

predicted to lead to shifts in high elevation species' ranges (Rehfeldt et al. 2006, Hu et al. 2010).

Seager et al. (2007) predicts that the aridity of the 1950's and recent early 2000's drought will be

the new climatology of the southwestern United States within years or decades.   The use of

provenance studies allows us to isolate the effects of inherited growth characteristics from

characteristics that arise from the growing environment. These studies take seeds from various

locations and plant them in one location to compare the growth and survival in a common

growing environment (Schmidtling 1994). If climate change occurs as expected, trees will need

to grow in conditions other than those they are adapted to.

Although Colorado has seen an increase of 1.1°C in temperature in the last 30 years, there has

been no detectable trend in precipitation yet (Lukas et al. 2014). However, climate change

models suggest that drought events are likely to become more frequent in Colorado's high

elevation forests over the next century (Seager et al. 2007). Recent bioclimate modeling

suggests that a warmer, drier climate will alter the range of Engelmann spruce (*Picea*

engelmannii Parry ex Engelm.) in central and southwest Colorado by the year 2060 (Rehfeldt et

al. 2006, 2015). Anticipated warming and drying will result in climatic conditions in the driest

locations that support Engelmann spruce-dominated forests becoming inconsistent with

conditions currently associated with the species. (Rehfeldt et al. 2006). Since Engelmann spruce is an important species in Colorado for recreation, timber, and habitat, including Canadian lynx (*Lynx canadensis*) habitat (Devineau et al. 2010), we must improve our understanding of the effects of drought on the growth of this high elevation tree species to help guide future management decisions.

Multiple forest types, including subalpine forests containing Engelmann spruce, already have documented cases of increased mortality due to drought and heat (Bigler et al. 2007, Allen et al. 2010). While several mechanisms may determine the future range of Engelmann spruce, tree vigor is likely to be critically important (Noble and Alexander 1977, Alexander 1987, Bentz et al. 2010). How Engelmann spruce responds physiologically to drought will play a role in where the species can survive and reproduce in the future. Researchers can use a framework of resistance and resilience to quantify a tree's ability to maintain their vigor during drought or return to their pre-drought level of vigor following drought. Resistance, for the purposes of this study, is defined as the ability of a tree to repel drought while also maintaining growth rates. We define resilience as a tree's ability to return to its pre-disturbance condition or growth rates following a drought. Forest resistance and resilience to disturbances will likely play a role in future range shifts. If forests are resistant and resilient, range shifts won't be as severe, but if they are not, disturbances may facilitate species composition shifts in a changing climate.   This study examines how much resistance and resilience is an inherited trait that may vary between populations of spruce.

By examining the effects that drought has on spruce from various seed sources, we also hope to inform future management decisions regarding assisted migration and planting site-adapted trees. Projections of climate change suggest trees will need to migrate quicker than they can in most cases (Zhu et al. 2012). Altering seed transfer guidelines, or assisted migration by land managers, has been suggested as a way to mitigate potential losses in species diversity due to climate change (Vitt et al. 2010, Williams and Dumroese 2013). Currently, land managers in Colorado do not commonly use non-local seed and focus primarily on using partial cutting to initiate natural regeneration in spruce dominated stands. In areas affected by fire, bark beetle, or low natural regeneration rates planting is commonly used to regenerate spruce, but planted seedlings are typically from local seed (Alexander 1987). Typically, seed zones or seed transfer guidelines are used to restrict the movement of seed to a region or a specified distance away from the source. This is done to reduce the risk of planting non-local seed that is maladapted to local conditions (Johnson et al. 2004).

This study aimed to examine whether trees grown from the seed of populations of Engelmann spruce in warm, dry locations out-performed trees from cool, wet areas during and after a severe drought event. Because drought conditions are forecasted to become more prevalent throughout the western US in the future (Seager et al. 2007), this information could guide the adaptation of seed transfer guidelines in response to changing conditions. Our hypothesis is trees from warmer and drier environments will be better adapted to drought, meaning they will be more resistant and resilient to drought. Conversely, trees from cooler, wetter seed sources will see reduced growth during drought (lower resistance) and have less ability to return to pre-drought growth rates following the drought (lower resilience) than trees adapted to warmer, drier climates. To

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test this hypothesis, we calculated resistance and resilience values from ring width values to quantify the differences in growth rates for each provenance between our three periods of interest. Our periods of interest are the five years before, during, and after the drought event from 2000-2004. This drought is estimated to be among the most severe of the last 500 years (Andreadis et al. 2005).

3.2 Methods

3.2.1 Study Area

We measured increment cores collected from an Engelmann spruce provenance study established in 1970 on the White River National Forest in the Moniger Creek area of the Holy Cross Ranger District (Shepperd et al. 1981). The study area just north of Vail, Colorado, sits at an elevation of 2930 m and is on a relatively flat north-eastern aspect. At the time of planting there was no vegetation due to logging and fire. The site receives 610 mm of precipitation annually, mostly as snow. 30-year normal average annual minimum and maximum temperatures at the planting site range from -4°C to 11°C (PRISM Climate Group 2014).

A randomized, complete block design was used with 4 trees from each of the 20 different provenances planted in 12 replicated blocks, for a total of 960 trees planted. An approximate 2.4 m by 2.4 m grid was maintained when planting, but was not exact in order to plant seedlings in the shade of stumps or logs to protect against high light intensity (Shepperd et al. 1981). Of the 20 seed sources planted, source latitudes range from 50°N to 33 °N (Fig. 8). Elevations of the

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seed sources range from 777 m to 3230 m. Local average temperatures range from 0.88°C to 9.96°C, while precipitation values range from 423 mm of precipitation annually to 1918 mm (Table 3 [PRISM Climate Group, Wang et al. 2016]).

3.2.2 Sampling design

We collected increment cores from six to eight trees from each provenance in the summer of 2016. Of the 12 blocks, eight were randomly selected to be sampled. Trees from each provenance were randomly selected within each block and were sampled at a height of 30 cm. Some blocks sampled had no survivors from certain seed sources, resulting in the decreased number of cores for some provenances.

3.2.3 Lab analysis

Cores were mounted and sanded using progressively finer grit sand paper until the annual rings were clearly visible under a microscope. All trees were live when cored, so cross-dating was not done visually beforehand. Each core was measured under a microscope using the program MeasureJ2X to create a chronology of ring widths by year. The tree-ring program COFECHA was used to check for potential inaccuracies in our measurements by checking for correlations between chronologies (Holmes 1983). Any potential problem cores were measured again.

Table 3: Climate data and site information for all 20 seed sources and the planting site. Climate data was obtained from PRISM for US sources and ClimateWNA for Canadian Sources. From left to right, abbreviations stand for latitude, longitude, elevation, precipitation, mean annual temperature, minimum annual temperature, and maximum annual temperature. Δ values are the difference between each climate variable at the planting site and the original provenance.

| Provenance	Location	Lat	Long	Elev. (m)	PPT (mm)	Tmean (°C)	Tmin (°C)	Tmax (°C)	Δ PPT	Δ Tmean (°C)	Δ Tmin (°C)	Δ Tmax (°C)
Gila NF	NM, USA	33.0	-108.0	2499	567.61	9.96	3.16	16.76	-43.02	6.44	7.16	5.72
Coconino NF	AZ, USA	35.3	-111.7	2865	671.55	6.93	-1.11	14.97	60.92	3.41	2.89	3.93
Santa Fe NF	NM, USA	36.1	-105.7	2895	711.14	5.01	-1.94	11.96	100.51	1.49	2.06	0.92
San Juan NF	CO, USA	37.3	-106.8	3230	898.65	3.21	-3.96	10.39	288.02	-0.31	0.04	-0.65
Dixie NF	UT, USA	37.8	-112.0	3017	744.84	3.62	-2.92	10.16	134.21	0.10	1.08	-0.88
Pike NF	CO, USA	39.0	-105.0	2712	655.33	4.90	-2.36	12.16	44.70	1.38	1.64	1.12
Gunnison NF	CO, USA	39.0	-107.2	3169	946.32	2.48	-4.45	9.40	335.69	-1.04	-0.45	-1.64
Grand Mesa-Uncompahgre NF	CO, USA	39.0	-108.0	3200	1170.97	0.88	-5.78	7.53	560.34	-2.64	-1.78	-3.51
Roosevelt NF	CO, USA	40.0	-105.5	2743	621.01	4.09	-2.80	10.99	10.38	0.57	1.20	-0.05
Larimer County 2	CO, USA	40.9	-105.6	2865	572.43	2.76	-3.82	9.34	-38.20	-0.76	0.18	-1.70
Larimer County 1	CO, USA	41.0	-105.5	2407	475.95	5.22	-1.58	12.02	-134.68	1.70	2.42	0.98
Cache NF	ID, USA	42.3	-111.3	2590	1025.31	4.06	-1.82	9.93	414.68	0.54	2.18	-1.11
Wallowa-Whitman NF	OR, USA	45.0	-118.2	1417	687.93	6.51	0.44	12.58	77.30	2.99	4.44	1.54
Payette NF	ID, USA	45.0	-116.0	1889	1015.92	3.73	-3.31	10.76	405.29	0.21	0.69	-0.28
Wenatchee NF	WA, USA	48.2	-121.0	777	832.54	6.00	1.04	10.96	221.91	2.48	5.04	-0.08
Okanogan NF	WA, USA	48.2	-121.0	1280	1918.71	3.21	-1.38	7.80	1308.08	-0.31	2.62	-3.24
Kidd Creek	BC, CA	49.2	-116.1	1432	816.00	3.60	-1.40	8.68	205.37	0.08	2.60	-2.36
Powers Creek	BC, CA	50.0	-119.8	1249	672.00	4.50	-0.60	9.55	61.37	0.98	3.40	-1.49
Inlet Creek	BC, CA	50.0	-116.3	1402	546.00	3.40	-2.30	9.08	-64.63	-0.12	1.70	-1.96
Cutting Permit 31	BC, CA	50.0	-120.1	1562	423.00	3.50	-1.40	8.40	-187.63	-0.02	2.60	-2.64
Planting Site	**CO, USA**	**39.7**	**-106.5**	**2926**	**610.63**	**3.52**	**-4.00**	**11.04**	—	—	—	—
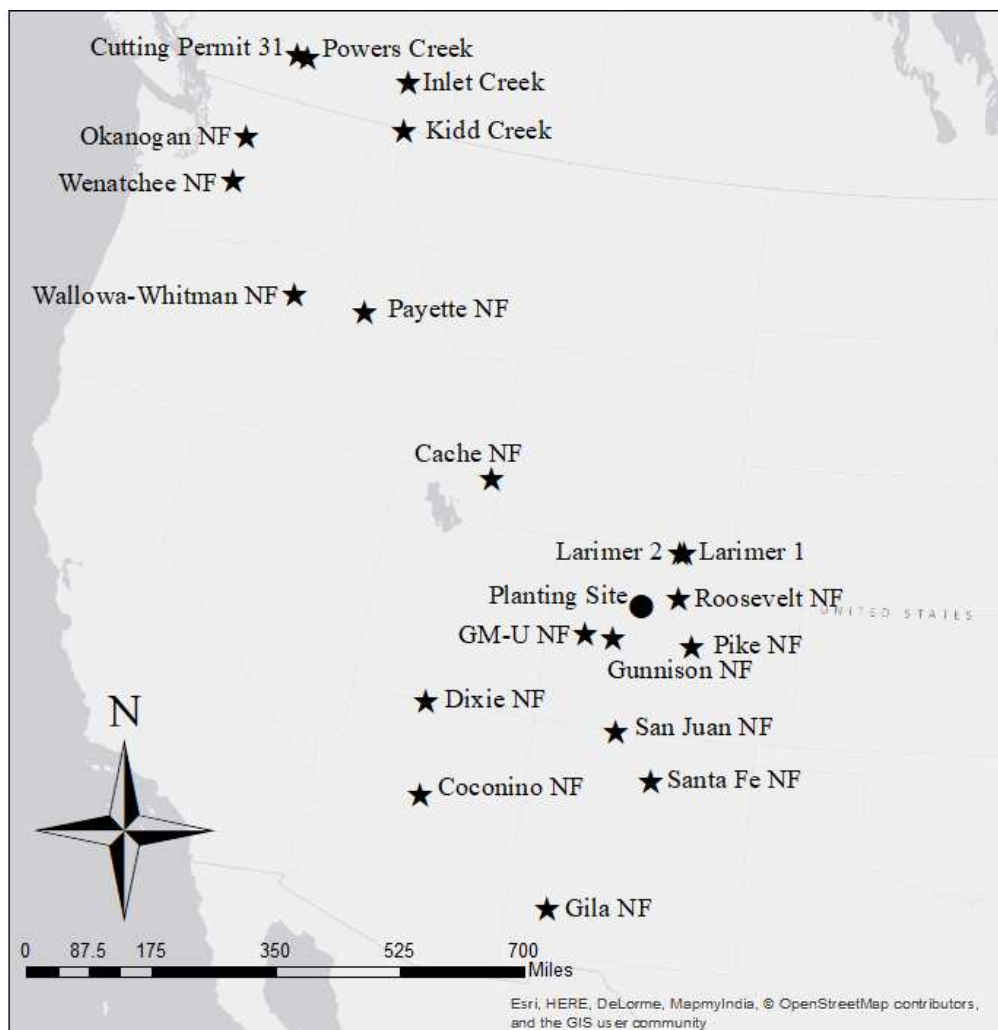
Figure 8: Locations of all 20 seed sources and the common planting site in the provenance study established in 1970.

3.2.4 Ring Width Chronologies

Ring width index (RWI) chronologies were produced for individual trees using a linear regression technique as it is the best option for relatively short series such as ours, since short series may have unusual growth patterns that a negative exponential curve cannot match (Cook and Holmes 1986). This technique fits a regression line to the raw ring width measurements and creates a unitless index (RWI) by dividing the resulting residuals by the fitted value. This results in an index in which yearly measurements above 1 are considered above average, values of 1 are average, and any values below 1 are considered poor growing years compared to the long term growth trend.

