THESIS

ASSESSMENT OF STABLE ASPEN COMMUNITIES ON THE ROAN PLATEAU, COLORADO

Submitted by

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ABSTRACT

ASSESSMENT OF STABLE ASPEN COMMUNITIES ON THE ROAN PLATEAU, COLORADO

Since the late 20th century, a growing scientific debate over the prospective future decline or persistence of aspen cover across North America has prompted interest in understanding aspen structure and regeneration dynamics over regional and landscape scales. While research has heavily focused on 'seral' aspen dynamics in response to altered fire regimes and conifer encroachment, less is understood over 'stable' aspen dynamics, as defined by their ability to maintain aspen dominate overstories with little to no conifer presence. This research focused on the stable aspen atop Colorado's Roan Plateau, found in non-contiguous 'island-like' patches among the Plateau's prevalent and narrow ridges. These unique patches of stable aspen are believed to be susceptible to increasing temperatures and drought conditions and yet, there is little known of their regeneration and stand dynamics. This research's main objective was to characterize the aspen on the Roan Plateau to better understand stable aspen stand dynamics by identifying the dominant decades and patterns of aspen establishment, the distribution of aspen mortality and regeneration across the Plateau and land ownerships, and investigate any likely drivers for aspen regeneration with varying browsing pressure and environmental site characteristics.

I examined 30 aspen stands, 15 on public lands and 15 on a private ownership, using established forest inventory protocols. All of the aspen stands sampled on the Plateau were characterized as stable, with 70% of the stands showing continuous aspen establishment occurring through the late 19th century through the 21st century. Aspen mortality and regeneration varied across the Plateau and land ownerships, with 83% of sampled stands considered self-replacing based on regeneration and subcanopy tree densities. While annual mean temperature, aspect, percent stand mortality, and percent browsing damage were found to significantly influence aspen regeneration, the most significant predictor variable threshold was percent stand mortality. Browsing damage negatively influenced regeneration densities, but a one-meter^3 exclosure cage did not significantly promote aspen suckering from ungulate browsing. Without the threat of conifer encroachment in these stable aspen stands, I identify the largest influence to aspen regeneration, and subsequently aspen persistence on the Roan Plateau, to be browsing damage occurring at levels that exceed regeneration establishment with compounding influences from senescing canopy trees and stress from increased temperatures and drought events into the future. Future monitoring of the stable aspen on the Roan Plateau is necessary to understand their temporal and natural range of variation.

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CHAPTER 1- ASSESSMENT OF STABLE ASPEN COMMUNITIES ON THE ROAN PLATEAU, COLORADO

1.1. INTRODUCTION

In the western United States, quaking aspen (*Populus tremuloides* Michx.) provide significant cultural and ecological benefits; through supporting biologically diverse habitats, increasing water yield, providing livestock forage, wood products, and great aesthetic beauty (Shepperd, 1990; Bartos, 2000). As the most widespread native tree species in North America, aspen is adapted to a multitude of climate and environmental gradients that vary in topography, precipitation, soil depth and type, plant associations, and disturbance type (Rogers et al., 2014). With such a diverse range of habitat, it has long been noted that aspen characteristics vary at different regional levels (Mueggler 1985). Being shade-intolerant and relatively short-lived (roughly 150 years; Mueggler, 1989), aspen stand development is driven by the species' unique ability to prolifically self-replace through clonal root suckering, which is largely seen after disturbance events such as forest fires and overstory harvesting (Mitton and Grant 1980; Bartos and Campbell 1988; Shepperd, 1993; Frey et al, 2003). As a result, aspen research has focused heavily on the successional or 'seral' aspen function, and understanding its need or lack thereof for disturbance to regenerate, or otherwise gradually succumb to conifer encroachment (Bartos and Mueggler 1981; Long 1994; Mittanck, 2010; Rogers et al. 2010).

Less understood are 'stable' or persistent aspen, believed to characterize nearly a third of the total aspen found in the West (Mueggler, 1989, Rogers, 2002; Kashian et al., 2007). These persistent aspen communities are characterized by their ability to maintain aspen-dominated overstories (>80% aspen basal area) with little to no conifer presence and function by self-regenerating seemingly without disturbance (Mueggler, 1985; Roger, 2002; Bartos and Campbell, 1998, Kurzel et al., 2010; Roger et al., 2010). Stable aspen typically do not experience frequent large-scale disturbances like massive fire, insect, or blowdown events, but are able to regenerate at low, nearly constant levels through time (Mueggler 1985; Shepperd, 1990; Kurzel et al., 2007). Once considered an anomaly across the West (Mueggler, 1981; Shepperd et al., 2006), stable aspen are now being observed at greater regional and landscape extents (Mueggler, 1985; Manier and Laven, 2002; Kashian et al., 2007; Roger et al., 2010) and may need to be managed differently based on their stand characteristics and conditions (Kurzel et al., 2007; Rogers et al. 2014).

Since the late 20th century, there is increasing interest in the future trajectory of aspen in response to altered fire regimes, herbivore impacts, and increasing temperature and drought events (Kay, 1995, 2001; Romme et al., 1995; Baker et al., 1997; Kay and Bartos, 2000; Hanna and Kulakowski, 2012). The concern is that with a lack of landscape-level disturbances, aspen populations are declining at local and regional scales, being replaced by shrub, meadow, or conifer communities (Bartos 2007; Hanna & Kulakowski 2012). A general decline in aspen has been observed across much of the West, attributed partially to fire exclusion and the successional processes of conifer encroachment (Hogg et al., 2008; Worrall et al., 2008; Rehfeldt et al., 2009; Hanna and Kulakowski, 2012). In Bretfeld et al. (2016) 40-year resampling of plots on the Colorado Front Range showed a decrease in aspen across all size classes and a loss of aspen in nearly 25% of their plots (Peet, 1981). In Coop et al. (2014) study in the central Rocky Mountains, a decrease in 33% of aspen stand density and 8% basal area was observed over a 46 year period, with elevated loss from 1994-2010. In many cases, decline was advanced by various abiotic and biotic factors that deteriorate tree and stand health (Worrall et al. 2008; Hanna and Kulakowski, 2012), such as insect and pathogen disturbances (Krebill, 1972), lack of self-replacement (Schier, 1975), heavy browsing by ungulates (Ripple and

Larsen, 2000), deteriorating root systems (Shepperd et al., 2001), and extreme drought events (Fairweather et al., 2008; Hanna and Kulakowski, 2012).

Without landscape level disturbance present in these systems, slow decline of aspen in the West occurs when aspen are 60-100 years old; however, from 2002 to 2008, aspen decline was observed in aspen as young as 2-6 years (Frey et al. 2004). In 2005, rapid aspen mortality was seen in southern Colorado, showing a 58% increase in mortality over a one year period (Worrall et al., 2008). This rapid aspen mortality, now termed “sudden aspen decline” (SAD), is characterized by the abrupt dieback and mortality of canopy and root systems on a landscape scale, and is believed to impact many of Colorado’s aspen forests (Simon, 2009; Worrall et al., 2008, 2010). By 2008, it was estimated that SAD affected an estimated 17% of aspen across Colorado, with predicted increases of aspen mortality into the future (Rehfeldt et al., 2009; Worrall et al. 2010; Worrall et al., 2013), especially in lower elevation regions (Yang et al., 2015). There is increasing evidence that forests across the globe will have increased mortality with increasing, severe, and frequent drought and temperature changes (Dutzik and Willcox, 2010; Dai, 2013; Steinkamp and Hickler, 2015). Now that aspen decline has been seen throughout its entire range (Worrall et al., 2008), interest in understanding aspen function has grown with rising concerns over potentially declining aspen populations (Kay, 1997; Bartos and Campbell 1998; Campbell and Bartos 2001; Frey et al., 2004; Marchetti et al., 2011; Carter et al., 2017).

My research focuses on the aspen residing atop the Roan Plateau, located in northwestern Colorado. Rising above the Colorado River Valley, the Roan Plateau is home to a multitude of resource values including diverse wildlife and habitat, scenic views, and productive natural gas resources. These resources drive a variety of land uses, such as recreation, hunting, ranching, and natural gas extraction on both public and private lands. Among the prevalent and narrow ridges of the Roan Plateau, non-continuous patches of persistent aspen are distributed over a mosaic of land ownerships, providing benefits for ecosystem function and great aesthetic values (Fig. 1). These island-like stable aspen stands are believed to be susceptible to adverse climatic effects (Rehfeldt et al., 2009; Worrall et al., 2013), and yet there is little known on their regeneration and stand dynamics (Kulakowski et al., 2004; Rogers et al., 2010). This research will provide an assessment for aspen on this landscape, an ecologically valued species with rising concern over potential future decline. By providing information on aspen regeneration and stand structure, aspen managers and researchers alike will have an increased understanding of these stable aspen dynamics.

The main objective of this research was to characterize the aspen on the Roan Plateau to better understand its persistent aspen stand dynamics on a landscape scale and assess its relative risk or resilience into the future. More specifically, I aim to: 1) describe current aspen condition across the Plateau, 2) identify relationships between aspen mortality and stand and site characteristics, and 3) investigate the factors that influence aspen regeneration. Regeneration will be assessed by a) investigating relationships between regeneration and stand and site variables, b) assessing aspen recruitment dynamics through age structure patterns, c) measuring the effects of browsing damage, and d) identifying the most important stand characteristics for predicting aspen regeneration on the Roan Plateau. Lastly, I will 4) identify any differences in stand and site characteristics between public and private land ownership. Investigating these factors will advance understanding about how these stable island-like aspen systems might persist under changing climatic regimes.

1.2. METHODS

1.2.1. SITE DESCRIPTION

The Roan Plateau

The Roan Plateau is roughly 596 km^2 in size, located in the south-central region of the greater Piceance Basin. The Plateau's elevation ranges from 2,200 - 2,800 m, cut by creeks and tributaries, creating steep and narrow ridges (Bureau of Land Management, 2016). Soils are primarily loamy and well-drained, formed from Green River shale and Uinta sandstone (Hail, 1992; USDA, 2011). Precipitation on the Plateau generally consists of highly localized summer storms that are heavily influenced by topography and elevation (Bureau of Land Management, 1983). Vegetation on the Plateau consist of five dominant cover types: sagebrush shrubland, mixed mountain shrubland, aspen woodlands, mixed conifer woodlands and riparian/wetland systems (Bureau of Land Management, 2016). The Plateau has multiple resource values with abundant wildlife, scenic views, and productive natural gas resources. Wildlife is diverse and includes sage grouse, elk, and mule deer, which are known to use the Plateau for their winter range (Lendrum, 2012). Multiple land use activities take place atop the Plateau and include hunting, OHV use, cattle and sheep ranching, and natural gas extraction.