3.2.5 Statistical analysis

Resistance and resilience values for each provenance were compared to each other using a mixed-model repeated-measures analysis of variance (ANOVA) using the nlme package in R (Pinheiro et al. 2016). We used an autoregressive of order 1 (AR1) correlation structure, which assumes adjacent years are more highly correlated than non-adjacent years (Sullivan 2008). Provenance was included as a covariate in the model. Tree was treated as a random effect in our model. We used the 5 years before, during, and after the 2000-2004 drought event as our time periods (Fig. 9). These time periods were used to give us a 5 year-average growth value for each provenance in each distinctly different period, based on regional PDSI values. These periods also allowed us to calculate resistance and resilience values in a similar fashion to other studies (D'Amato et al. 2013, Bottero et al. 2017). A means comparison based on our model was used

to identify significant differences of resistance and resilience between provenances during and

after the drought. To control the type 1 error rate, we used Tukey adjusted p-values. We used a

similar means comparison to identify differences in diameter at breast height (DBH) between

provenances in 1996, to establish differences in radial growth between provenances prior to the

drought.
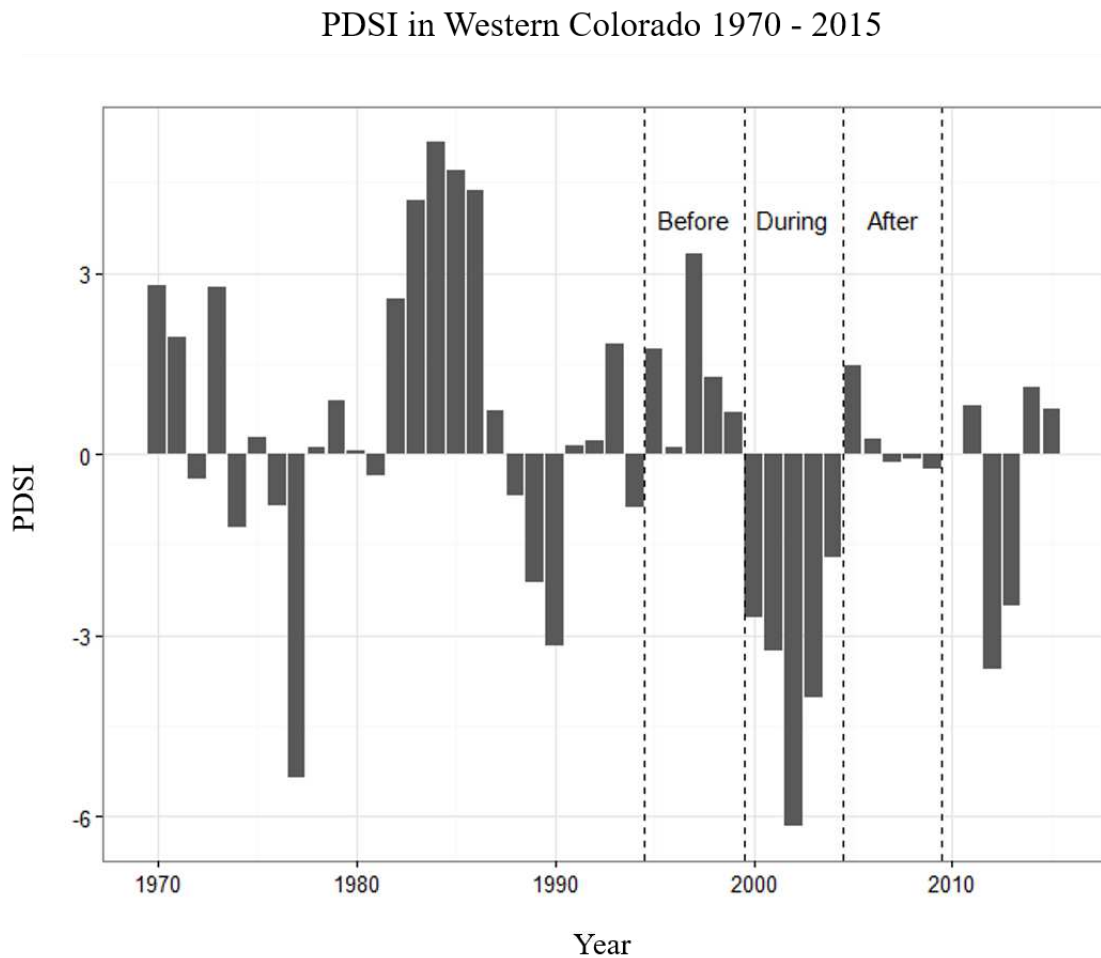
Figure 9: Palmer Drought Severity Index (PDSI) values for Western Colorado climate division from 1970 – 2015. Negative PDSI values indicate drier than average years. PDSI values less than -2 indicate moderate drought, while severe and extreme droughts are those with values less than -3 and -4 respectively (Palmer 1965). PDSI data acquired from National Climatic Data Center (NCDC).

Resistance and resilience were analyzed using a similar modeling approach. First, resistance was calculated by dividing the average RWI of the five years during drought by the average RWI of the five years before drought for each tree. Resilience was calculated using the average RWI of the five years following drought divided by the average RWI of the five years before drought (D'Amato et al. 2013). Values over one indicate the provenance is resistant or resilient, while values below one indicate a lack of resistance or resilience to drought. Separate mixed effects models were used to analyze the effect of provenance on both resistance and resilience. Our models used tree as a random effect. Means comparisons for RWI, resistance, and resilience were derived from our models was used to find significant differences ($p < 0.05$) between provenances.

3.3 Results

3.3.1 RWI Model Results

Mixed effect modeling to analyze the response of RWI during and after drought yielded some significant variables. Our model found period (before, during, and after drought) to be highly significant ($p < 0.0001$), while the interaction between period and provenance was also significant ($p = 0.0001$).   Provenance by itself was not important in the model ($p = 0.1654$).

3.3.2 Survival and growth before drought

After 45 years, survival was still high amongst all trees at 73%. There were few significant differences between provenances in survival rate with most provenances having around 60-70% survival as of 2014. Most of the mortality occurred in the first ten years following planting. The Gila seed source did have the lowest survival as of 2014 with less than 50% of the trees still alive (Mike Battaglia, unpublished data). Overall though, most of the trees were still alive across provenances.

Diameter growth before drought was similar among almost all provenances, with most provenances having a diameter of 5-10 centimeters after 25 years. However, the Gila National Forest source was the only one under 5 cm on average. (Fig. 10). The Gila National Forest seed source was growing significantly slower than six other seed sources. Five of these seed sources were from wetter areas than Gila, but one, Cutting Permit 31 in British Columbia, was drier and colder (Table 3).
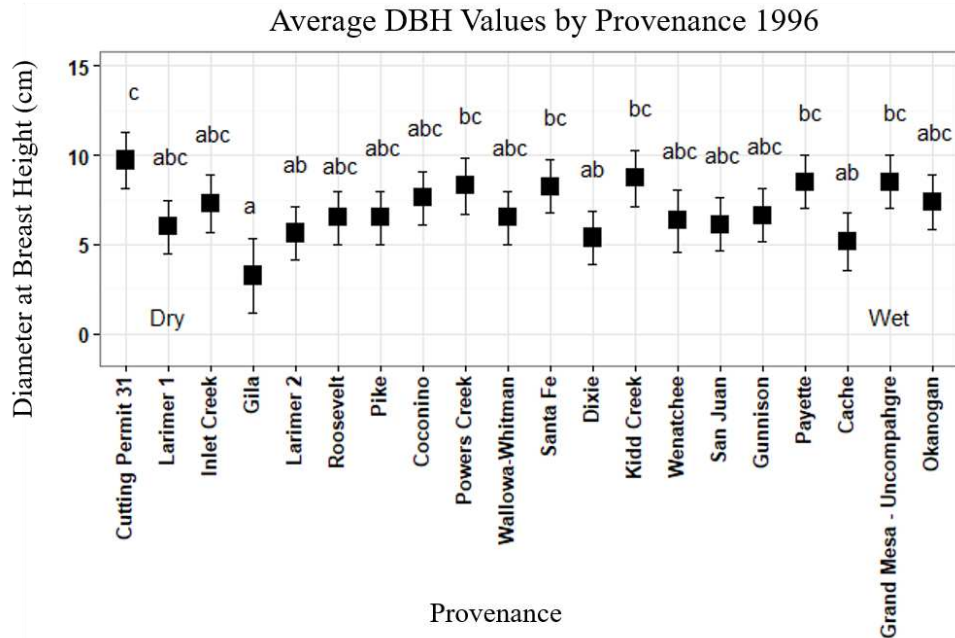
Figure 10: Compact lines display showing significant differences in DBH between provenances before drought in 1996. 6-8 trees are included for each provenance. Provenances are in order from driest to wettest in terms of average annual precipitation. Provenances sharing a letter are not significantly different. Error bars show 95% confidence intervals around the mean.

3.3.3 Growth during drought – Resistance

Our analysis found few significant differences in resistance between any provenances during the drought (Fig. 11a). Most of the provenances maintained their growth rates during the drought compared to growth rates before the drought with resistance values around 1. The exception was Inlet creek, which demonstrated a lower resistance than the Larimer 2 (Fig. 11a).

3.3.4 Growth after drought – Resilience

We found almost no significant differences in resilience between provenances (Fig. 11b). However, Gila was found to be more resilient than every other seed source, with a mean

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resilience value of 1.26, indicating this provenance's RWI values were on average 1.26 times greater than before the drought. Many other provenances had mean resilience values below 1, indicating, on average, they were unable to return to their pre-drought growth rates.
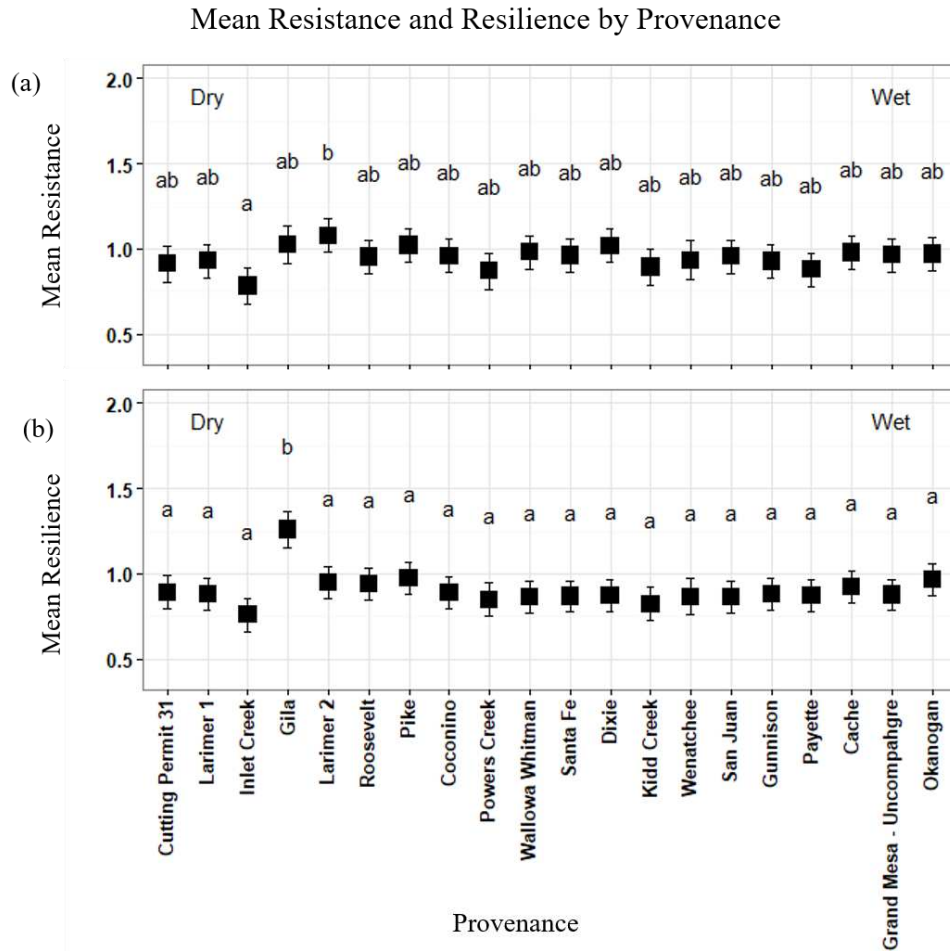
Figure 11: Compact lines display showing any significant differences in resistance and resilience between provenances. Resistance and resilience values above 1 indicate greater growth during and after drought, respectively, when compared to the period before drought. Values below 1 indicate slower tree growth during and after drought. Shared letters between provenances indicate no significant differences, as is the case with almost all our provenances. Error bars indicate 95% confidence intervals around the mean.

3.4 Discussion

Provenance studies provide insight into how various seed sources respond to common conditions, including extreme climate events. This information can be used to anticipate species responses to increased drought conditions predicted to occur in the future (Andreadis et al. 2005, Seager et al. 2007). This study attempted to detect differences between drought responses of various seed sources of Engelmann spruce in a planted study near Vail, Colorado. We hypothesized that warmer, drier provenances would be more resistant and resilient to drought conditions whereas trees from wet sources would respond negatively to drought. We calculated resistance and resilience indices to compare growth during and after the drought to pre-drought growth. We found almost all provenances responded similarly in growth during and after the drought event.

As Williams and Dumroese (2013) point out, anthropogenic climate change is predicted to alter conditions quicker than many species can adapt. Therefore, the climate across much of Engelmann spruce's range is likely to become inconsistent with the current climate envelope spruce inhabits. However, our results show that Engelmann spruce from widely varying seed sources appear to respond similarly to drought. This leaves managers with a decision to make about whether to use seed from different seed zones in the future. Research in the southern United States on southern pine species has found that planted trees grow best if the minimum annual temperature at the planted site is within 2.7°C of the seed source location (Schmidtling 2001). Our results suggest this is not the case with Engelmann spruce as five of our provenances had annual minimum temperatures greater than 2.7°C different than the planting site (Table 3).

We also did not see wildly different mortality rates between provenances as of 2014, except for the Gila seed source (Mike Battaglia, unpublished data).

The other option for managers is to allow species range shifts to occur naturally, which other research predicts will result in lost habitat for many tree species and the loss of some products humans rely on (Rehfeldt et al. 2006). Some argue that range shifts should be allowed to happen naturally (Noss 2001). Managers' decisions under a changing climate depend on how flexible trees are in their response to climate. Our results suggest that Engelmann spruce from a variety of genetic backgrounds, once established, perform similarly in climate conditions different from those of their source location. This suggests a high degree of environmental tolerance in spruce, especially considering the peak of the drought event we studied was considered extreme based on PDSI values. However, PDSI is a regional value (Palmer 1965), and the elevation or local climate of our planting site may have lessened the impact of the 2000-2004 drought.

Much of this comes back to the concepts of resistance and resilience (Derose and Long 2014). If forests are resistant to change, they will be able to withstand a changing climate in the future and maintain their current species composition. We found most provenances to have resistance values close to one, indicating growth and vigor didn't change drastically during drought. We found that resilience values were also similar across all provenances and values were close to one, with one exception, which suggests these trees were not impacted following the drought.

A few factors should be considered for our results as well. First, our trees are relatively young (i.e. <50 years old) for spruce, with the fully mature spruce trees being 300 to 600 years old

(Alexander 1987). Other studies have found that tree age is an important factor in tree drought response, with older trees generally being less vigorous and resilient to drought (Martinez-Vilalta et al. 2012). In addition, provenance studies can take decades to show real differences between seed sources. Johnson et al. (2004) cites an example where an extreme, prolonged cold spell killed non-local Douglas-fir trees which had been growing relatively well for 40 years. In contrast, the local population was more resistant to this cold spell (Johnson et al. 2004). Lastly, these are trees grown in open conditions, and stand structure and density have been shown to have effects on tree growth. Trees grown in less dense conditions specifically have been shown to be more resistant to drought (Bottero et al. 2017, Gleason et al. 2017).

While the trees in our study withstood a very severe period of drought, it's possible that their young age helped them to survive this dry spell, as smaller trees have less hydraulic limitations than larger, taller trees (Carrer and Urbinati 2004). In addition, a study in Arizona found Engelmann spruce at higher elevations to be less sensitive to regional drought than spruce at lower elevations (Adams and Kolb 2005). The provenance study we analyzed is at a high elevation of 2930 m, which could have shielded our trees from regional drought to an extent. Adams and Kolb (2005) used a ratio of RWI between wet and dry years to examine multiple species' responses to periods of drought. Much like our study, PDSI was used to indicate wet and dry years with wet years having PDSI values > 2 and dry years having PDSI values < -2 (Adams and Kolb 2005). Our study had PDSI values far below -2 during drought, so the fact that we found few differences in resistance and resilience suggests drought may not be limiting at this elevation.

3.5 Conclusion

This study characterized responses to a period of drought in an Engelmann spruce seed source study. We wanted to discover if trees from different seed sources had different vigor levels during and after a severe drought event. In addition, we used a resistance and resilience framework to analyze how trees from various seed sources responded and recovered in response to the drought. Overall, we found that most provenances had similar responses, but a couple interesting findings stood out. Our data did not support our hypothesis of seeing more resistance and resilience from dry, hot provenances, except for the Gila seed source being more resilient. Our lack of significant differences between the resistance and resilience of the various seed sources suggests these trees may not have experienced the drought or water is not a limiting factor at these high elevations.

This study can guide management decisions in the future, as land managers decide how to alter management in response to anthropogenic climate change. In addition, continued monitoring of this provenance study should be done to check for differences in survival and growth as these trees age. However, our results suggest these trees were either sheltered from the drought at this altitude or are not limited in growth by water availability.

CHAPTER 4: CONCLUSION

Recent bioclimate modeling predicts we will see a shift in the range of spruce in southwest Colorado (Rehfeldt et al. 2015), and we attempted to gain insights into the mechanisms that may result in changes in spruce seedling establishment or tree vigor. We did so by examining a interannual weather variability and a drought event from 2000-2004, with the assumption that drought events such as this will become more common in the future. Understanding how spruce will respond to a warmer, drier climate is important for land managers developing plans to mitigate the effects of a changing climate.

This two-part study attempted to analyze the influence of interannual climate variability and drought on Engelmann spruce regeneration and mature tree vigor. We hypothesized regeneration would decrease in warmer, drier years, whereas tree vigor would be less impacted by drought in trees from warmer, drier provenances. In other words, trees adapted to warmer, drier conditions would be more resistant and resilient to a period of severe drought. In both cases, our hypothesis was not found to be the case. We saw very weak effects of interannual climate variability on regeneration, indicating spruce in high elevation stands that have been partially cut may be adequately sheltered from local climate and were not negatively impacted by the drought. With mature tree vigor, we found few significant differences between radial growth of trees of varying genetic backgrounds indicating Engelmann spruce may have a high environmental tolerance, especially in cold, wet conditions typical of high altitudes.

While we did not find strong effects of climate on regeneration or vigor, it is possible the effects are simply not prevalent yet in the high elevation stands we sampled. Our results suggest to management that seedling establishment is not strongly impacted by interannual weather variability and Engelmann spruce trees appear to have a high environmental tolerance at high elevations, regardless of genetic background. More research should be done on regeneration in lower elevation spruce stands that receive less moisture than those we studied to analyze the effects of drought on the lowest elevational limit of the species. In addition, continued monitoring of the provenance study should be done, as relatively young trees such as those we studied can take decades to show any maladaptation to climate. Provenance studies established at various elevations would also lend insight into the adaptability of spruce.

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APPENDIX A: CHAPTER 2 STUDY SITE LOCATIONS

Table A1: Coordinates and elevation data for all 24 sampled sites on the Gunnison National Forest in Chapter 2.

| Study Site	Latitude	Longitude	Elevation (m)
BM1	38.07	-106.89	3375.09
BM2	38.07	-106.88	3347.05
BM3	38.07	-106.89	3417.46
BM4	38.05	-106.85	3354.97
BM5	38.04	-106.85	3386.67
CC1	38.11	-106.96	3135.52
CC2	38.10	-106.97	3269.32
CC6	38.10	-106.96	3166.91
CC7	38.09	-106.97	3189.47
CC11	38.08	-106.98	3242.50
DC4	38.31	-106.39	3372.96
DC24	38.31	-106.36	3346.74
DC32	38.31	-106.37	3362.29
SC1	38.90	-106.70	3452.51
SC3	38.88	-106.75	3452.82
SC4	38.84	-106.66	3330.89
SC8	38.89	-106.71	3343.70
SC9	38.90	-106.70	3351.62
SC10	38.90	-106.70	3443.06
SC12	38.85	-106.66	3312.91
SC16	38.90	-106.70	3307.73
SC19	38.87	-106.76	3390.64
SC20	38.89	-106.69	3504.63
SC21	38.85	-106.66	3469.58
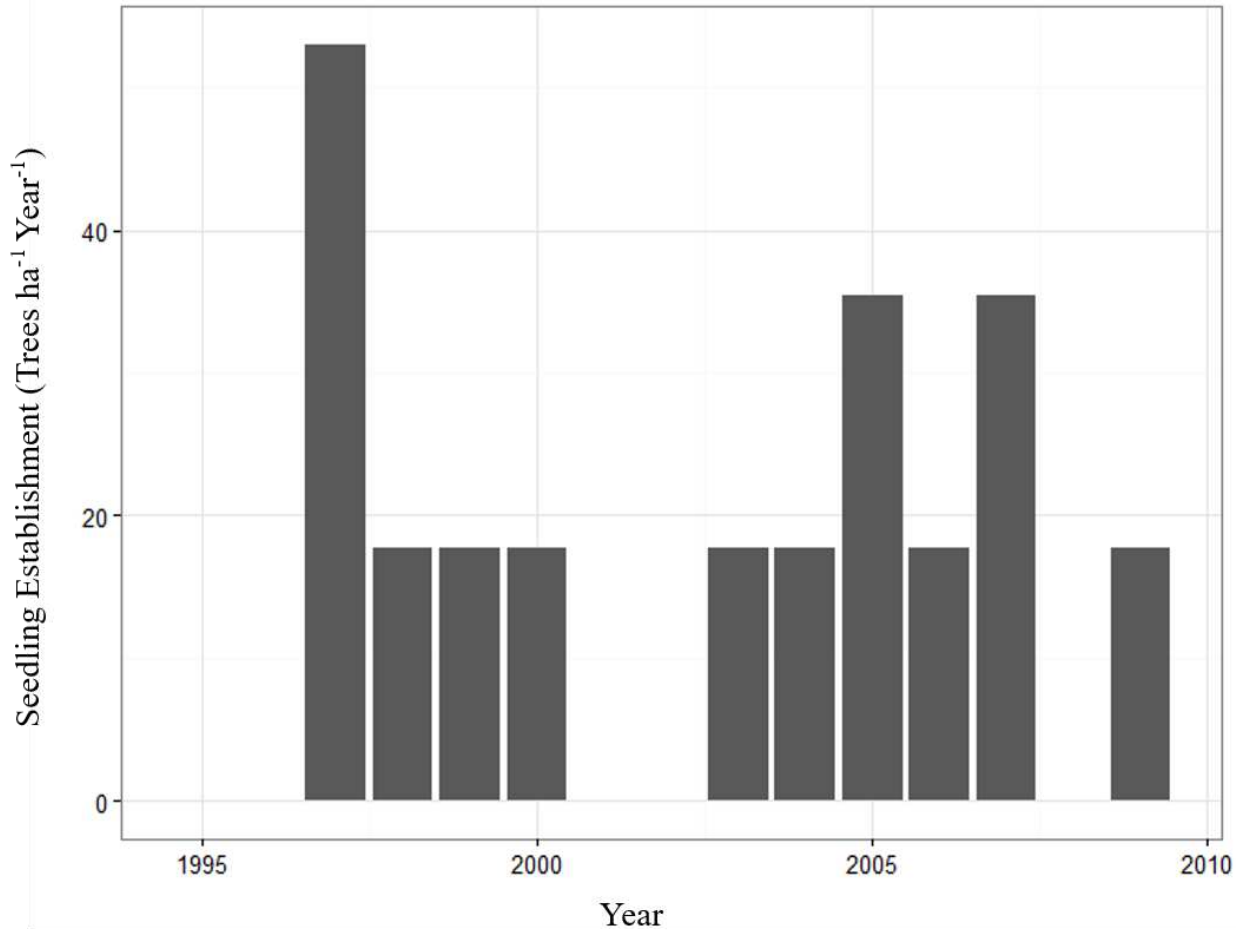
Figure B1: Annual seedling establishment density from year after treatment to 2009 for study site BM1 located on the Gunnison National Forest.
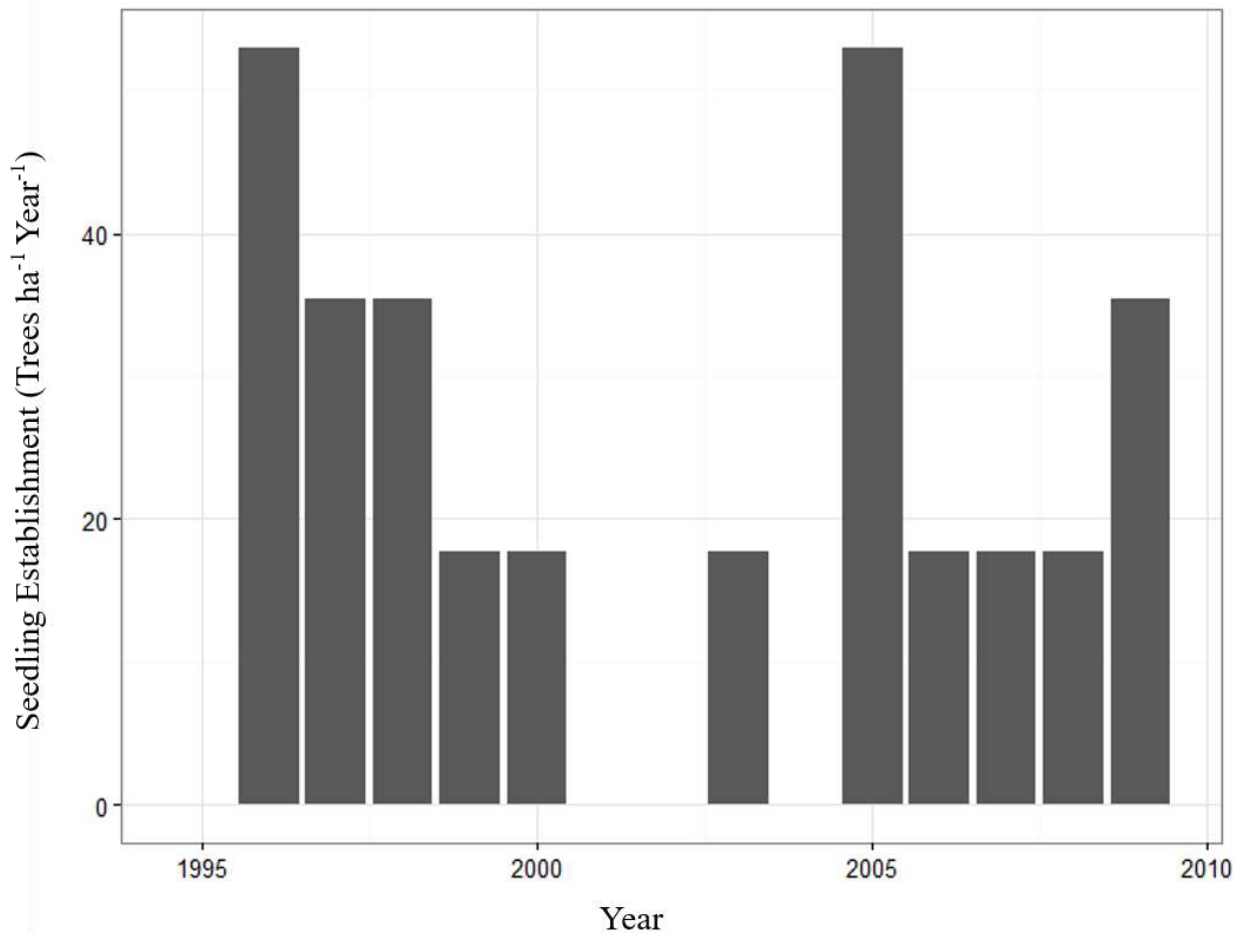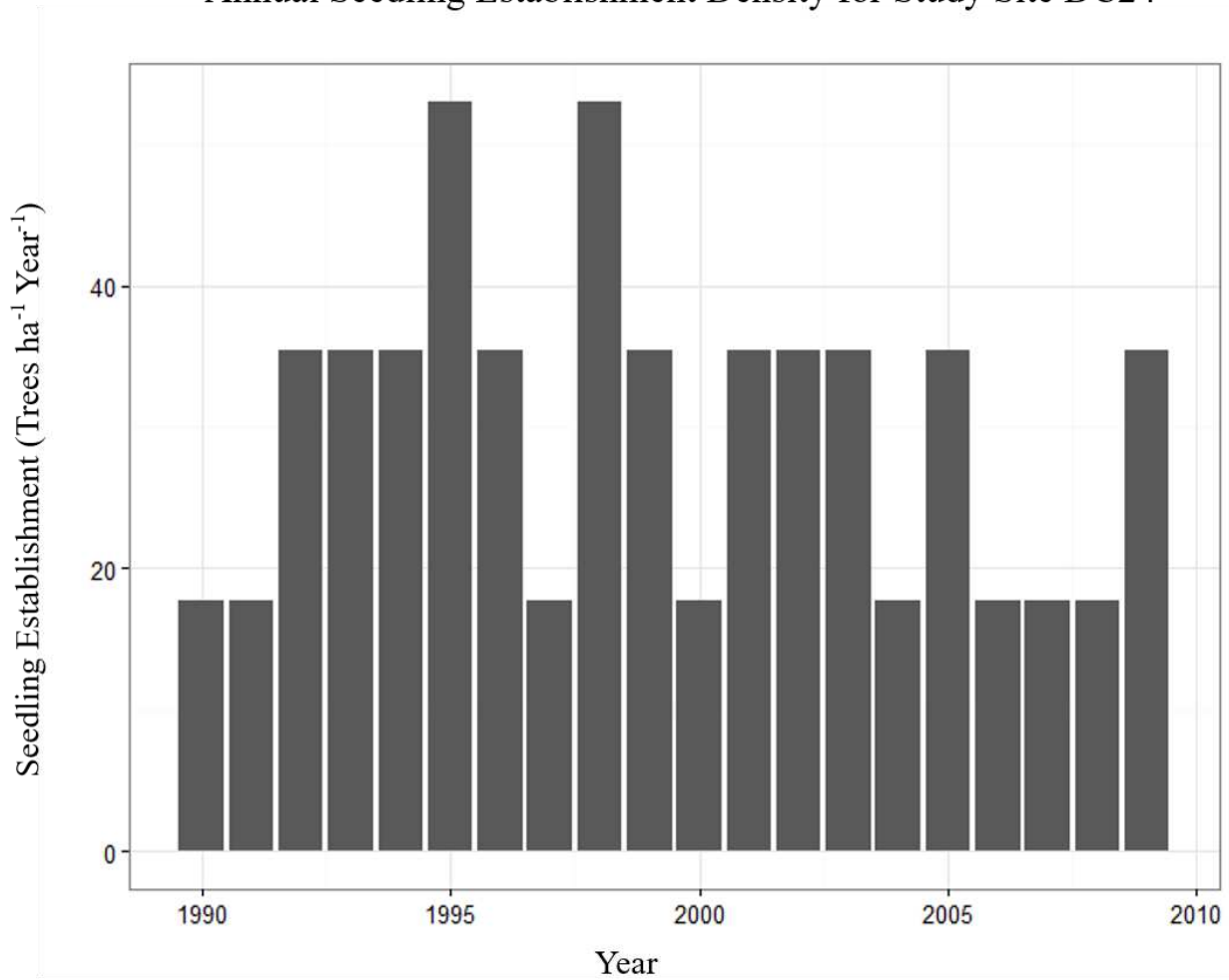
Figure B2: Annual seedling establishment density from year after treatment to 2009 for study site BM2 located on the Gunnison National Forest.
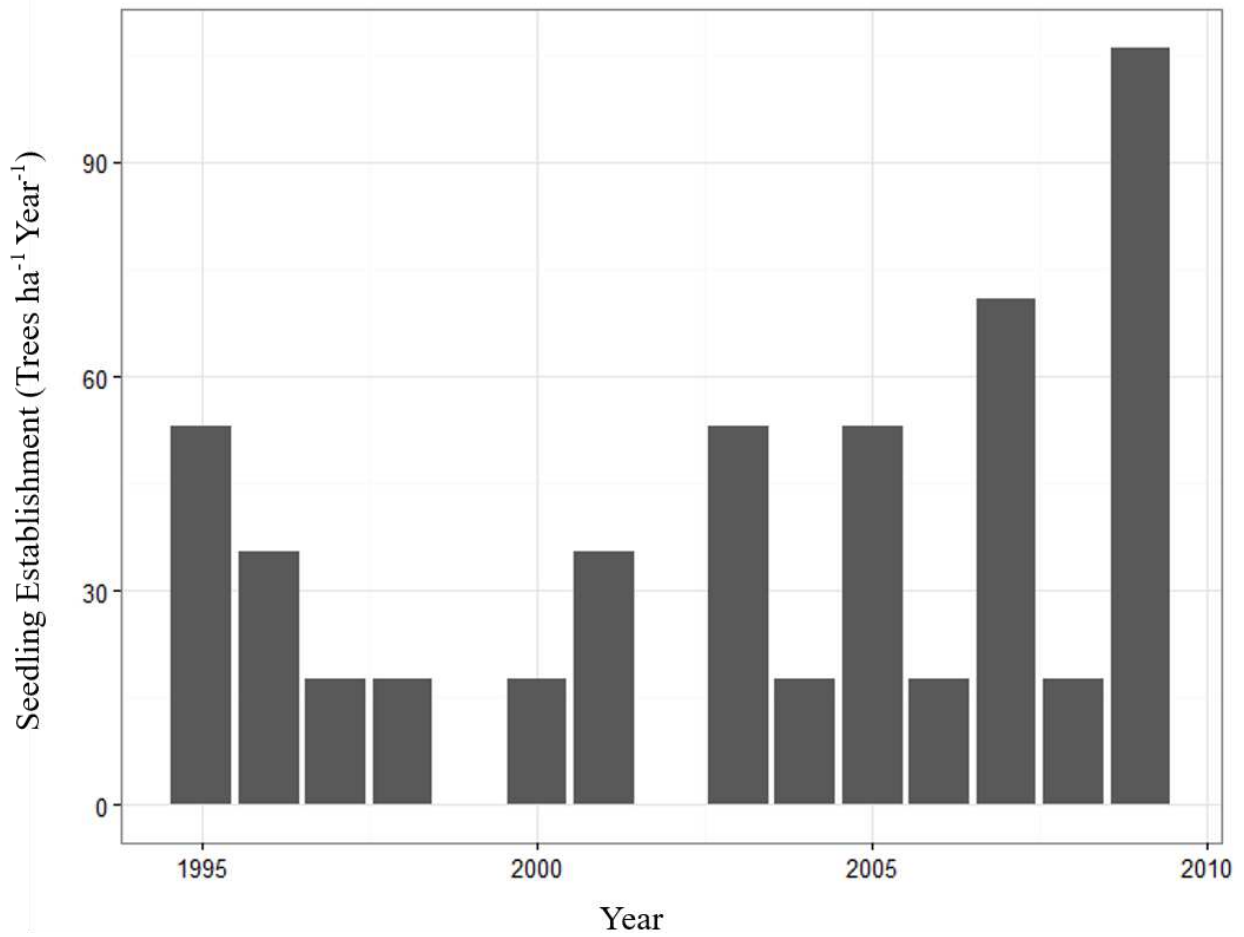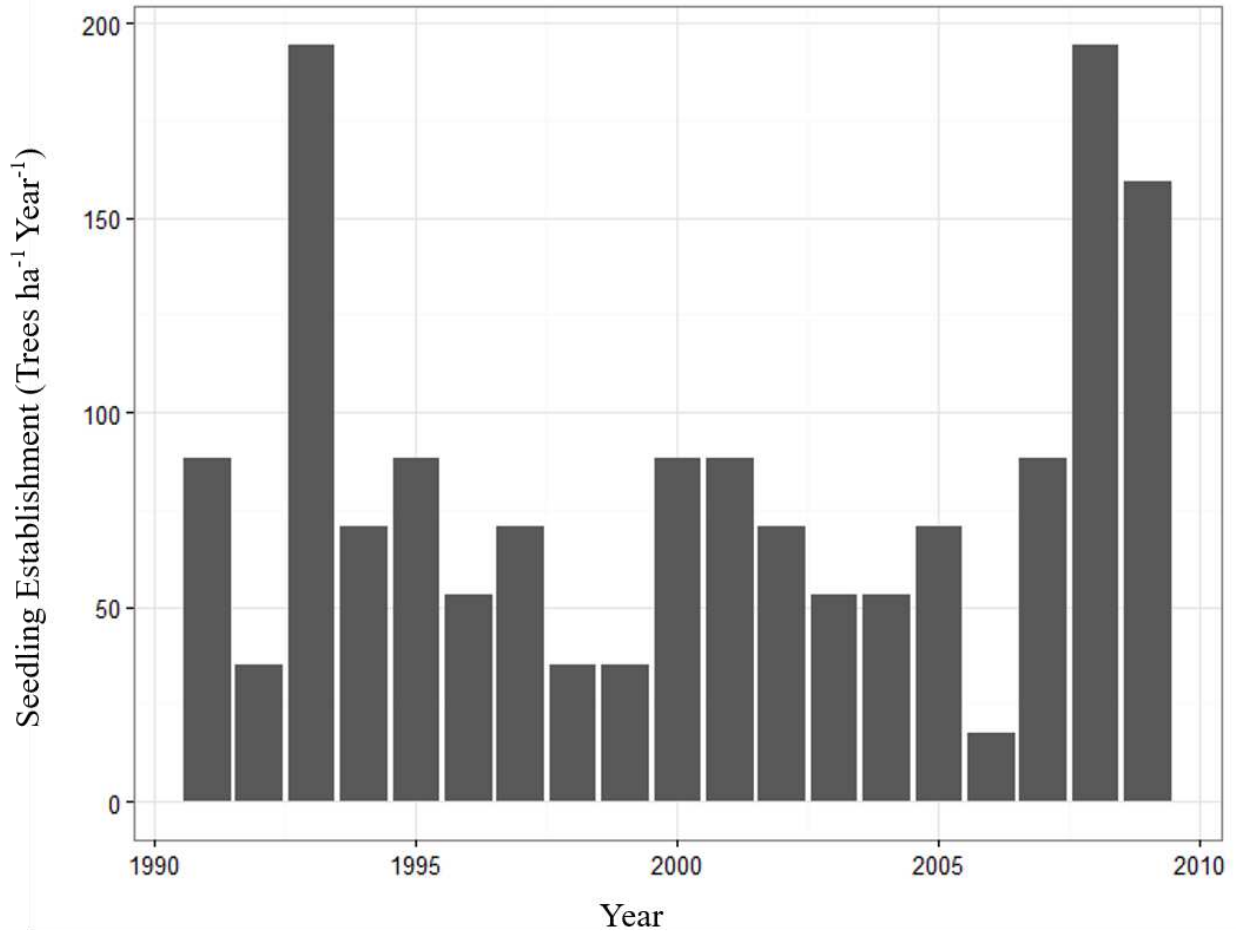
Figure B3: Annual seedling establishment density from year after treatment to 2009 for study site BM3 located on the Gunnison National Forest.