The Roan Plateau has a rich history of livestock grazing and energy development uses. After the Homestead Act of 1862, the Piceance Basin's population increased with mining, farming, and ranching for both cattle and sheep (Mehls, 1982). Cattle grazing quickly became prolific on the Plateau. By the early 1900's, upwards of 24,000 head of cattle were grazing the Plateau and creating detrimental vegetation and soil impacts (Hughes, 1979). Documented through the 1900's, impacts from overgrazing and overstocking can be still seen in areas on the

Plateau. The Roan Plateau, formerly named the Naval Oil Shale Reserves, is believed to contain major oil-shale resources. Natural gas exploration on the Roan began during World War I but did not gain traction until the 1950's, when its demand grew and extraction techniques were better developed (Mehls, 1982). It is now estimated that the Roan Plateau contains 15.4 trillion cubic feet of recoverable natural gas (Bureau of Land Management, 2004). Study sites were located on the Roan Plateau, residing on public and private land (Fig. 2). All study areas are currently utilized for cattle grazing and energy development.

Private land

Fifteen study sites were located on a private property owned by Chevron. The property is located north of Parachute, Colorado. The entire property's elevation ranges from below the Plateau at 1,720 m to 2,700 m atop the Plateau, with aspen forests located at 2,400 m and above. Average annual temperature is 5.3 °C and mean annual precipitation is 51.6 cm (PRISM, 2016) with October receiving the most precipitation on average (WRCC*, 1947-2016*). Annual average snowfall is 161 cm (WRCC*, 1947-2016*). Historically, the property was used for oil shale development and is now used for multiple purposes, including agriculture production, natural gas extraction, and wildlife benefit (Personal communication with Craig Tysse, 2014).

Public land

Fifteen study sites were located on public properties. Fourteen sites were located on property managed by the Bureau of Land Management and one site was located on property managed by the Piceance State Wildlife Area. These public lands total roughly 22,000 ha on the Roan Plateau, ranging from 2,500 meters to 2,700 m in elevation (Bureau of Land Management, 2016). Average annual temperature of 5.4 °C and mean annual precipitation is 58.9 cm with, on average October receiving the most precipitation (PRISM data, 2016; WRCC*, 1947-2016*). Annual average snowfall is 161 cm (WRCC, *1947-2016*). The Bureau of Land Management assisted the Navy in managing the surface resources for the Roan Plateau for 62 years before being granted full management control in 1997 (Bureau of Land Management, 2016). Management of the public properties is for multiple uses, including energy development, cattle and sheep grazing, recreation, and wildlife management. Mule deer and elk hunting is popular sport on public lands during the fall months.

1.2.2. DATA COLLECTION

To initially identify potential study areas within aspen stands on the Roan Plateau, I used ArcGIS (ESRI 10.1, 2015) to randomly generate 200 points that were proportionally allocated to the aspects and dominant soil types (USDA, 2016) where aspen reside on the Roan Plateau. I visited points in the field that were within 1000 m of an accessible road and within the sampling boundaries. At the GPS point, 50 m were paced following a randomly selected azimuth and was treated as a temporary plot center.

At each suitable random point, one plot was established. Each plot consisted of a cluster of four 10 m fixed radius circular subplots arranged at a fixed 30 m distance (Fig. 3; USDA, 2005). A random azimuth was generated at 120° increments apart and 30 m from the temporary plot center (Subplot 1) to identify the remaining three subplots. The plot was considered acceptable if every subplot had at least one live or dead aspen stem; if not acceptable, the plot could be randomly rotated to ensure all subplots fit the study plot criteria. This process was repeated until fifteen stands on public land and fifteen stands on private land were selected and sampled.

Over the summer of 2015, thirty plots, made up of 120 subplots, were sampled on the Roan Plateau. At each subplot, I recorded elevation (m), aspect (degrees), slope (%), evidence of past disturbance as defined by visual evidence of burnt logs, fire scars, visible disease, and visible damage from insects or wildlife. Measurements for every tree with a bole within a 10 m radius from the subplot center was recorded. I recorded diameter at breast height (dbh) for every overstory tree (trees $\geq$ 3 cm dbh) within each 10 m radius subplot. I recorded tree species, dbh, and tree status as live, dead, or dead and down for each tree within the subplot following Worrall et al. (2008). Aspen regeneration (trees < 3 cm dbh) were counted by four size classes (class 1: < 0.3 m height; class 2: 0.3 - 1 m height; class 3: 1 - 1.37 m height; class 4: > 1.37 m height, >0 - 3 cm dbh) and the presence or absence of damage from browsing was recorded. Browsing damage was considered to be visible terminal or lateral branch stripping or removal (Kota and Bartos, 2010).

To determine the approximate establishment age and distribution of aspen trees, I systemically selected ten overstory aspen trees within each subplot. Every *n*th/10 live aspen tree was selected to be cored based off the total number of overstory aspen trees (*n*) within the fixed 10 m radius subplot (Kurzel et al., 2007). The selected trees were cored at 0.7 m above the base of the tree and measured for diameter in three locations: at the base, at 0.7 m height, and at dbh. If a tree did not have an extractable core due to internal rot, it was replaced by a tree similar in diameter and conditions (Kurzel et al., 2007). Due to the frequency of aspen rot, the range in aspen density within subplots, and the challenges of reading aspen cores, not every subplot had ten extractable or readable cores; a total of 985 dateable aspen cores were collected to determine the decade of recruitment (defined by reaching 0.7 m in height; Binkley et al. 2014). Forty-nine aspen suckers (> 1 m height) were randomly collected across all plots between the subplot boundaries to include in establishing the age structure for a subset of aspen regeneration.

To further investigate browsing pressure on aspen regeneration, a paired exclosure experiment was conducted on the fifteen public land plots over a one-year period. In June 2015, fifteen one-m^3 ungulate exclosure cages were installed at each public land plot; one of the four subplots at each plot were randomly selected using a random number generator, selecting the first number that corresponded to a subplot number. The exclosure cage was installed adjacent to the edge of the 10 m radius subplot, parallel to the center subplot (Fig. 4). If the center subplot was randomly selected for the exclosure cage, it was placed on the north edge of the subplot. For every exclosure 'cage treatment', a 'no cage treatment' was located 5 m towards the selected subplot's center. Aspen suckers were counted by size class (class 1: < 0.3 m height; class 2: 0.3 - 1 m height; class 3: 1 – 1.37 m height; class 4: >1.37 m height; >0 - 3 cm dbh) for both the cage and no cage treatments. Measurements were taken upon installation of the cage in June 2015 and again in August 2016.

1.2.3. DATA ANALYSIS

Laboratory methods

I identified the decade of establishment for aspen sampled on the Roan Plateau using standard dendrochronology techniques. Aging aspen cores can be challenging due to their diffuse-porous wood structure and faint annual tree-rings (DeRose and Gardner, 2009). To minimize the effects from these challenges, the techniques used were directed through the literature (Asherin and Mata, 2001; Kaye et al, 2005; DeRose and Gardner, 2009; Rogers et al., 2010) and personal trainings with Peter M. Brown (Rocky Mountain Tree-Ring Research, Inc.; Personal communication, 2016) and Kristen Pelz (USFS; Personal communication, 2016). The core samples were air dried in paper straws, glued to wooden mounts, and surfaced using five different grains of sandpaper (Asherin and Mata, 2001). Cores were sanded again before being aged with use of a dissecting microscope. The ‘shadow technique’ was implemented by directing a backlight against the mounted core to highlight the more translucent spring wood in contrast to the darker, late-season wood (DeRose and Gardner, 2009; Rogers 2010). The rings were counted from 2015 to the pith “establishment” year. If the core did not capture the pith, a concentric circle guide was used to estimate up to ten missing years (Kaye et al., 2005). The regeneration suckers were cut into cookies from the sucker base, surfaced using five different grains of sandpaper, and aged using a dissecting microscope. After ages were recorded, data were rechecked (in subset) by Ben Gannon (Colorado Forest Restoration Institute; Personal communication, 2016). To compensate for the difficulty in accurately identifying the year of aspen tree establishment, the trees were binned within their 10-year decade of establishment. Stand establishment was based on the binned ages of sampled stems (ramets) and should not define the greater genet age, which can persist through multiple generations (Rogers et al., 2010).

Analytical methods

All abiotic and biotic variables were computed, scaled to the hectare, and averaged for each plot (see Table 1). Abiotic variables consisted of: elevation (m, measured with a handheld GPS unit); 30 year mean annual precipitation (cm, PRISM, 2016); 30 year mean annual temperature (C°, PRISM, 2016); slope (%); trigonometric aspect was computed as “north-ness” (*cos(*aspect*(radian))+1*); and “east-ness” (*sin(*aspect*(radian))+1*). The value for trigonometric aspect are given as a continuous measure represented on a scale from 2 to 0. For north-ness, values of 2 represent most north, and values of 0 represent most south (Roberts, 1986). Likewise for east-ness, values of 2 represent most east and values of 0 represent most west. Biotic variables consisted of: basal area (m^2 ha^{-1}); overstory stems (ha^{-1}); mortality as the proportion of dead aspen trees (ha^{-1}) to the total aspen stand (ha^{-1}); dead basal area ($m^2\ ha^{-1}$) as the proportion of dead aspen basal area to the total stand aspen basal area (%); and browsing damage as the proportion of aspen suckers (ha^{-1}) with evidence of terminal or lateral branch browsing in the last two years to the total stand suckers (%, Kota and Bartos, 2010). Oldest establishment was identified as the oldest sampled pith date age for each plot. All analysis was performed in R 3.3.2 and evaluated for significance with an alpha = 0.05 (R Core Team, 2016).

To characterize the current condition for aspen on the Roan Plateau, summary statistics were averaged across all plots sampled for all abiotic and biotic variables (Revelle, 2016). The distributions of aspen basal area and stems per hectare were defined by size class (Wickham, 2009). I then fit a linear trend between aspen diameter and age across the Roan Plateau using the ggplot2 package (Wickham, 2009).

To investigate the factors related to aspen mortality on the Roan Plateau, I ran a series of non-parametric analyses to identify the relationships and their strengths between mortality and site and stand characteristics. Correlations were performed between percent stand mortality and a suite of abiotic (elevation, annual precipitation, annual temperature, slope, north-ness, east-ness) and biotic variables (percent aspen basal area, mean live and dead basal area, browsing damage, oldest establishment). A Spearman's rank correlation calculated *p*-values and Rho values, used to measure the strength of association between two variables, with +1 being a perfect positive correlation while a -1 being a perfect negative correlation.

To identify the factors that influence aspen regeneration, I assessed aspen stand establishment and recruitment dynamics, the influences of browsing on aspen suckering, and the relationships and influences between various stand characteristics and regeneration densities. To execute this, I identified 1) the relationships between regeneration and stand and site characteristics, 2) the modes of aspen establishment from age structure patterns, 3) the success of stand self-replacement, 4) the quantitative effect of browsing on suckering densities, and 5) the most influential variables for predicting regeneration on the Roan Plateau.

I investigated the relationships of a suite of environmental and stand variables on aspen regeneration densities. To identify the degree that regeneration and various site and stand characteristics are related, a non-parametric Spearman's rank correlations was computed between regeneration densities and abiotic (elevation, annual precipitation, annual temperature, slope, north-ness, east-ness) and biotic variables (percent aspen basal area, mean live and dead basal area, browsing damage, oldest establishment). The significance and strength of the relationships were measured using calculated *p*-values and Rho values.

To determine the patterns in aspen age structure on the Roan Plateau, aspen establishment histograms were first created for each plot by decade of establishment (in 10-year bins; Appendix 1). I then identified patterns in age structure by running an unsupervised cluster analysis to identify and group similarly structured plots. A partitioning around medoids (PAM) cluster analysis was used to investigate and partition plots into a predefined set of clusters based on similarities or differences between their establishment and stand variables (Kaufman and Rousseuw, 1990). Variables included the frequency of aspen stems by establishment decade (from 1840 through 2010), live aspen basal area, and dead aspen basal area. Variables were standardized and computed into a pairwise distance matrix to best isolate the patterns in establishment distribution and structure between plots (R Core Team, 2016; Felde et al., 2014). The optimal number of clusters, k, was determined ($k = 2$) by testing multiple combinations of clusters and selecting the value with the highest cluster quality using the pamk() function in the fpc package (Hennig, 2015). Within the cluster package, the PAM cluster analysis used the Manhattan distance to partition the data, which examines the sum of absolute differences and is more robust to outliers when compared to the sum of squared Euclidean distance approach (Kaufman and Rousseuw, 1990; Mondal and Choudhury, 2013). An internal validation measure was used to evaluate the quality of the clustering analysis by assessing the silhouette width (S_i) of each cluster and the distance between the clusters centers. S*i* values that are closer to one indicate the cluster is ‘well fit’ while S*i* values closer to zero indicate ‘poor fit’ within the cluster and potential misclassification (Reynolds et al., 2004).

Since the PAM cluster analysis is an unsupervised means of partitioning data, some post-clustering splitting or merging of plots may be necessary based on external information (Mock et al., 2008). Adapted in concept from Mock et al. (2008) use of “threshold-clustering approaches” for grouping genetically distinct or similar aspen genets, I independently built establishment distribution criteria that defined three modes of aspen establishment distributions as pulse, having a unimodal age distribution; continuous, showing extended periods of establishment; and multiple, showing two or more establishment periods with extended gaps in time between events (Kulakowski et al., 2006; Kurzel et al., 2007). The establishment distribution criteria assessed the frequency of aspen establishment by decade to define establishment distribution for each plot (Table 2).

I identified whether aspen stands on the Roan Plateau are self-replacing and their distribution across land ownerships based on criteria examined in other studies (Ferguson et al., 2004; Bartos, 2007; Kurzel et al., 2007). Stands were defined as self-replacing based on the following criteria: regeneration levels needed to be >1200 suckers ha^{-1} (Ferguson et al. 2004; Bartos, 2007) and subcanopy trees, having diameters > 3 cm, needed to be > 100 stems ha^{-1} (Kurzel et al., 2007). The criteria for successful self-replacement was based on meeting either one or both aspen regeneration or the subcanopy trees densities since stable aspen do not necessarily establish regeneration at a constant rate (Kurzel et al., 2007).

To quantitatively assess browsing impact on regeneration over a one year period, the exclosure experiment was assessed using a non-parametric paired Wilcoxon signed rank test to compare differences in aspen regeneration densities between cage and no cage treatments (R Core Team, 2016). The test was performed with a continuity correction, which addresses tied values within the dataset ranking. Significant difference between treatments is assessed using calculated *p*-values.

To predict the influence of site and stand characteristics on regeneration densities, I constructed two comparable models to identify ecological predictors from stand and site variables: elevation, annual mean precipitation, annual mean temperature, slope, north-ness, east-ness, percent browsing damage and percent mortality for aspen regeneration density on the Roan Plateau. First, a mixed-effect model was built using a test of AICc selection, an adjusted version of AIC (Akaike information criterion). Aspen regeneration (stems ha^{-1}) was modeled as a continuous response variable against all combinations of abiotic variables (elevation, annual mean precipitation, annual mean temperature, slope, north-ness, and east-ness) and two biotic variables (percent browsing damage and percent mortality). To minimize misleading results from data dredging, the biotic variables that were significantly correlated from the univariate analysis of regeneration and most logical for the analysis were included for model selection (Pakeman et al., 2011). In the MuMin package, a series of models were generated using the dredging function, which fit all possible model outcomes (Bartoń, 2016). The model with lowest AICc value was selected and checked for normality of residuals and for outliers using the Bonferonni adjusted *p*-value ($p = 0.0146$; Fox and Weisberg, 2011). A fitted generalized linear model with a Gaussian distribution was constructed using the variables from the AICc selected model (R Core Team, 2016). I then identified the most significant ecological predictors and their corresponding thresholds for aspen regeneration densities using a non-parametric model within the PARTY package (Hothorn et al. 2006). A regression tree analysis modeled all abiotic variables (elevation, annual mean precipitation, annual mean temperature, slope, north-ness, and east-ness) and two biotic variables (percent browsing damage and percent mortality) against aspen regeneration densities.

I tested for significant differences between land ownerships using a non-parametric Wilcoxon-rank sum test (R Core Team, 2016). Significant difference was measured using calculated *p*-values for the public and private properties between all abiotic and biotic variables. Abiotic variables included elevation, annual mean precipitation, annual mean temperature, slope, north-ness, and east-ness. Biotic variables included percent of aspen basal area, total, live, and dead basal area, stems per hectare, regeneration per hectare, percent browsing damage, and oldest establishment.

1.3. RESULTS

For the 30 aspen plots sampled on the Roan Plateau, all plots consisted of >80% mature aspen basal area (including live, dead, and down trees). Eight plots sampled (27% of study area) had 100% overstory aspen basal area. One plot had conifer species present, but the conifers were not located within the plots sampled. Other tree species sampled included Rocky Mountain maple (*Acer glabrum*; 1.1% total basal area), gamble oak (*Quercus gambelii*; 0.08% total basal area), and unknown down and dead (2.9% total basal area). Mean live basal area was 13.9 (± 1.5 standard error) m^2 ha^{-1}. There was considerable variation between plots in live basal area, ranging from 4.1 to 34.5 m^2 ha^{-1}. On average, total stem density (all live, dead, down trees > 3 cm dbh) was 1,444 (± 183 SE) stems ha^{-1} and showed considerable variation between plots, ranging from 215 to 5,419 stems ha^{-1}. For aspen (all live, dead, down aspen > 3 cm dbh), mean stem density was 1,347 stems ha^{-1}, with a range from 214 to 5,045 stems ha^{-1}. Mean live overstory for aspen was 892 (± 166 SE) stems ha^{-1}, ranging from 72 to 4,512 stems ha^{-1}. While aspen basal area was most frequent in the 25 - 30 cm diameter class, most of the boles were 5 – 10 cm in diameter across the Roan Plateau (Fig. 5). A mean of 41.6% of the total stand basal area was dead and down aspen, ranging from 0.8 to 80.7% of the stand basal area. Mean stand mortality was 41.8% dead, ranging from 1.4 to 80.6%. Average standing dead was 28% of the total stand, ranging from 1.4 to 55.2%. Mean aspen regeneration was 737 suckers (± 99 SE) ha^{-1} and was heavily varied across sampled stands, ranging from 72 to 1,989 suckers ha^{-1}. An average of 44.4% of suckers sampled had browsing damage observed. Aspen age on the Roan Plateau was strongly related to tree diameter; aspen diameter and age was significantly related (p-value <0.001), showing a tight linear fit with an adjusted R^2 of 0.78 (Fig. 6).

Aspen stand mortality, as the percent of all dead aspen to the total stand, greatly varied across the Roan Plateau. Across the Plateau, 12 plots showed ≥50% mortality, with seven plots on private ownership and five plots on public lands. The Spearman's rank correlation for percent stand mortality showed positive correlations with percent browsing damage (0.49) and negative correlations between regeneration densities (-0.55) (Table 4). East-ness had marginal significance (p-value = 0.052) and suggests a negative correlation (-0.36) to stand mortality.

Aspen regeneration was related to one abiotic variable and three biotic variables. Spearman's rank correlation for regeneration densities showed moderate positive correlations with north-ness (0.38) and older stand establishment (0.40). Regeneration showed moderate negative correlations with browsing damage (-0.37) and percent stand mortality (-0.55) (Table 5).