Annual Seedling Establishment Density for Study Site BM4
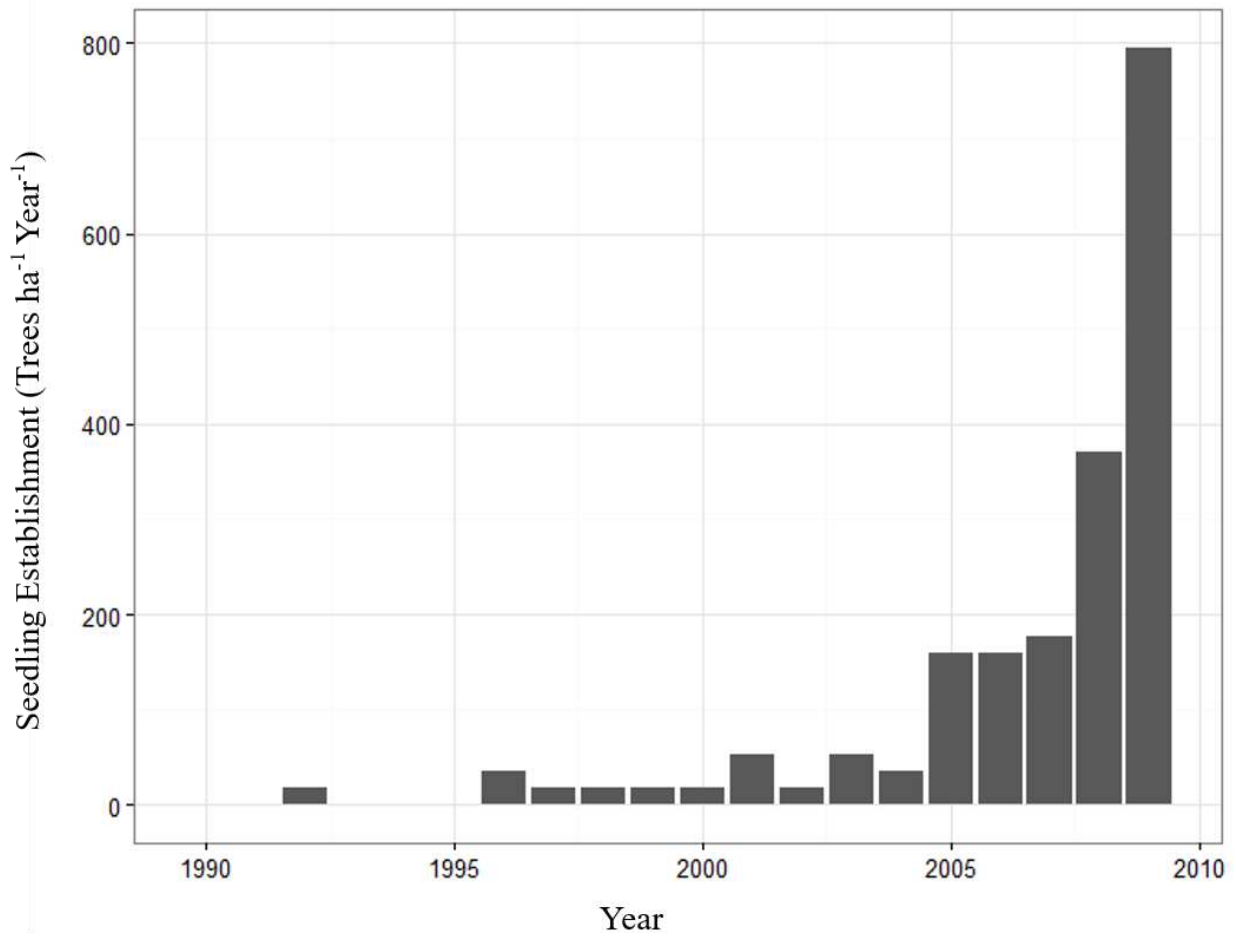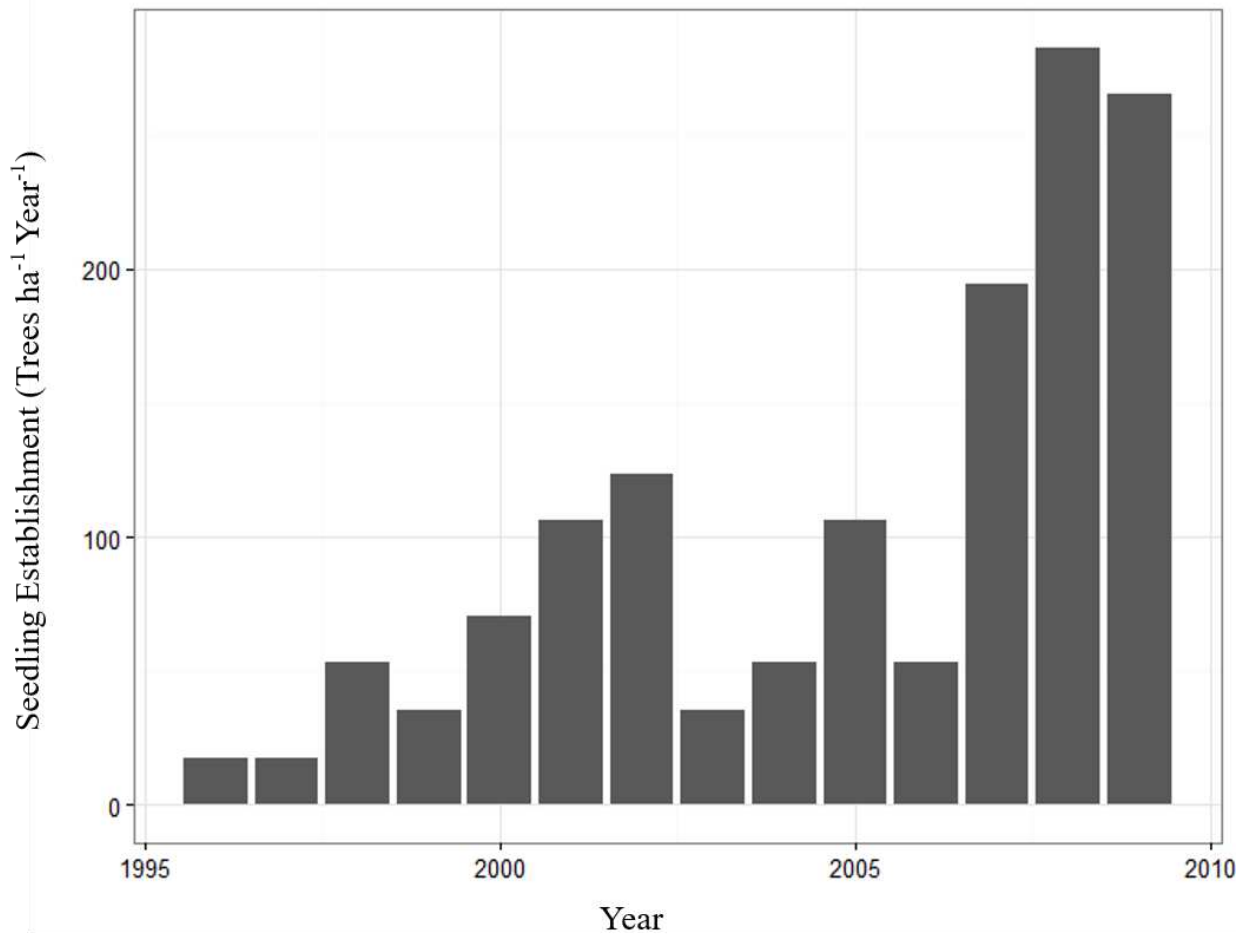

Figure B4: Annual seedling establishment density from year after treatment to 2009 for study site BM4 located on the Gunnison National Forest.
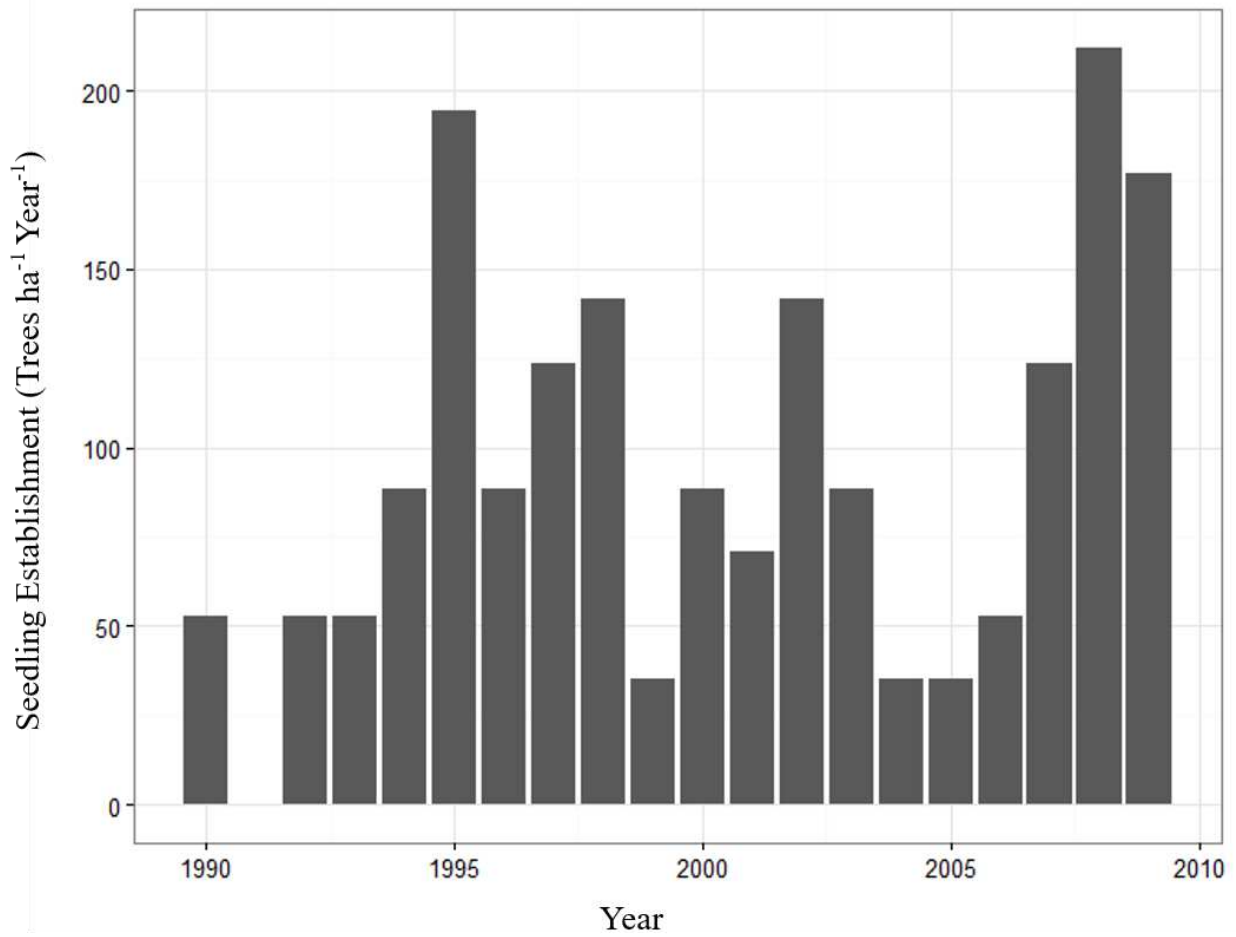
Figure B5: Annual seedling establishment density from year after treatment to 2009 for study site BM5 located on the Gunnison National Forest.

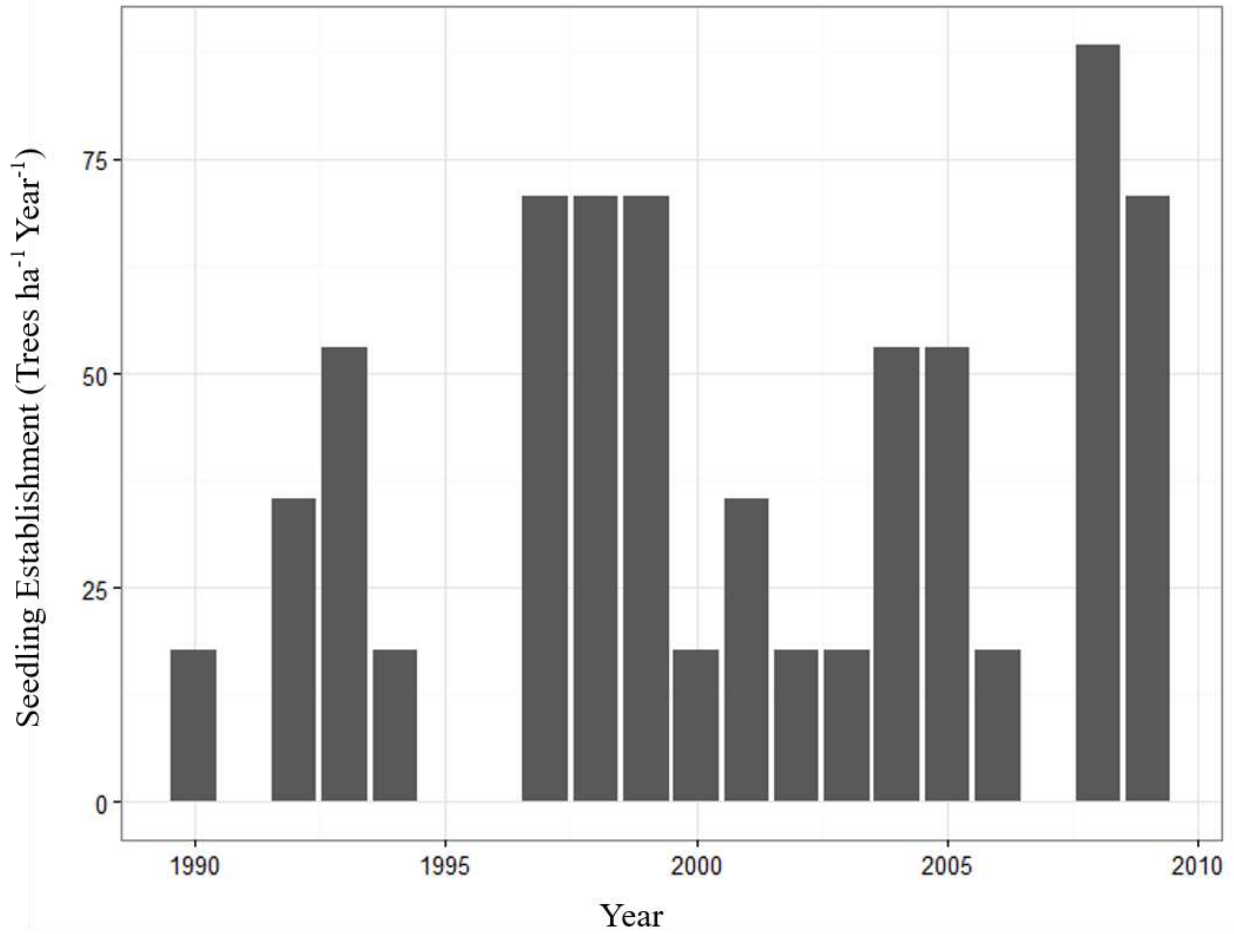# Annual Seedling Establishment Density for Study Site CC1
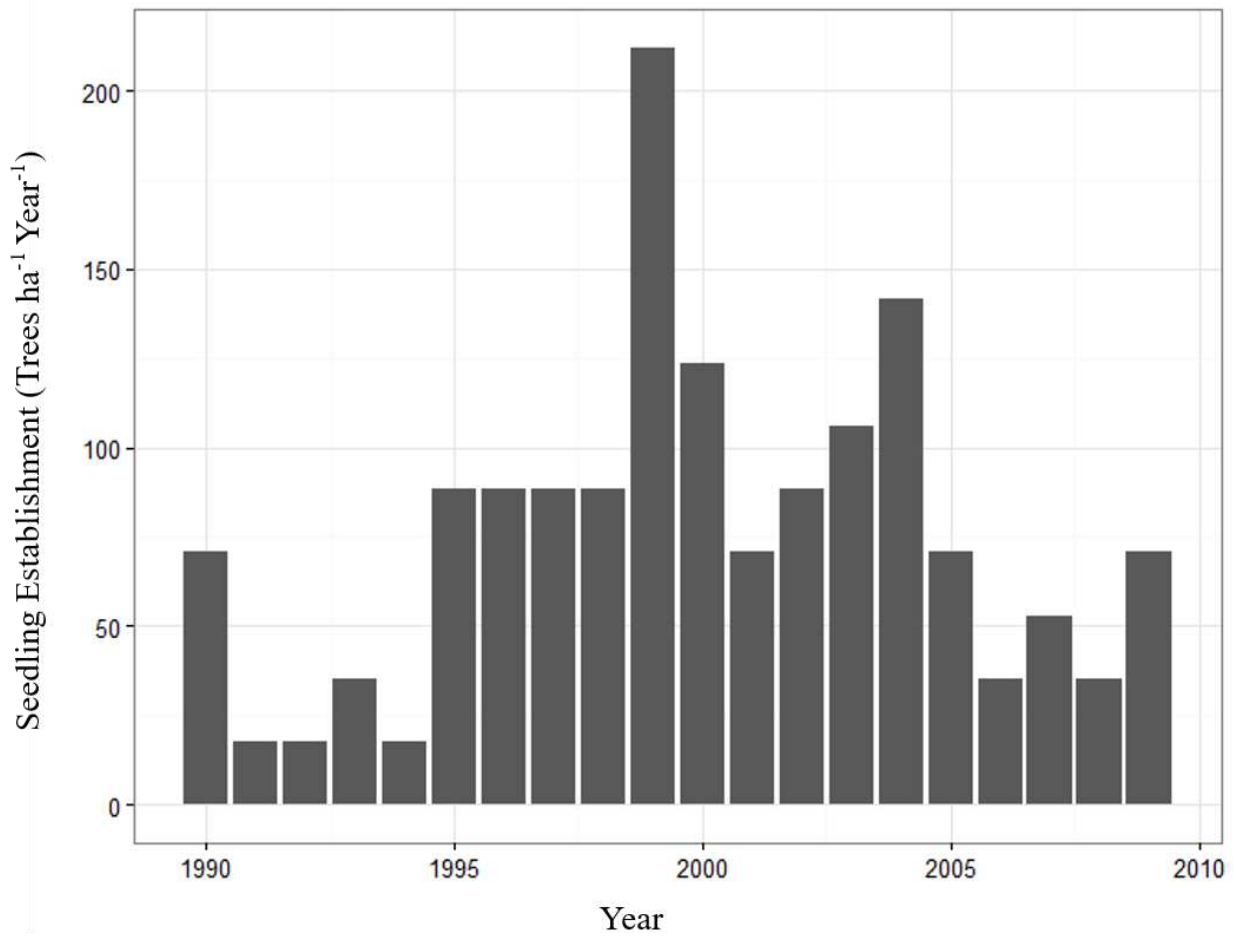
Figure B6: Annual seedling establishment density from year after treatment to 2009 for study site CC1 located on the Gunnison National Forest.
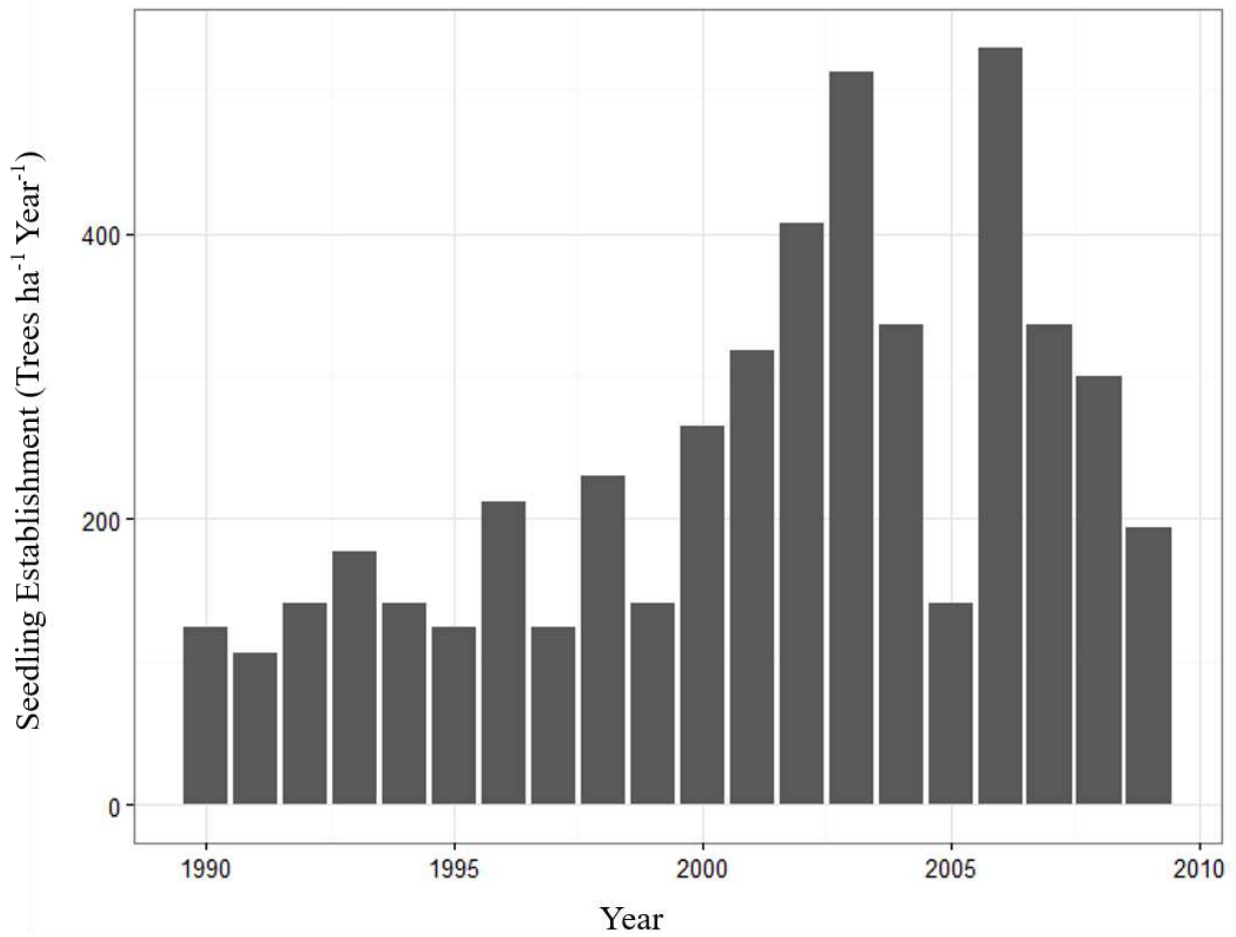
Figure B7: Annual seedling establishment density from year after treatment to 2009 for study site CC2 located on the Gunnison National Forest.
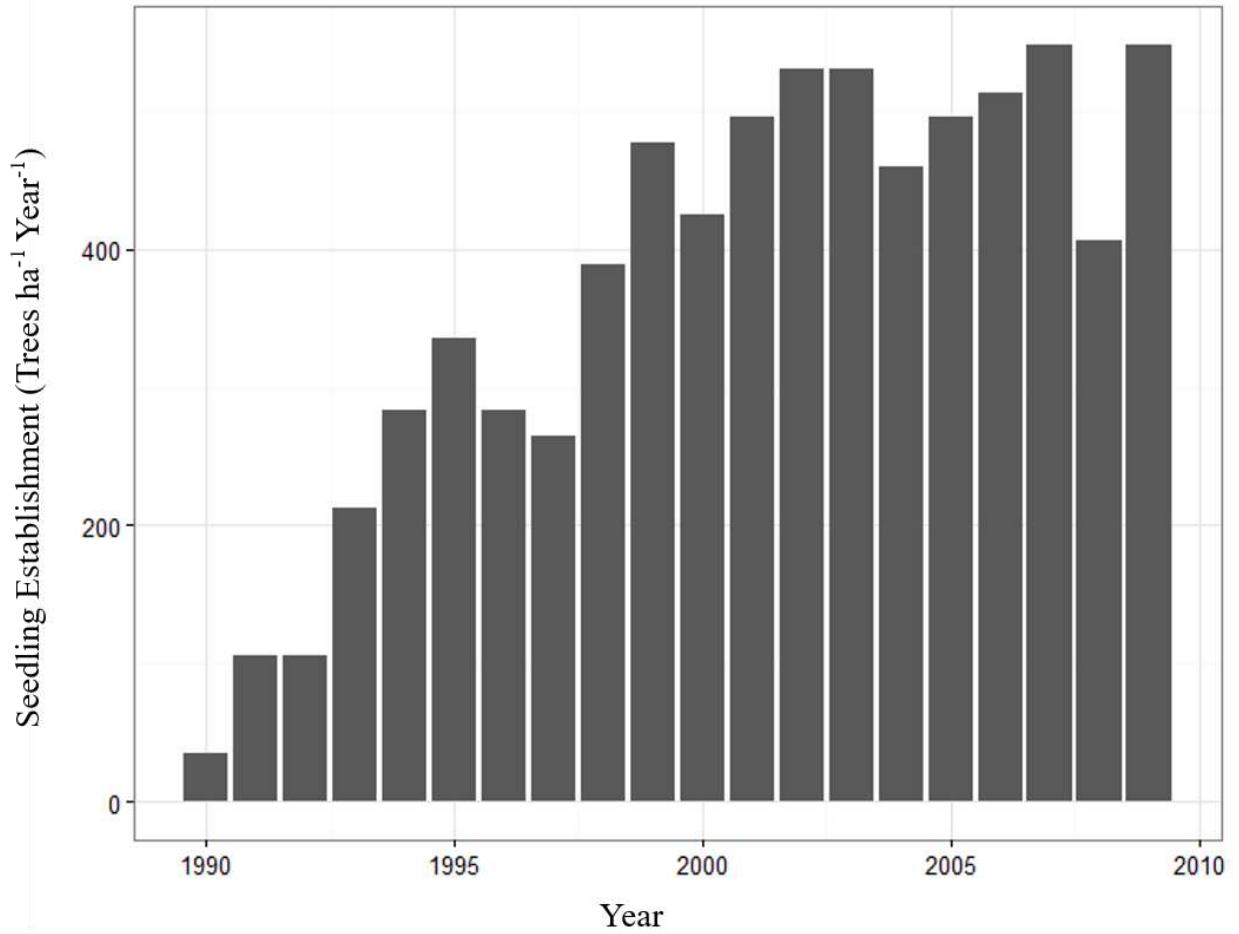
Figure B8: Annual seedling establishment density from year after treatment to 2009 for study site CC6 located on the Gunnison National Forest.