A cluster analysis was used to define patterns in age structure and recruitment dynamics, and found two distinct groups based on their similarities in establishment distribution and basal area. The cluster analysis was weak to moderate in grouping strength, with an average silhouette width (S_i) of 0.33 and cluster separation of 12.7 (Appendix 2). Group 1 had 26 plots total (15 public land plots, 11 private land plots) with a silhouette width of 0.34. Group 2 had 4 plots total, all found on private land ownership, with a silhouette width of 0.27. Group 1 had an average stand age of 52 years old (± 2 SE) with plots showing high and varied establishment periods in the 1930's through the end of the 20th century. Group 2 was characteristically much older, having an average stand age of 100 years old (± 16 SE) where all aspen within plots established around 1880 through the early 1990's. Group 1 had a mean maximum age that was roughly 40 years younger than group 2. Using my age establishment criteria over the 30 sampled stands (Table 2), I defined one plot (3% of study area) as having a pulse establishment mode, 21 plots (70% of study area) as having a continuous mode of establishment, and eight plots (27% of study area) as having a multiple establishment mode. The pulse plot was found on public land and had a mean age of ~19 years old with no trees older than 25 years. Continuous establishment was seen for 43% of plots on public land and 27% plots on private lands, having a mean age of 61 years old for trees >12 cm dbh and a mean age of 24 for trees <12 cm dbh. The first decade of establishment sampled was varied, with plots first establishing in the late 1800's (plot CH, BI, CE, CG), early 1900's (plot BO, CA, BJ, BM, BN, CL, BF, BB, BH, BK, BC, CJ) and mid 1900's (plot BD, BL, CO, CI, BE). Multiple establishment modes were found for 3% of plots on public land and 23% plots on private land, having a mean age ~100 years old for trees >12 cm dbh and a mean age of 11 years old for trees <12 cm dbh. Multiple establishment plots had aspen that were generally older, with oldest establishment periods sampled around the mid-1800's (plot CK, CN), late 1800's (plot CB, CC, CD, CF, CM), and early 1900's (plot BG). All stands identified in group 2 from the cluster analysis were defined as having multiple establishment modes. Across the Roan, 50% of stands sampled have aspen >100 years old.

Five sampled aspen plots (17% of study area) were not found to be self-replacing, as they did not meet either criteria for regeneration (>1200 stems ha^{-1}) or subcanopy tree densities (>100 stems ha^{-1}). A total of 83% of plots sampled were considered self-replacing (25 plots). Nineteen plots sampled (63%) met one criteria, being subcanopy tree density. Six plots sampled (20%) meet both criteria for regeneration and subcanopy density.

The assessment of aspen regeneration for the exclosure experiment on public lands showed a marginal difference in aspen suckering. The Wilcoxon signed rank test found a p = 0.089 for aspen size class 1 and 2 (<0.3 m height, 0.3 - 1 m height respectively) when comparing the caged treatment to the no cage treatment over one year (Fig. 7). While the results were not significantly different at the alpha = 0.05 level, the caged treatment showed nearly a 3-fold increase in size class 1 (mean 1,330 increase in suckers ha^{-1}) and a 6-fold increase in size class 2 (mean 3,333 increase in suckers ha^{-1}) aspen suckering after one year.

The most significant predictors for aspen regeneration density were identified by both their values and predicted thresholds through building multiple regression models. The lowest AICc model selected four variables: annual mean temperature, east-ness, percent browsing damage, and percent stand mortality (Table 7). The generalized linear model showed significance for predicting regeneration densities with increases in annual temperature, west-facing aspects, and decreases in percent stand mortality and marginal significance for decreases in percent browsing damage (Table 7). The regression tree analysis found only one important predictor variable from all predictor variables input into the model as percent stand mortality. An important ecological break was identified at 37% for percent of stand mortality (p =

0.039; Fig. 8). It predicted that aspen stands with less than or equal to ~37% stand mortality have mean aspen regeneration densities of 1,097 suckers ha^{-1}. Stands that have >37% percent stand mortality have predicted mean regeneration densities of 557 stems ha^{-1}. The regression tree had an r^2 value of 0.23.

The non-parametric Wilcoxon-rank sum test showed significant differences for four abiotic variables and three biotic variables between public and private properties. There were differences in elevation (p = 0.030), annual precipitation (p = 0.005), slope (p = 0.008), and east-ness (p = 0.025; Table 6) between public and private land. Public property was higher in elevation, had less rise in slope, greater annual precipitation, and had more east facing aspects when compared to the private property (Table 6). Significant differences between properties were identified for three biotic variables; mean dead basal area (m^2ha^{-1}, $p < 0.010$), percent browsing damage (p = 0.026), and mean oldest aspen establishment (p = 0.006; being the oldest age found in each stand). The median differences between property was 5.5 (m^2ha^{-1}) for dead aspen basal area, 14% browsing damage, and 40 years with oldest tree establishment with the private property having the upper values for all three biotic variables. Regeneration densities were not significantly different between land ownerships (p = 0.507).

1.4. DISCUSSION

The characteristics of the stable aspen on the Roan Plateau are comparable to stable aspen communities across the West. Mean aspen basal area for canopy trees on the Roan (~12 m^2ha^{-1}) was lower than in the "low to mid-elevation, self-replacing aspen stands" found on the Colorado Front Range (27.6 m^2ha^{-1}; Kashian et al., 2007), the stable aspen on the Uncompahgre Plateau (32.1 m^2ha^{-1}; Smith and Smith, 2005), and the stable aspen on Cedar

Mountain, Utah (~20 m^2ha^{-1} at 12.5 cm dbh; Rogers et al. 2010). Canopy density on the Roan Plateau (304 ha^{-1} for trees ≥12 cm dbh) was comparable across the West, with density on the Roan slightly below Cedar Mountain, Utah (315 stems ha^{-1} at 2.5 cm dbh minimum; Rogers et al., 2010). Overstory density on the Roan Plateau (891 live stems ha^{-1}) was lower than in Dudley et al. 2010 sample of the mountainous aspen of the White River National Forest (~1,243 live stems ha^{-1}) and Medicine Bow National Forest (~3,122 live stems ha^{-1}) but higher than on the Routt National Forest (~836 live stems ha^{-1}). Aspen mortality on the Roan Plateau was higher than in other areas of Colorado. Standing dead for the Roan (~28%) was higher than that found in Dudley et al. 2010 roadside survey of the White River National Forest (4%), Routt National Forest (5%), and the Medicine Bow National Forest (24%). Aspen regeneration density on the Roan (737 suckers ha^{-1}) was much lower than those from Dudley et al. 2010 aspen stand assessment plots from 2010 of in the White River National Forest (~1,856 suckers ha^{-1}), Routt National Forest (~3,778 suckers ha^{-1}), and the Medicine Bow National Forest (~5,567 suckers ha^{-1}). When compared to other stable aspen communities across the West, regeneration densities for the Roan were low. In Kashian et al. self- replacing aspen stands on the Colorado Front Range had regeneration densities >2,000 stems ha^{-1} (2007), well above densities observed on the Roan. Even with regeneration being limited, Cedar Mountain, Utah had mean density of 2,760 ha^{-1} for suckers 0.3 – 1.3 m height and 600 ha^{-1} for suckers 0 – 2.5 cm dbh (Rogers et al. 2010); mean densities on the Roan were 200 ha^{-1} and 614 ha^{-1} respectively. Percent browsing damage on the Roan (~44%) was lower than on the Colorado Front Range (58%; Kashian et al., 2007) and on Cedar Mountain, Utah (79%; Rogers et al. 2010). Overall, the Roan Plateau was comparable in mature canopy density, overstory stem density, and browsing damage, lower in values for canopy basal area and regeneration densities and higher in values for percent standing dead when compared across the West. The Roan Plateau is best compared to studies of stable aspen in mid-elevation, xeric locations across the West (Kashian et al., 2007; Rogers et al., 2010).

Aspen mortality is highly variable across the Roan Plateau, driven by a range of environmental and site characteristics. One explanation for this variability may be the Plateau's topography acting as a driver for soil moisture conditions (Frey et al., 2004; Worrall et al., 2008; Kaiser et al., 2013). Elevation has been found to effect aspen mortality throughout the West, but has been inconsistent in its influence. Although increased mortality has been observed and expected in xeric lower elevation sites (Frey et al., 2004; Rehfeldt et al., 2009; Worrall et al., 2008, 2013), mortality has also been observed to decreased at low elevations and increased at high elevations (Bretfeld et al., 2016). While other studies identify elevation and slope to influence stand mortality (Frey et al., 2004; Rogers et al., 2010; Worrall et al., 2013; Tai et al., 2017), these were not explanatory for aspen on the Roan Plateau due to their narrow range of variation among stands in this study. Assessing and characterizing aspen forests across a wider extent of the Roan Plateau may benefit our understanding on the relationship between elevation and aspen mortality.

Aspect can largely play a role in aspen mortality (Frey et al., 2004; Worrall et al., 2013). As a result of exposure to solar radiation and decreased soil moisture content, tree stress is more prevalent on south and west facing aspects (Safranyik and Carroll, 2006). On the Roan, aspects that were more west-facing were found to marginally increase percent stand mortality and this trend is supported across aspen sampled in the West (Kashian et al., 2007; Rogers et al., 2013; Bretfeld et al., 2016). Variation in mortality may also be a result of browsing damage; I found that browsing damage was positively related to percent stand mortality, indicating stands with greater browsing damage may experience difficulties establishing and maintaining new canopy and subcanopy trees (Kaye et al., 2005).

Aspen regeneration dynamics may define aspen stand structure and can be influenced by variations in environmental conditions, establishment mode, and browsing disturbance (Long and Mock, 2012). Across the Roan Plateau, regeneration densities varied greatly with a range from <100 to nearly 2,000 suckers ha^{-1}. Some of this variability may be explained by site aspect; I found aspen regeneration was best supported on north aspects, which generally have higher soil moisture content. This relationship has been observed in Rogers et al. assessment of stable aspen in Cedar Mountain, Utah (2010) and Wolf Creek Ranch, Utah (2013). On the Colorado Front Range, Bretfeld et al. (2016) resampled aspen populations after a 40-year period and found a climate-driven shift of stands towards northeast aspects. This relationship between aspect and aspen suckering suggests the importance of local site conditions and the potential limitations drier sites may impose on aspen densities (Frey et al., 2004; Bretfeld et al., 2016). Future monitoring to see how regeneration densities are affected over time with anticipated increases in temperature and drought conditions should be performed by revisiting sampled plots and expanding aspen sampling, especially on south-facing slopes and xeric sites.