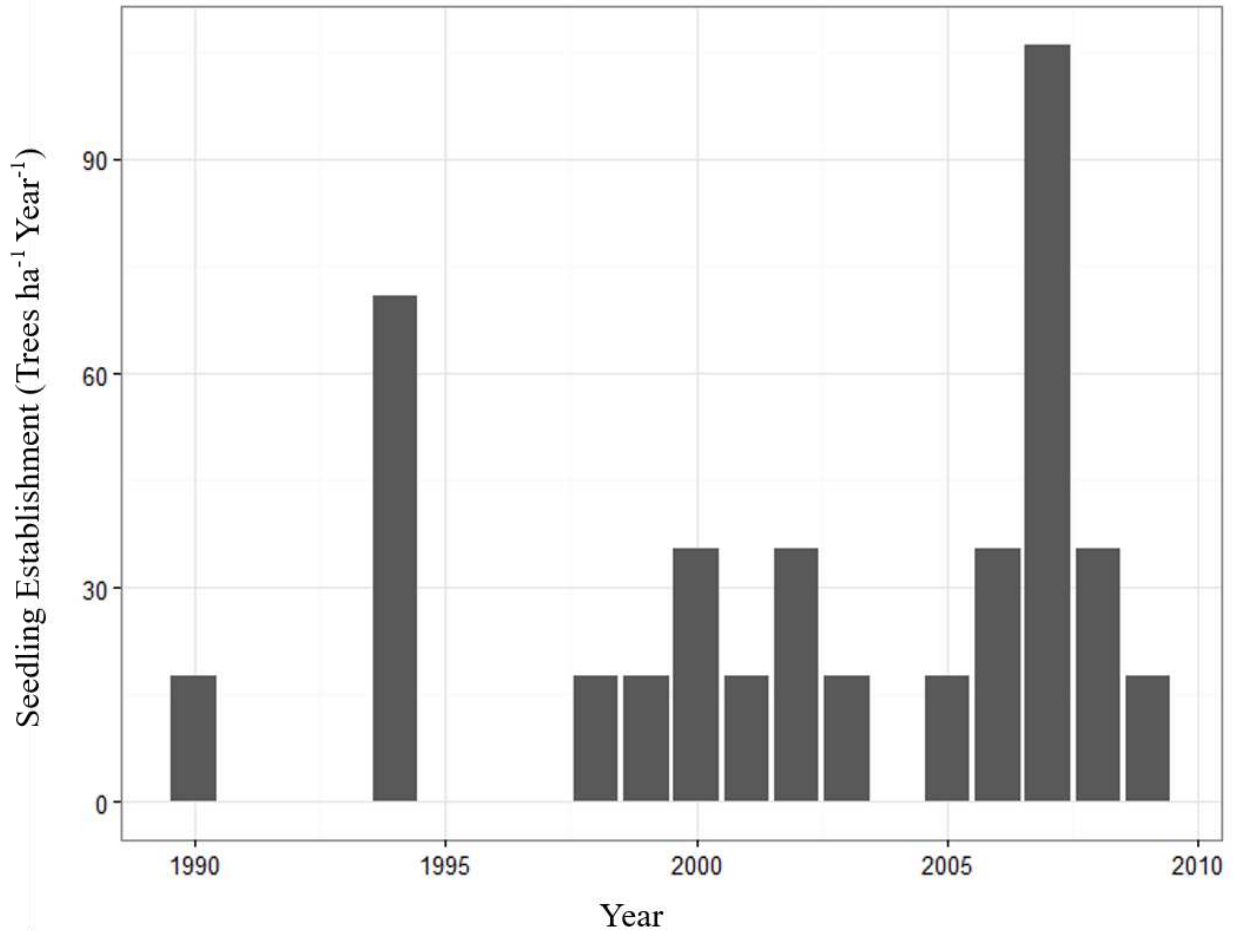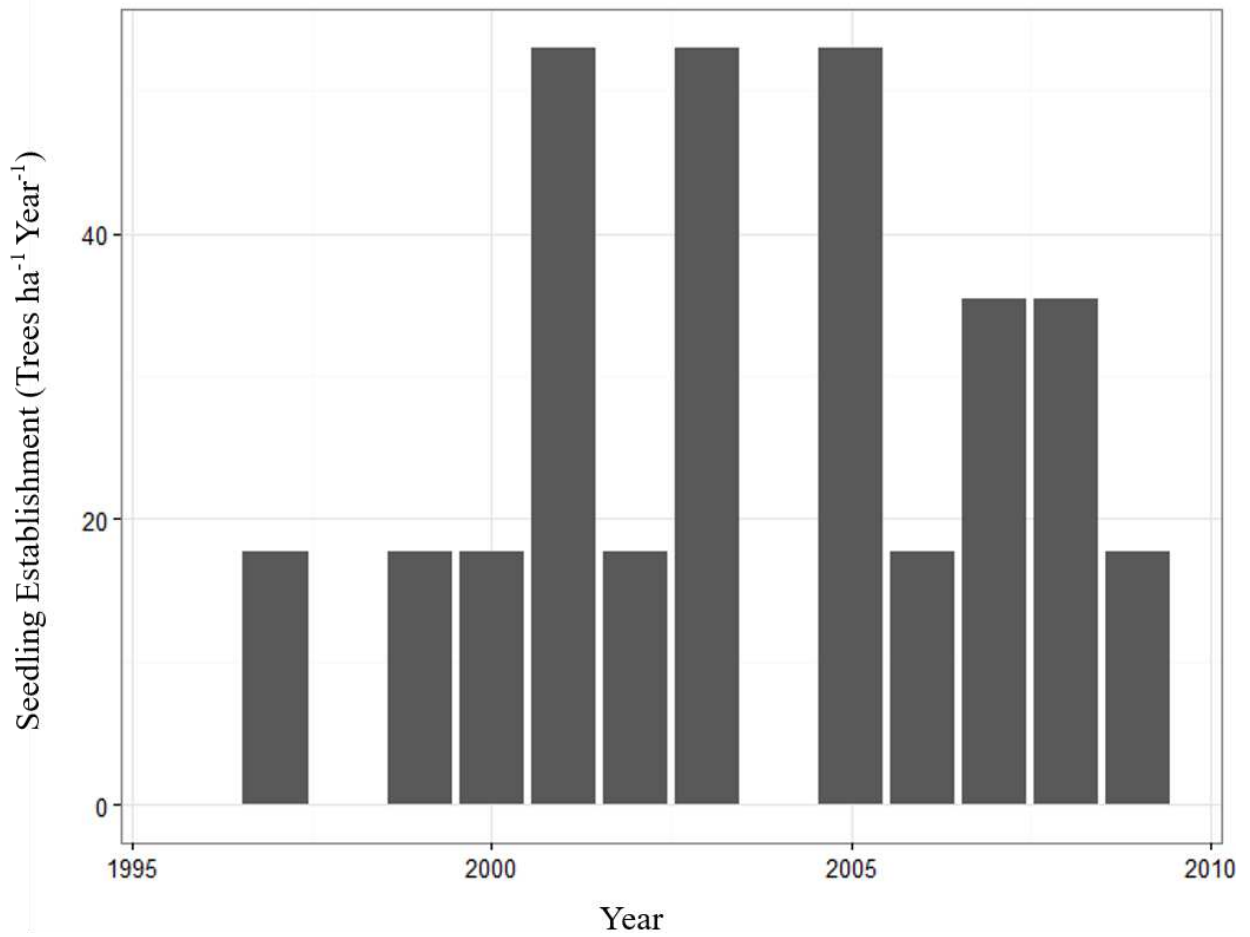# Annual Seedling Establishment Density for Study Site CC7
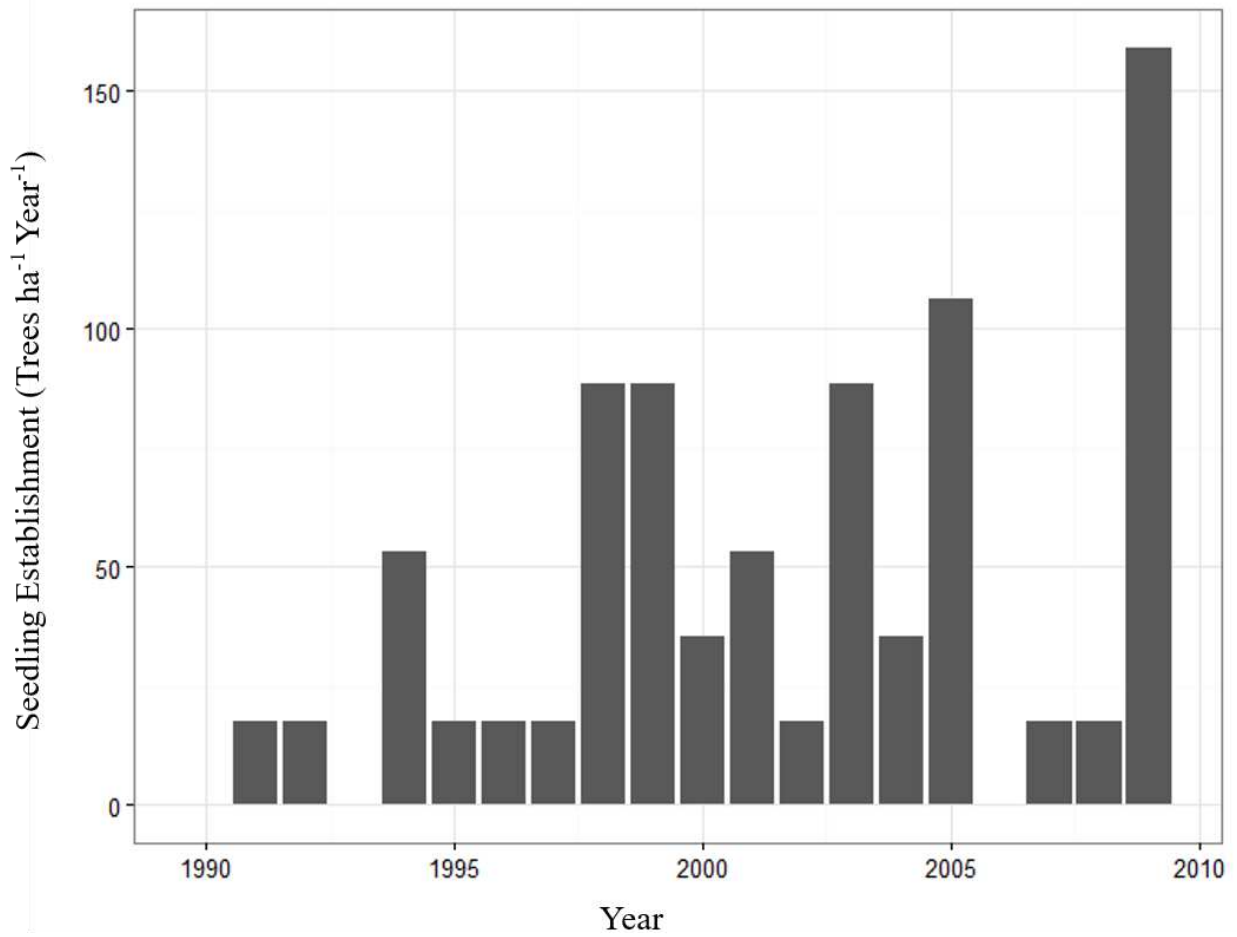
Figure B9: Annual seedling establishment density from year after treatment to 2009 for study site CC7 located on the Gunnison National Forest.