The variety in stand structures seen in the aspen on the Roan Plateau further support the idea that stable aspen communities do not need large-scale disturbance events to regenerate and are much more diverse in their mode of establishment than previously believed (Mueggler 1985; Kurzel et al., 2007). Nearly 97% of the stands sampled on the Roan Plateau expressed continuous or multiple establishment distributions, often a distinctive trait of stable aspen structure (Mueggler 1985; Shepperd 1990). Interestingly for both distribution mechanisms, aspen establishment is occurring without severe fire or other severe disturbance events within these stands. Continuous stand development through understory suckering was the primary mode of establishment on the Roan Plateau and may be a result of gap phase openings within the canopy that allow light to reach the forest floor which support regeneration suckering (Cummings et al., 2000; Kurzel et al., 2007). Stands with multiple establishment periods may be a result of non-catastrophic episodic events that drive cohort development (Kurzel et al., 2007). The multiple layers within these canopies indicate low-levels of continuous or episodic cohort development that promote uneven age and size stand structures and result in greater stand resilience from disturbance (Mueggler 1985; Shepperd 1990; Kurzel et al., 2007). While one stand did not exhibit a continuous establishment distribution, down burnt logs and charcoal present on the forest floor were evidence of a past fire that may have led to a responsive pulse of aspen over the 1990's.

I identified 83% of plots to meet at least one of the criteria to be considered self-replacing. The self-replacing aspen seen on the Roan is also seen across northwest Colorado; my findings are consistent with a 2007 study of mid- to high-elevation stable aspen in northwest Colorado, where 70% of sampled aspen stands were considered self-replacing (based on >2,500 suckers ha^{-1} or $\geq$100 subcanopy ha^{-1}; Kurzel et al. 2007). Interestingly, the majority of the stands that met the self-replacement criteria only met the subcanopy density requirement, which may be tied to an episodic response to the Colorado drought in the early 2000's (Elliott and Baker, 2004). Now residing in the subcanopy diameter range, aspen establishment was seen in all plots from 1990 - 2010, potentially a result from water-stress clone stimulation (Frey et al., 2003; Kulakowski, 2013).

Browsing damage can influence aspen stand structure and may limit the recruitment of aspen regeneration into the canopy. The Roan Plateau has long been utilized for grazing by livestock and wild ungulates (elk and mule deer), using the Plateau as their winter habitat range (Lendrum et al., 2012). Aspen regeneration may be decreased as a result of high populations of mule deer and elk causing negative impacts from concentrated browsing (Baker et al., 1997; Suzuki et al., 1999; Lendrum et al., 2012). Though cattle are known to use aspen regeneration as forage, especially towards the second half of the growing season, the steep slopes (greater than ~30%) and high density of down trees may deter cattle utilization within aspen stands (Smith et al. 1972; Fitzgerald et al., 1986; Asamoah et al., 2003; Kaye et al., 2005). I found browsing damage to be negatively correlated with regeneration density (Table 5), but with a one-year release from ungulates there was a release from browsing pressure for aspen suckering. With a larger sample size across landownerships (n > 15), a better understanding of the significance of browsing on aspen regeneration and the value of using small, cost-effective exclosure cages could be identified.

Several variables from my complementary analytical approaches were identified that best predict aspen regeneration densities on the Roan Plateau. The generalized linear model predicted regeneration densities to increase with increased temperature and more west-facing aspects, and decrease with increased stand mortality and browsing damage. Though the model selection included percent browsed as a predictor for aspen regeneration, it was not significant in the generalized linear regression ($p = 0.0857$). While the results from my generalized linear model identified multiple predictor variables, the regression tree analysis found only one most influential predictor variable for aspen regeneration density. My regression tree findings suggest that aspen stands with less than or equal to 37.7% mortality are predicted to have higher levels of success for aspen regeneration. Overstory tree mortality events release hormonal queues to the underground root system that stimulate clonal shoot initiation (Farmer 1962; Schier 1972) but interestingly on the Roan, I found stands with greater percent stand mortality experience lower regeneration densities. It is possible that when stand mortality is <38%, small gaps open within the canopy promoting aspen suckering success by allowing sunlight to reach the forest floor while also retaining soil moisture and protection from the elements (Frey et al., 2003; Dudley, 2011). Once a stand has reached a mortality threshold >38%, aspen regeneration may not be as successful, potentially as a result of weak clonal stimulation along with increased exposure to harsh or damaging conditions (Frey et al., 2003; Kurzel et al., 2007). Expanding sampling across the Roan Plateau and other arid regions to see if this identified mortality threshold is consistent across larger extents should be considered.

On a more local-scale, land ownership showed variations in stand and site conditions (Table 6). Much of the variation may just be a result of specific stand characteristics; the older forests that are primarily found on private ownership may just be residing within a different stage of stable aspen's natural range of variation, which potentially extends longer than the last century (Kulakowski et al. 2006, 2013; Rogers, 2014). Variations in dead aspen basal area may be contributed to differences in aspect. The private property had significantly more west-facing plots, which was an abiotic trait significantly related to stand mortality and may be contributing to property differences. Even with differences in abiotic and biotic conditions, land ownership did not have a significant difference in regeneration. Though different management strategies may contribute to some of the variation, access to detailed records on land use history and management practices for the sites on both land ownerships were not available in detail, which could greatly enhance the value of these results.

This research was a snapshot of the current status of aspen on the Roan Plateau, but what does the future of these aspen look like? Aspen in the West naturally begin to senesce around 120 years old (Meuggler, 1989; Kaye et al., 2005; Kurzel et al. 2007). With 50% of stands sampled on the Roan having aspen greater than 100 years old, mature stem die off may increase within the next 20 years, as these trees have an increased susceptibility to "inciting" factors that can weaken the root system and lead to stand mortality (Worral et al., 2008). Aspen stand deterioration can be a result of insufficient aspen suckering (Schier, 1975); heavy browsing damage (Bartos and Mueggler, 1981; Romme et al., 1995; Baker et al., 1997; Rhodes et al., 2017); understory competition (Campbell and Bartos, 2001); fire exclusion (DeByle et al., 1987; Kay, 2007); compounding genetic influences (Mock et al., 2008); and increased temperature and drought conditions (Worrall et al., 2008; Hanna and Kulakowski, 2012). Unlike the concerns over aging in seral aspen stands, which often are similar in age and size distribution, senescing canopy trees are not usually the primary concern for stable aspen because of their varied ages, stand structure, and most significant, continuous regeneration dynamics. In my study, the primary mechanisms for patterns in stand structure are attributed to variations in aspen suckering densities which can be shaped by stand mortality, browsing influences, and the continuous establishment of aspen.

Aspen regeneration is a key indicator of future aspen persistence (Long and Mock, 2012). Without the threat of conifer encroachment in these stable aspen stands, I believe the largest influence to aspen regeneration on the Roan to be compounding effects from browsing damage occurring at a rate that exceeds regeneration establishment, senescing canopy trees that increase percent stand mortality, and greater clonal stresses from drought into the future (Frey et al., 2004; Kurzel et al., 2007; Rhodes et al., 2017). Though 83% of stands met the self-replacement criteria, regeneration densities were observed far below other stable aspen communities across the West and may be limited into the future if changes in their stand and site conditions shift outside their natural range of persistence.

Over the next century and beyond, I hypothesize that the greatest threat to aspen populations on the Roan Plateau will be warming temperatures that push the range of aspen habitat upslope in elevation (Kulakowski et al., 2013; Carter et al., 2017). A historic pollen and charcoal study of aspen from Colorado and Wyoming illustrated that between 4,500 and 2,000 cal. yr bp an upslope shift in aspen occurred after a 150-year long drought and sustained populations for ~500 years due to an increased climate-fire relationship (more frequent fires due to warmer temperatures; Carter et al., 2017). Aspen mortality in the West has been highlighted in lower elevations where stable aspen primarily reside and subsequently are assumed to experience the greatest mortality into the future (Frey et al., 2004; Rehfeldt et al., 2009; Anderegg et al., 2013; Worrall et al., 2013; Carter et al., 2017; Tai et al., 2017). Predicted shifts in the frequency and severity of fire, drought, and warming conditions favor aspen expansion in high elevations while hindering aspen regeneration at lower elevations (Romme et al. 2001; Elliott and Baker, 2004; Hanna and Kulakowski, 2012; Kulakowski et al., 2013; Carter et al., 2017; *but see* Bretfelt et al., 2016 *for an exception*). Colorado's climate has become increasingly warmer over the last century (Bretfeld et al., 2016), and with low spring snow densities followed by dry summer and fall conditions aspen are predicted to narrow in their geographic and elevational range (Meier et al., 2015). While aspen on the Roan reside at its highest elevation gradients, the Plateau's unique topography may mitigate the effects from extreme temperature, droughts, and other disturbance and allow aspen to persist in areas where it is predicted to decline (Sibold et al., 2006; Dobrowski, 2011).

Though many site and stand characteristics were assessed within this study, there are likely influences on aspen stand structure that were not directly assessed or limited in scope. Abiotic conditions including annual precipitation, slope, and elevation had a narrow range of variation among stands, but may have played a role in the distribution of mortality and regeneration that was not observed in this study. Soil moisture may also contribute to stand structure on the Roan; I did not explore this specifically but used aspect as a proxy for soil moisture. Seasonal precipitation is largely influential for aspen success, with many studies showing that high snowpack year can result in the protection of aspen from browsing and promotion of establishment (Elliott and Baker, 2004; Frey et al., 2004; Martin and Maron, 2012; Meier et al., 2015). Aspen research should consider monitoring soil moisture levels within stands on the Roan Plateau seasonally to identify if there are any influences on aspen establishment and persistence.

Biotic conditions that were not directly assessed or limited in scope may also contribute to aspen stand and site characteristics. Aspen age structure is dynamic and provides its own challenges. Establishing distinct age patterns is challenging due to the variability in establishment distribution, lack of a standard practice of categorizing establishment patterns, and that aspen potentially express multiple modes of establishment (Roger et al., 2010). Stands sampled were assumed to be clonal, but without genetic testing it is unclear if multiple stands are coexisting within the same space (Long and Mock, 2012). Future studies should assess the genetic variability of these island-like patches of aspen to see if these stands were once all contiguous or if genetic diversity exists amongst stands, as recent studies indicate aspen are more genetically diverse than once believed (Long and Mock, 2012; Krasnow and Stephens, 2015). Understory competition and shrub invasion have been cited to suppress aspen regeneration (Campbell and Bartos, 2001; Kurzel et al., 2007). In this study understory cover was notably varied across stands but was not quantified, however Kurzel et al. (2007) identified similarly thick shrub layers within self-replacing stands, and considered lower elevations to exhibit more threat from understory competition over mid- to high elevations. Lastly, not assessed in this study, insect and pathogens have been identified to contribute to aspen stand deterioration and are greater in effect in regions of low precipitation and high temperatures (Frey et al., 2004; Bell et al., 2015). Aspen on the Roan Plateau should be assessed for any pathogen, insect, and disease as contributing factors that may influence aspen establishment and persistence. Further investigation on these variables and characteristics which define the stable aspen of the Roan Plateau will assist both forest managers and the greater scientific community alike.

1.5. CONCLUSION AND MANAGEMENT IMPLICATIONS

My assessment of the aspen on the Roan Plateau found all stands sampled were stable aspen function (without conifer encroachment) and the majority of the stands regenerating seemingly without a large-scale disturbance. Ninety-seven percent of the stands sampled are characterized by a multiple or continuous establishment distribution and 83% of stands sampled are considered self-replacing. Aspen are not currently declining on a landscape-scale atop the Roan Plateau, but some aspen stands are at greater risk for the future than other stands. Because 50% of the stands sampled on the Plateau have trees greater than 100 years old, the aging of aspen stands raise concerns over cohort senescence coupled with insufficient regeneration/subcanopy densities in 17% of plots could lead to clone die-off. Negative impacts on aspen resilience may be seen into the next few decades, as trees reaching 120 years are more susceptible to stresses from drought, insects, disease, and browsing and may affect regeneration success (Frey et al., 2004).

Studies that examine the characteristics of forests across a landscape tend to focus on the overarching trends and patterns, which often can be challenging to translate for forest management application (Shepperd, 1990; Kashian et al., 2007), so I have identified the most significant and accessible variables for forest management on the Roan Plateau to consider: stand age, mortality, and regeneration densities. The extrapolation of aspen diameter and age (Fig. 6) showed a strong relationship and provided a useful regression equation for management application (Binkley et al. 2014). Forest managers on the Roan Plateau can measure the diameter of their trees and with use of the aspen diameter to age regression, extrapolate a tree age. This knowledge can assist managers in understanding the age distribution of their forests and identify stands with trees >100 years old to prioritize management that promotes aspen regeneration. This includes assessing mortality levels, with an understanding that stands exhibiting >38% stand mortality reach a predicted threshold to have significantly less regeneration. Forest managers can survey their aspen to identify if they are self-replacing based on criteria of either regeneration or subcanopy tree density (Ferguson et al. 2004; Kurzel et al. 2007). Lastly, browsing damages on regeneration should be monitored, and if there are concerns of regeneration mortality as a result of browsing, building exclosures to protect aspen regeneration has been successful on the Roan and across the West (Baker et al., 1997; Kay and Bartos, 2000; Ferguson et al., 2004; Rogers and Gale, 2017).

Increasing temperature and drought conditions are a threat to the future of aspen on the Roan Plateau. The frequency, extent, and severity of ecological disturbances are increasing across many forest systems (Dutzik and Willcox, 2010; Dai, 2013; Steinkamp and Hickler, 2015) and predicted increases in temperature and drought events are believed to reduce aspen regeneration densities into the future (Romme et al. 2001; Elliott and Baker, 2004; Hanna and Kulakowski, 2012; Kulakowski et al., 2013). While higher elevation aspen may benefit from increased disturbance events, such as fires and conifer forest mortality from insects and disease (Kulakowski et al., 2013), aspen on the Roan Plateau have persisted seemingly without major disturbance and may benefit from bottom-up topographic effects of the Plateau, which may mitigate future climate conditions (Sibold et al., 2006; Dobrowski, 2011). With management considerations based on existing forest function and conditions to promote aspen regeneration, aspen will continue to persist at different extents atop the Roan Plateau.

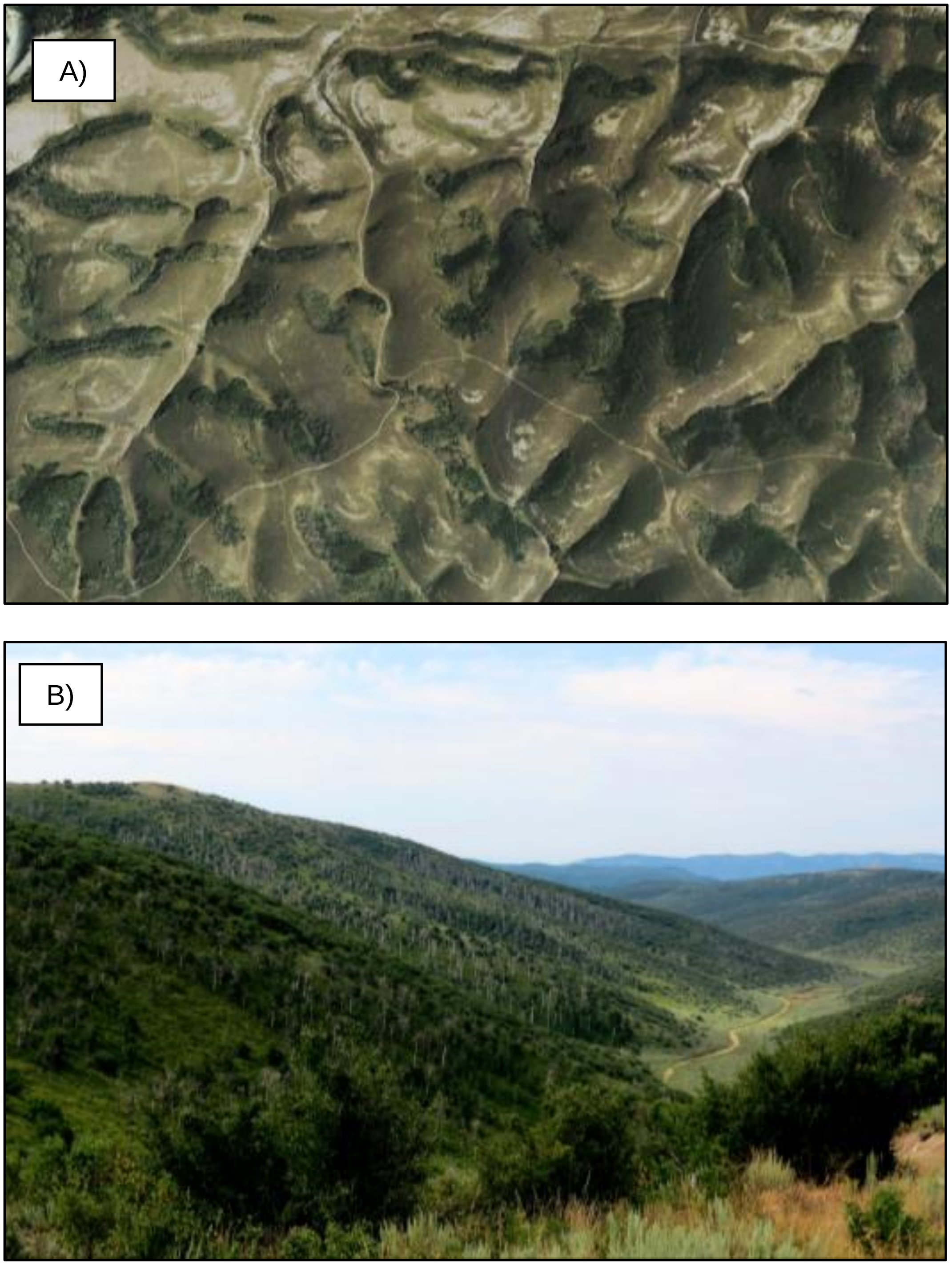
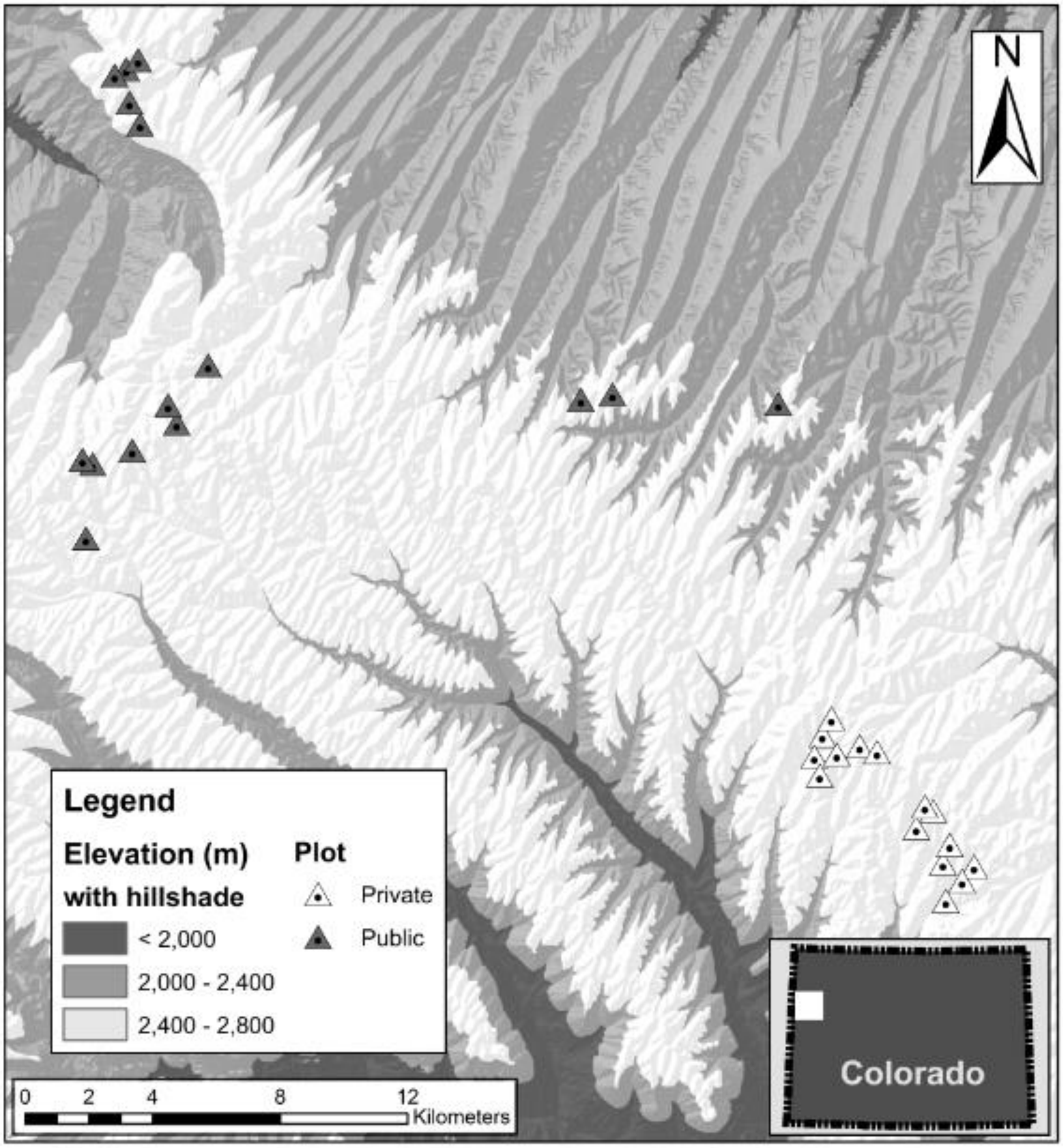