Figure B10: Annual seedling establishment density from year after treatment to 2009 for study site CC11 located on 0the Gunnison National Forest.
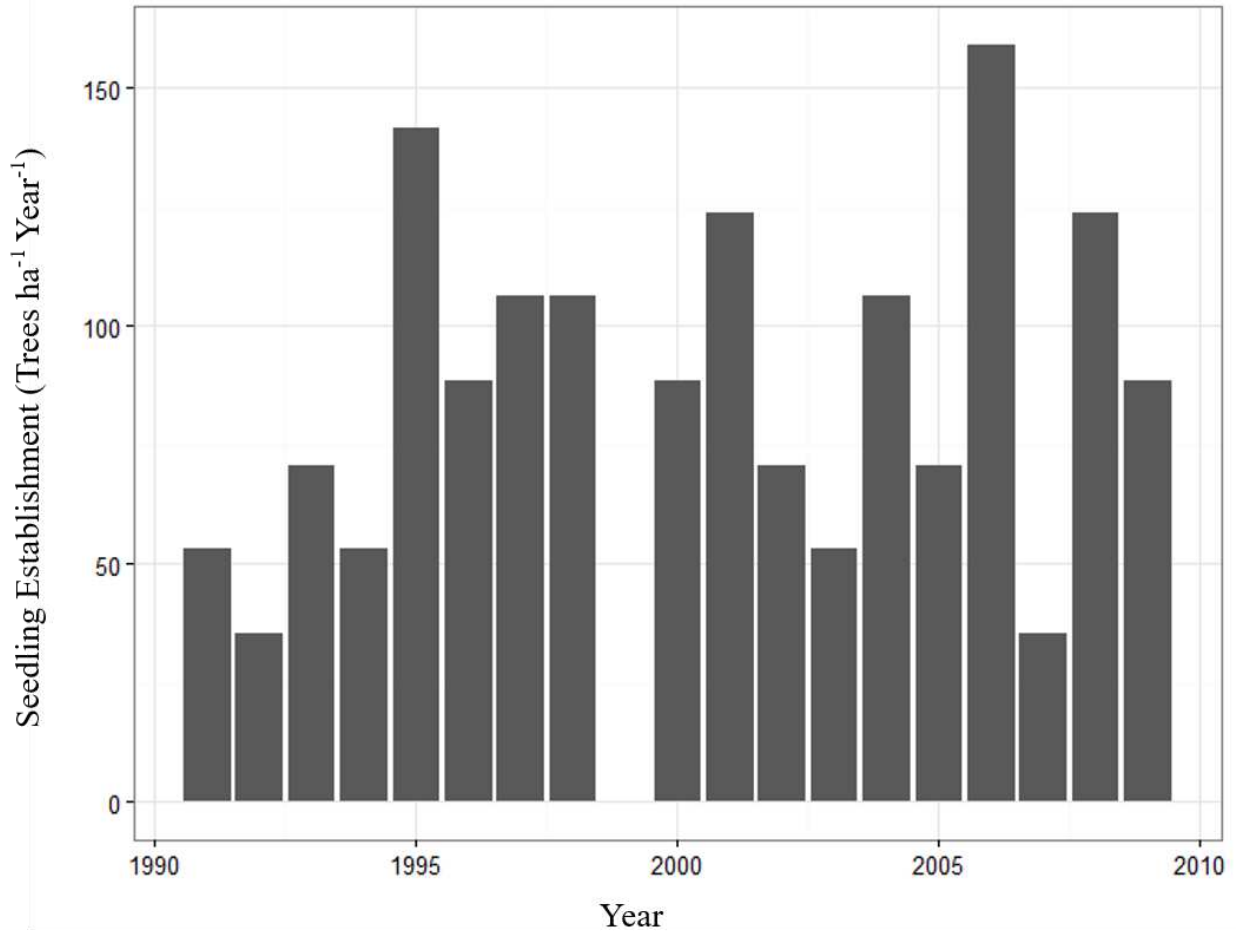
Figure B11: Annual seedling establishment density from year after treatment to 2009 for study site DC4 located on the Gunnison National Forest.

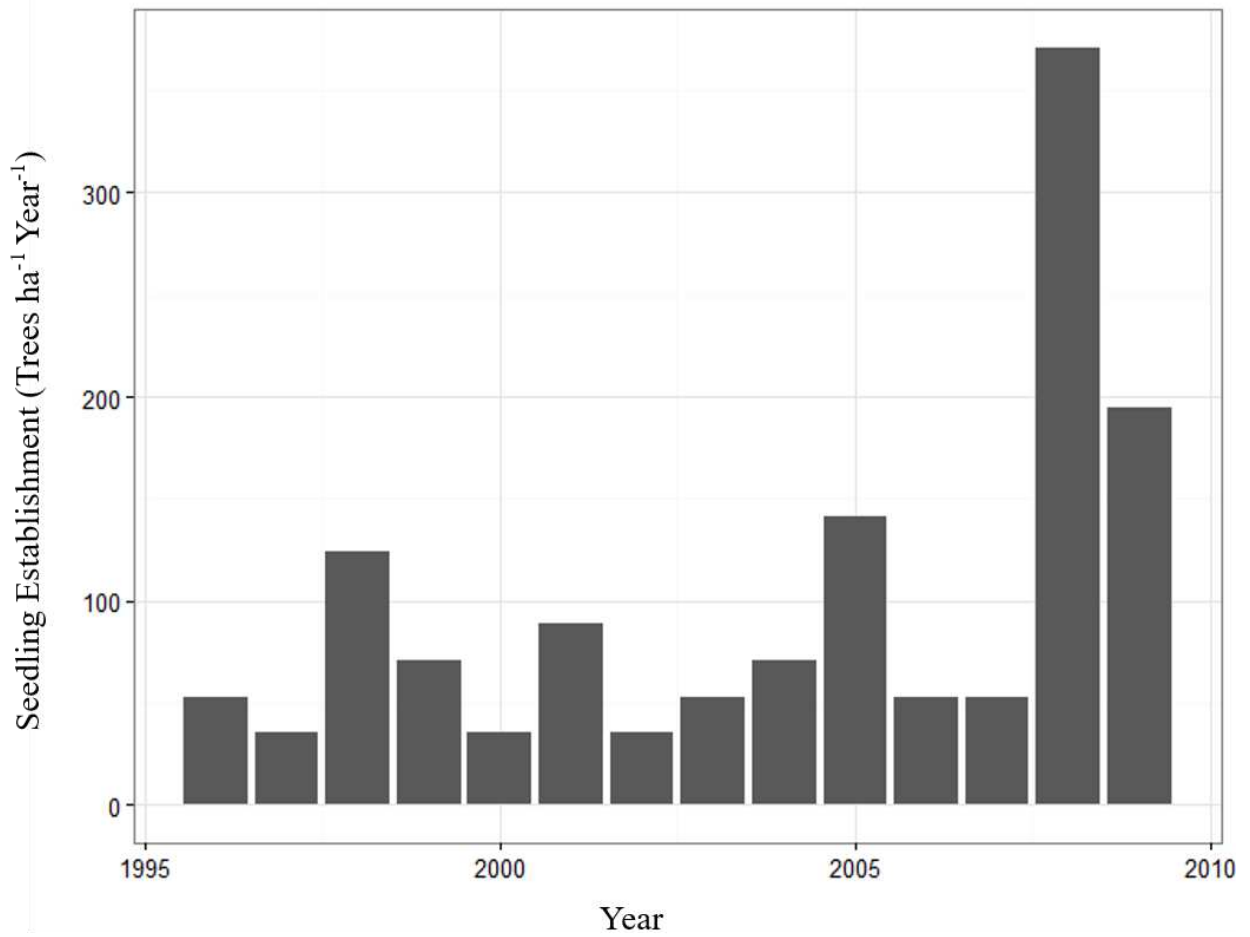# Annual Seedling Establishment Density for Study Site DC24

Figure B12: Annual seedling establishment density from year after treatment to 2009 for study site DC24 located on the Gunnison National Forest.

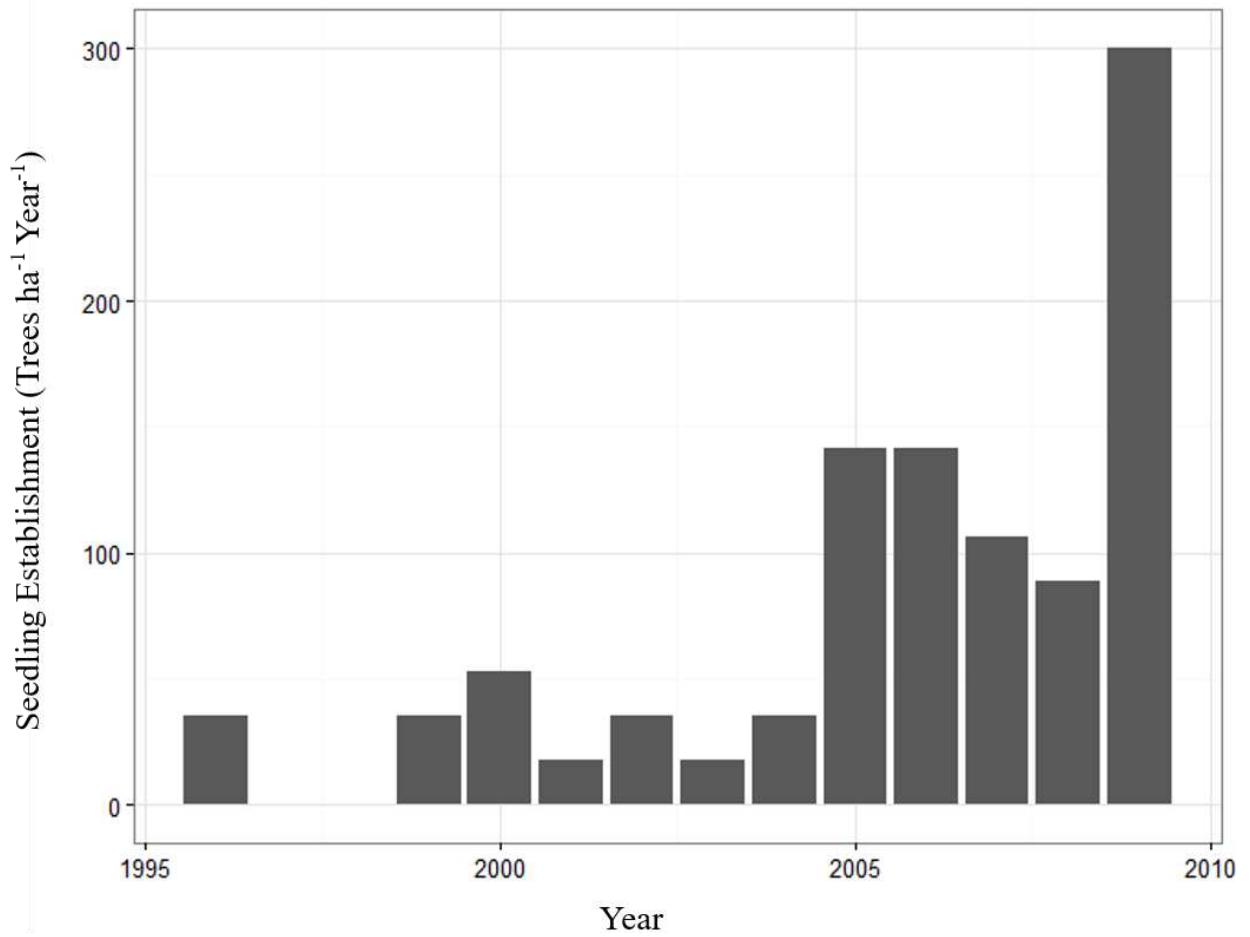# Annual Seedling Establishment Density for Study Site DC32

Figure B13: Annual seedling establishment density from year after treatment to 2009 for study site DC32 located on the Gunnison National Forest.

Figure B14: Annual seedling establishment density from year after treatment to 2009 for study site SC1 located on the Gunnison National Forest.
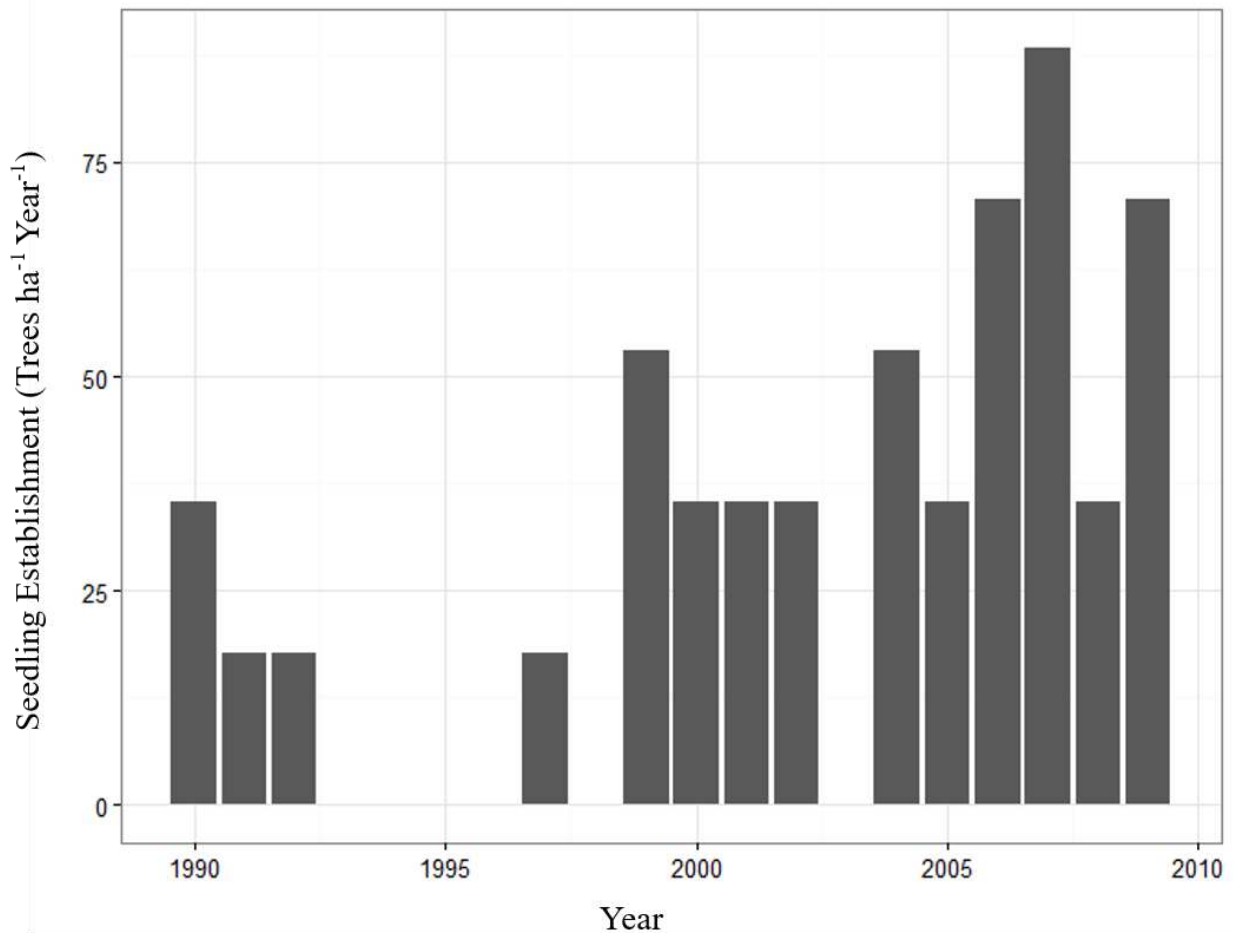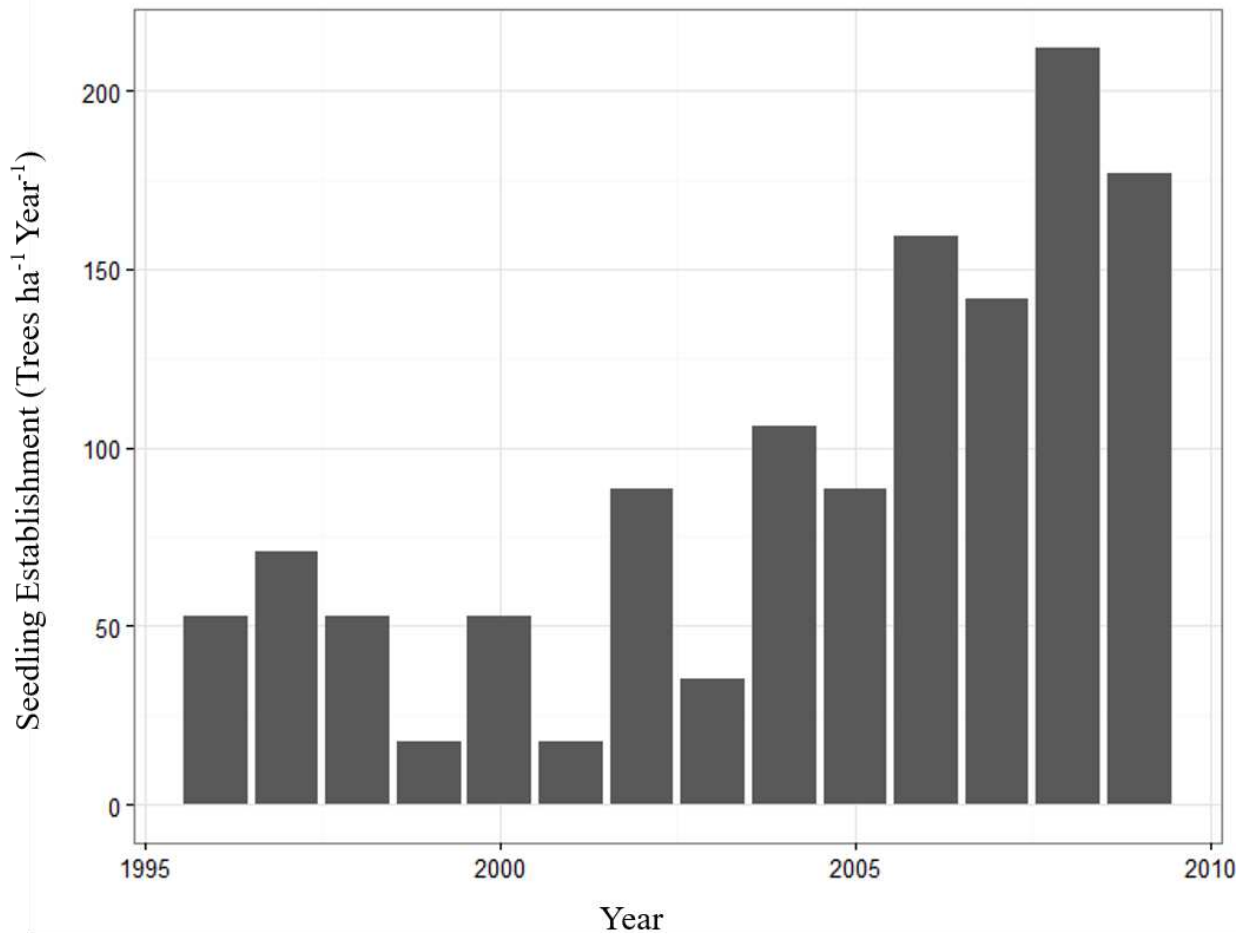
Annual Seedling Establishment Density for Study Site SC3