Figure 1. Island-like patches of aspen along narrow ridges atop the Roan Plateau A) depicted by green patches in Google Earth aerial imagery (2016) and B) from the ground looking south on the Plateau.



ArcGIS 10.1, Service Layer Credits: Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors
Map created by Kelsey Correia, 2017

Figure 2. Hillshade map of the study sites atop the Roan Plateau, Colorado, USA.

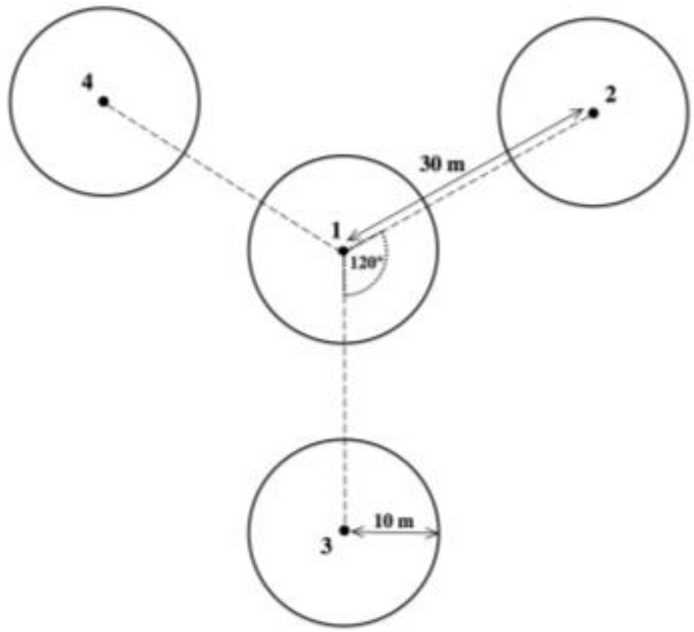


Figure 3. Study plot design. The center subplot was established first (subplot 1), and subplots 2-4 were established 30 meters from the center at 120° intervals. For the 30 plots on the Roan Plateau, each subplot had at least one aspen tree present.

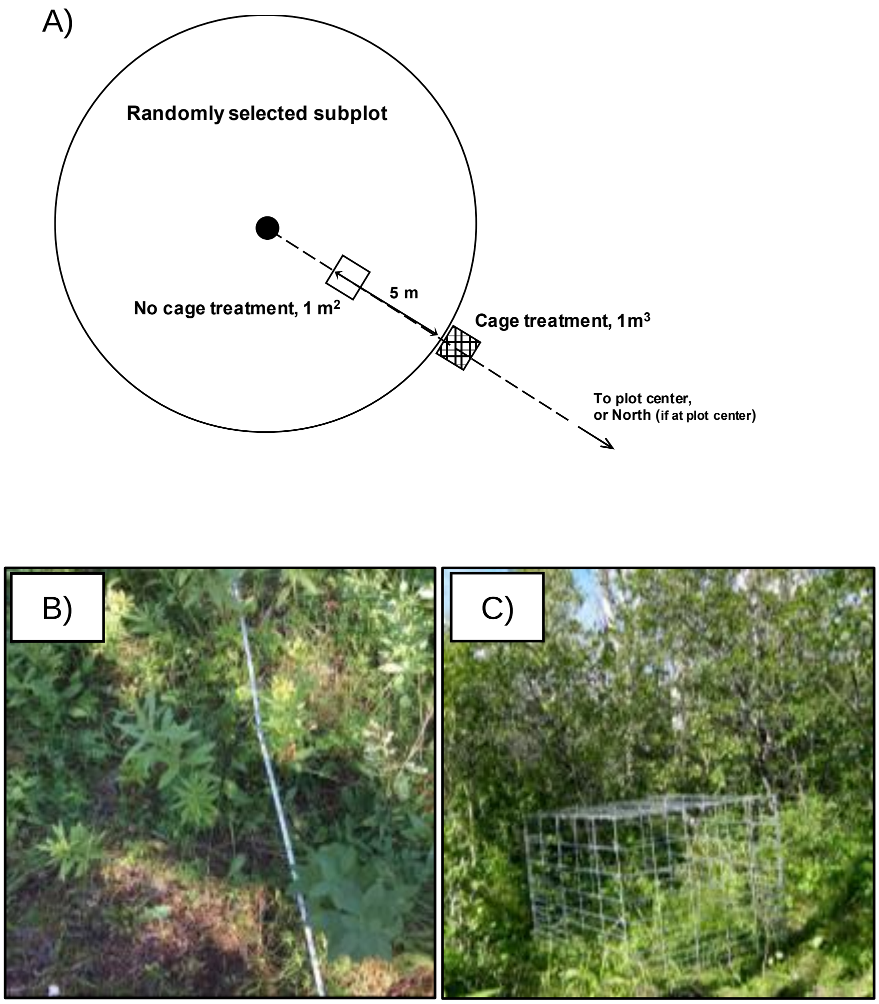


Figure 4. A) Browsing exclosure treatment design, B) photo of no cage treatment C) photo of cage treatment.

Table 1. All abiotic and biotic variables, units, and definitions.

Abiotic variable	Unit	Definition
Elevation	Meters	
Annual Precipitation	cm	PRISM 30-year normal, 2016
Annual Temperature	∘C	PRISM 30-year normal, 2016
Slope	%	Percent rise
North-ness	= *cos(*aspect*(radian))+1*	Aspect represented by a range of 0 to 2; value of 2 corresponds most north aspect and 0 being most south
East-ness	= *sin(*aspect*(radian))+1*	Aspect represented by a range of 0 to 2; value of 2 corresponds most east aspect and 0 being most west
Biotic variable	**Unit**	**Definition**
Stems	ha^{-1}	All aspen stems (live and dead) per hectare
Overstory	ha^{-1}	Live aspen stems per hectare
Mean basal area	$m^2 ha^{-1}$	Average (live and dead) aspen basal area meters^2 per hectare
Mean live basal area	$m^2 ha^{-1}$	Average live aspen basal area meters^2 per hectare
Mean dead basal area	$m^2 ha^{-1}$	Average dead aspen basal area meters^2 per hectare
Basal area mortality	%	Dead basal area/ total stand basal area * 100
Stand mortality	%	All dead or down aspen stems (>3 cm dbh) per hectare/total aspen stems * 100
Regeneration	Stems ha^{-1}	Aspen suckers (diameter < 3 cm DBH) per hectare
Oldest establishment	Year	Oldest sampled pith date age for each plot
Browsing Damage	%	Browsed suckers/total stand suckers *100

Table 2. Age distribution description and criteria. To refine the results from the cluster analysis, criteria was built based on the proportion of aspen establishment frequency by decade for each age distribution category.

Age distribution	Age distribution description	Age distribution criteria
Pulse	relatively unimodal age distribution	≥60% sample frequency in one decade (<10% others)
Continuous	Broad range of establishment	Maximum of a one decade gap between establishment periods
Multiple	Variety of tree establishment periods broken by gaps in establishment	≥2 decades between establishment periods (>10% establishment frequency)

Table 3. Average values (± 1 standard error) for plot characteristics on the Roan Plateau, Colorado, 2015.