Figure B15: Annual seedling establishment density from year after treatment to 2009 for study site SC3 located on the Gunnison National Forest.

Figure B16: Annual seedling establishment density from year after treatment to 2009 for study site SC4 located on the Gunnison National Forest.

Figure B17: Annual seedling establishment density from year after treatment to 2009 for study site SC8 located on the Gunnison National Forest.

Figure B18: Annual seedling establishment density from year after treatment to 2009 for study site SC9 located on the Gunnison National Forest.

Figure B19: Annual seedling establishment density from year after treatment to 2009 for study site SC10 located on the Gunnison National Forest.
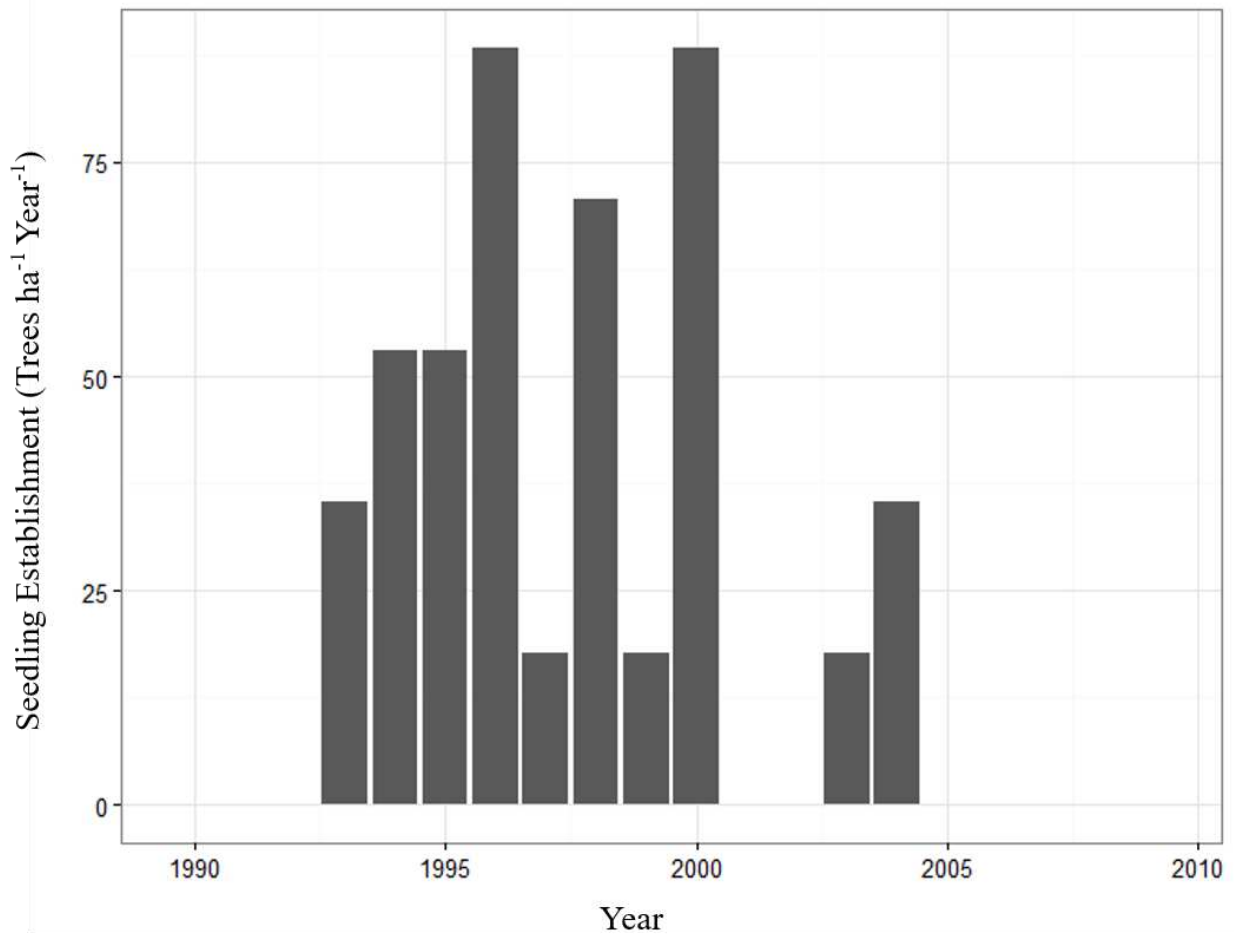
Figure B20: Annual seedling establishment density from year after treatment to 2009 for study site SC12 located on the Gunnison National Forest.

Figure B21: Annual seedling establishment density from year after treatment to 2009 for study site SC16 located on the Gunnison National Forest.

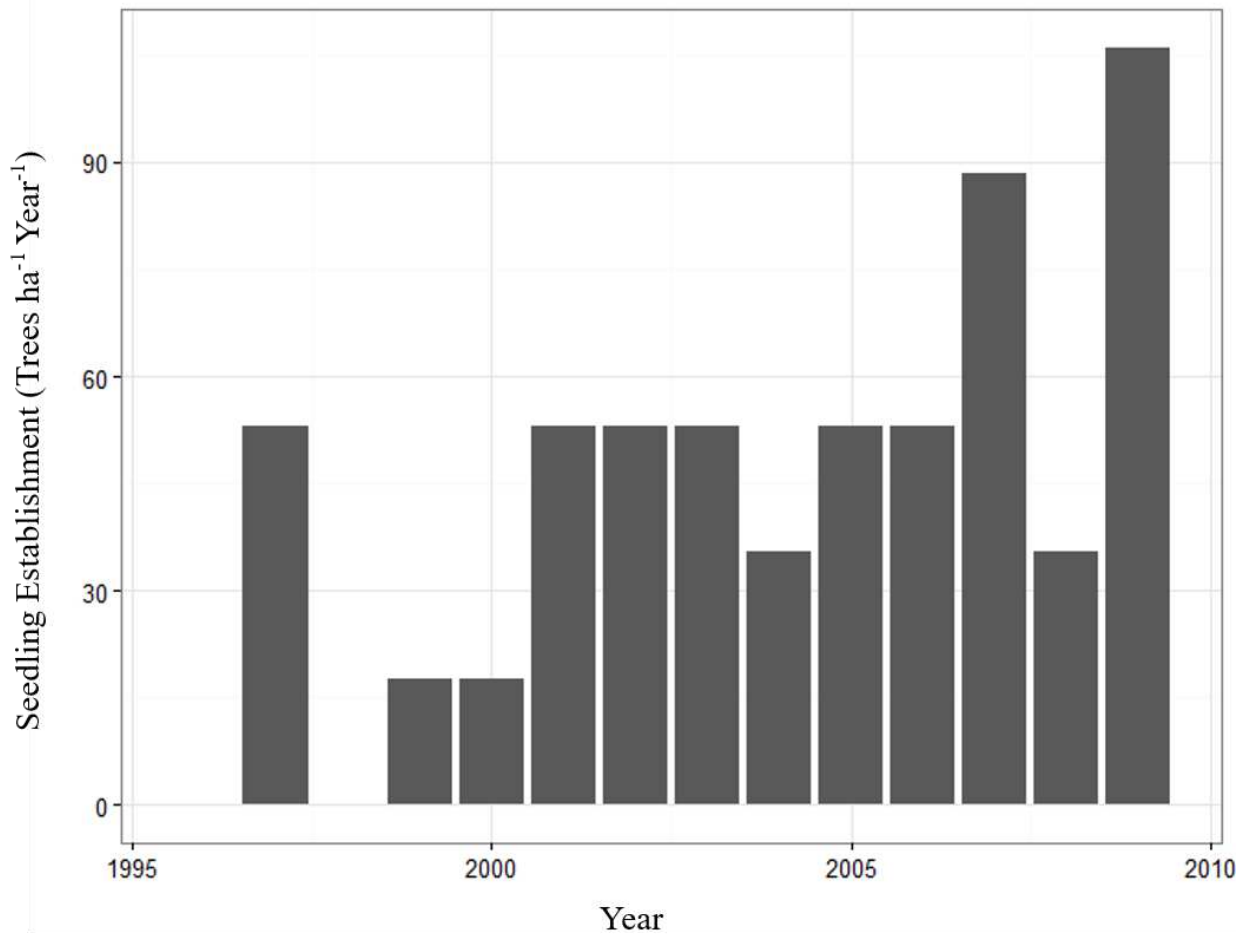# Annual Seedling Establishment Density for Study Site SC19

Figure B22: Annual seedling establishment density from year after treatment to 2009 for study site SC19 located on the Gunnison National Forest.

Figure B23: Annual seedling establishment density from year after treatment to 2009 for study site SC20 located on the Gunnison National Forest.
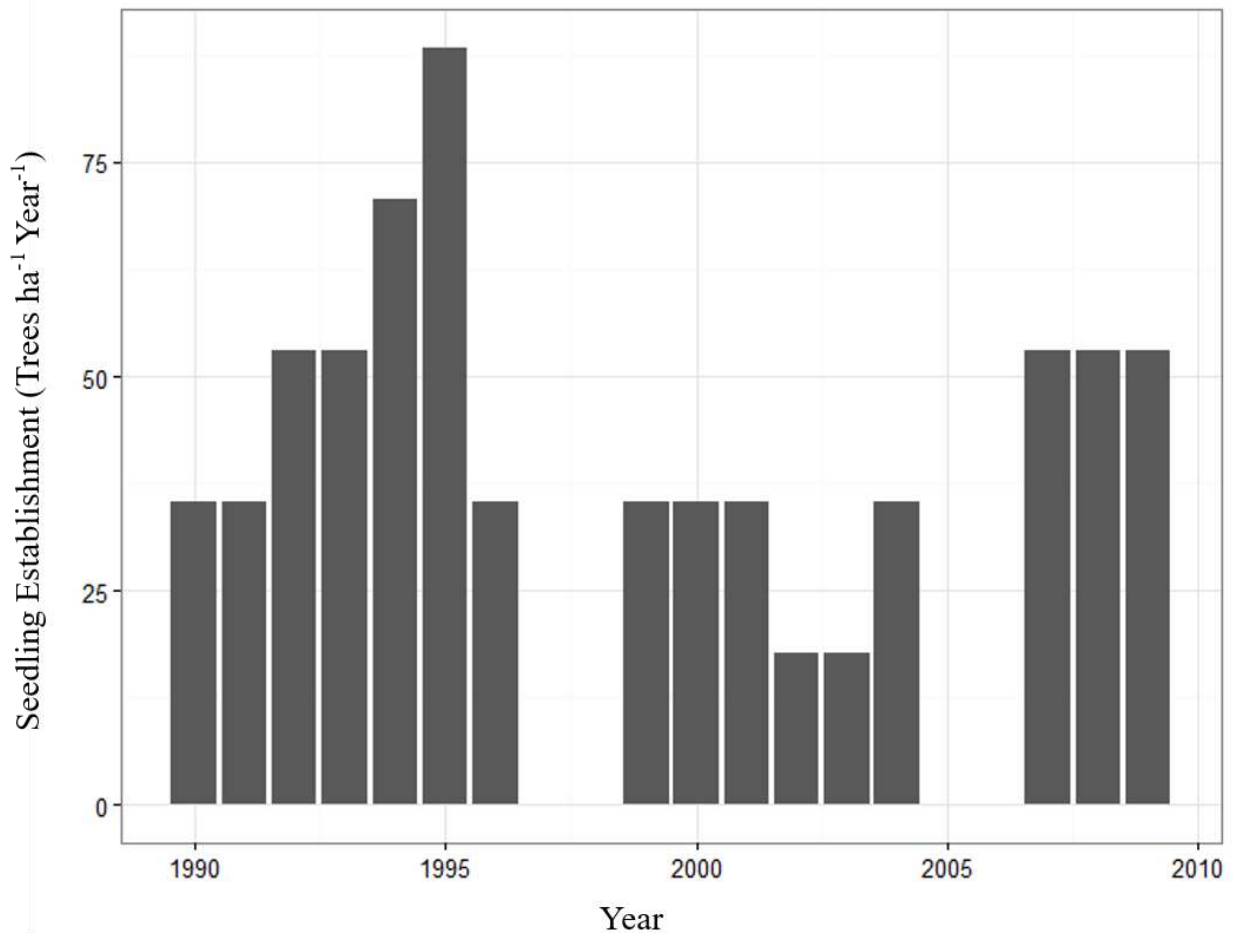
Figure B24: Annual seedling establishment density from year after treatment to 2009 for study site SC21 located on the Gunnison National Forest.