Variable	Mean ± SE
Elevation (m)	2,556 m ± 12 m
Annual Precipitation (mm)	552.7 mm ± 10.6 mm
Annual Temperature (∘C)	5.3∘C ± 0.1∘C
Slope (%)	30.6 ± 2.6
North-ness	1.52 ± 0.1
East-ness	0.83 ± 0.1
Aspen stand basal area (%)	95.5 ± 1.0
Stems ha^{-1}	1444 ± 183
Overstory ha^{-1}	892 ± 166
Mean basal area ($m^2 ha^{-1}$)	24.9 ± 1.9
Mean live basal area ($m^2 ha^{-1}$)	13.9 ± 1.5
Mean dead basal area ($m^2 ha^{-1}$)	11.0 ± 1.0
Basal area mortality (%)	41.6 ± 3.2
Stand mortality (%)	41.8 ± 3.3
Regeneration (stems ha^{-1})	737 ± 99
Browsed (%)	44.4 ± 3.5

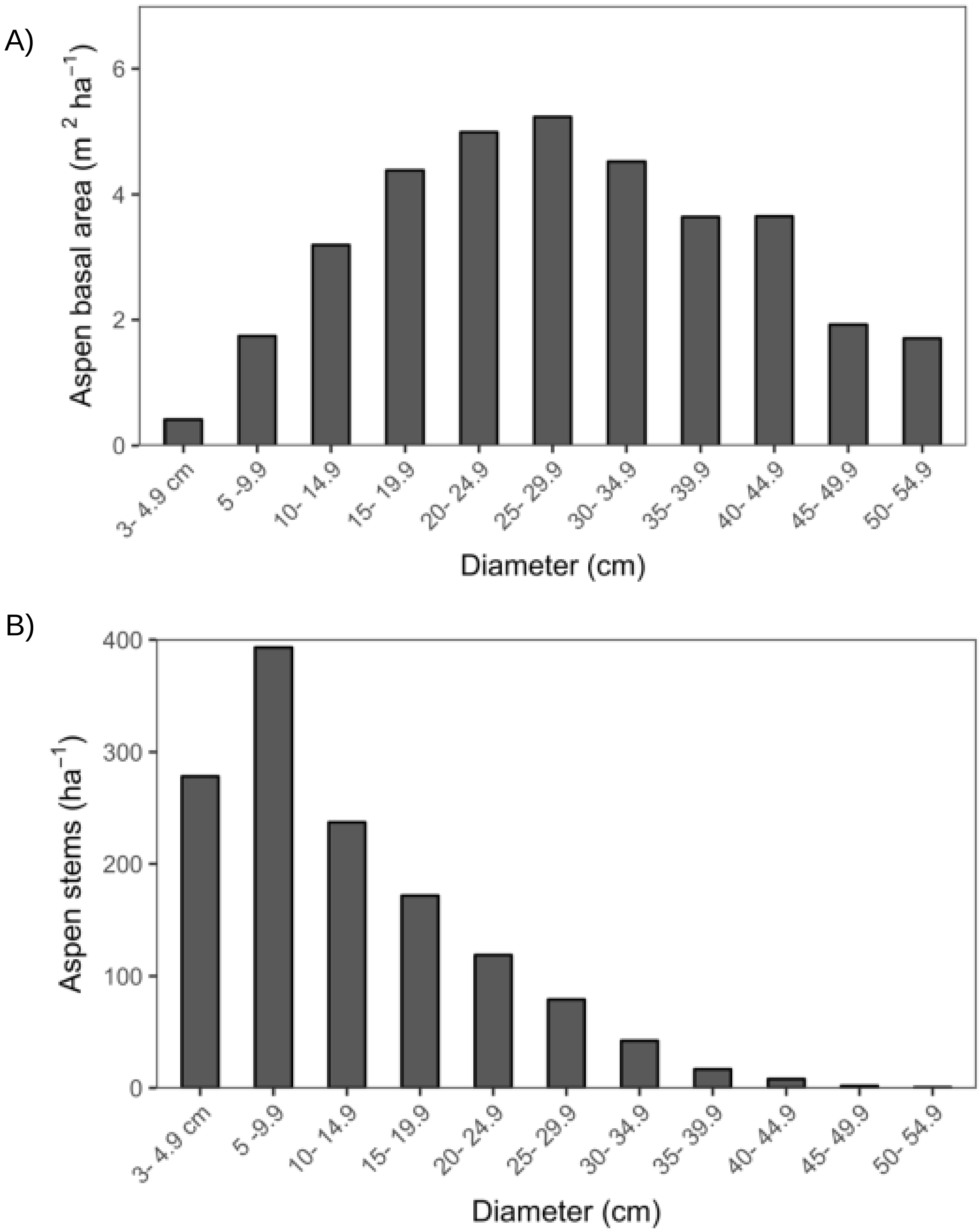


Figure 5. Aspen A) basal area (m^2 ha^{-1}) and B) trees ha^{-1} by diameter across the Roan Plateau, Colorado, 2015.

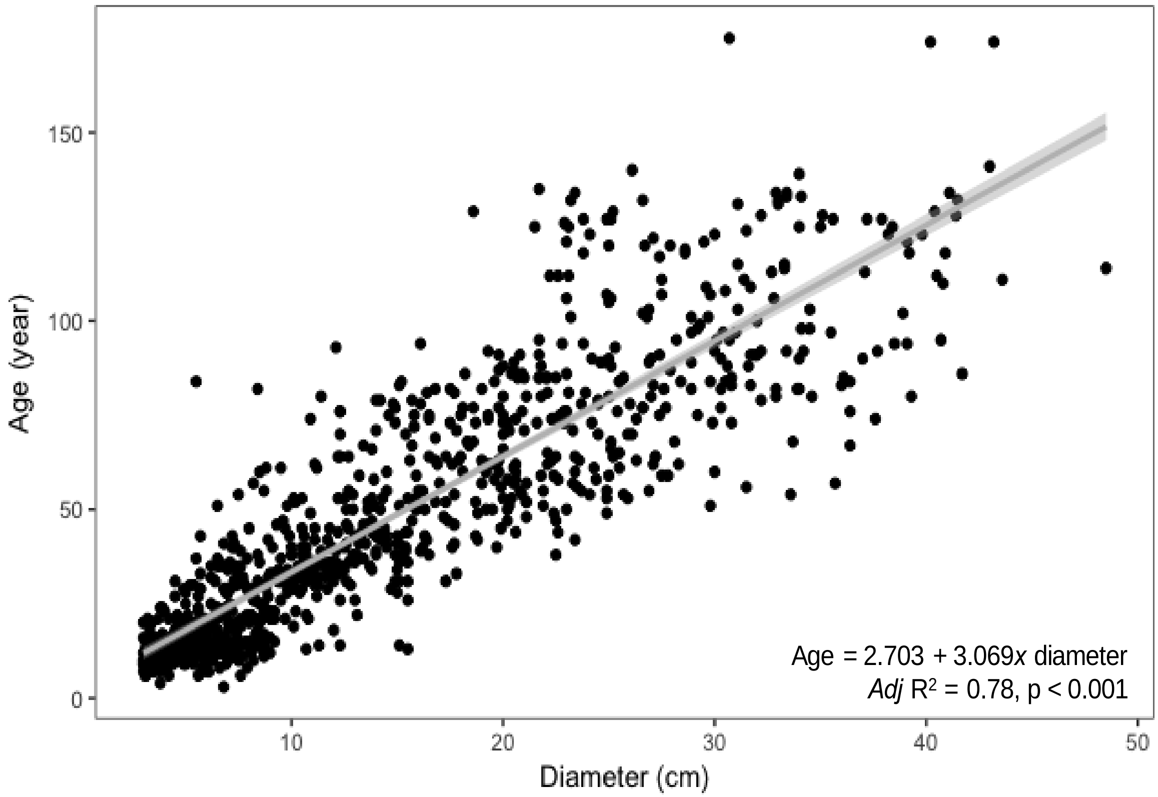


Figure 6. Relationship between tree age (year) and diameter (cm) for aspen on the Roan Plateau, Colorado, 2015; linear regression (dark gray line) with 95% confidence interval (light gray).

Table 4. Mode of establishment for plots sampled on the Roan Plateau, Colorado. The table was created with a cluster analysis of aspen stands using the sum of absolute differences by establishment frequency by decade, live basal area and dead basal area per plot. Results were manually assessed by group quality and criteria on the frequency and gaps in establishment decade.

Age distribution	**Age distribution description**	**Frequency of plots**		
		Public	Private	Total
Pulse	Relatively unimodal age distribution	1	0	1
Continuous	Broad range of establishment	13	8	21
Multiple	Variety of tree establishment periods broken by gaps in establishment	1	7	8

Table 5. Spearman's rank correlation for aspen regeneration (suckers <3 cm) and percent stand mortality against abiotic and biotic variables. Rho (ρ) and *p*-values are bold where significance exists.

	% Stand Mortality	
Variable	ρ	*P*-value
Elevation (m)	-0.002	0.994
Annual Precipitation (cm)	-0.132	0.487
Annual Temperature (∘C)	-0.006	0.975
Slope (%)	-0.042	0.827
North-ness	-0.283	0.130
East-ness	-0.358	0.052
Aspen basal area (%)	0.286	0.126
Mean basal area (m^2ha^{-1})	0.032	0.868
Mean live basal area (m^2ha^{-1})	-0.275	0.141
Browsing damage (%)	**0.493**	**0.006**
Oldest establishment (yr)	-0.280	0.134
Regeneration (ha^{-1})	**-0.548**	**0.002**

	Regeneration	
Variable	ρ	*P*-value
Elevation (m)	-0.002	0.992
Annual Precipitation (cm)	0.043	0.822
Annual Temperature (∘C)	0.089	0.638
Slope (%)	-0.008	0.967
North-ness	**0.384**	**0.036**
East-ness	-0.023	0.892
Aspen basal area (%)	-0.292	0.118
Mean basal area (m^2ha^{-1})	-0.049	0.798
Mean Live basal area (m^2ha^{-1})	0.030	0.876
Mean Dead basal area (m^2ha^{-1})	-0.247	0.188
Browsing damage (%)	**-0.368**	**0.046**
Oldest establishment (yr)	**0.400**	**0.028**
Stand Mortality (%)	**-0.548**	**0.002**

Table 6. Average values (± 1 standard error) for all abiotic variables and biotic variables, including percent aspen basal area, total, live, and dead aspen basal area, stems ha^{-1}, regeneration stems ha^{-1}, browsing damage, and oldest establishment for private and public property in the Roan Plateau, Colorado. P-values are derived from the Wilcoxon-rank sum test and is bold (*) where significant differences between the properties exist.

Variable	Public	Private	*p*-value	
Elevation (m)	2575 ± 21	2537 ± 11	**0.030**	*
Annual Precipitation (mm)	589.4 ± 16.6	516.1 ± 0.4	**0.005**	*
Annual Temperature (∘C)	5.4 ± 0.2	5.3 ± 0.1	0.709	
Slope (%)	25.1 ± 3.9	36.2 ± 2.9	**0.008**	*
North-ness	1.5 ± 0.1	1.6 ± 0.1	0.481	
East-ness	1.2 ± 0.2	0.5 ± 0.1	**0.025**	*
Aspen basal area (%)	95.7 ± 1.4	95.4 ± 1.6	0.660	
Mean BA ($m^2 ha^{-1}$)	21.5 ± 2.3	28.3 ± 2.8	0.202	
Mean Live BA ($m^2 ha^{-1}$)	13.3 ± 1.8	14.5 ± 2.3	0.935	
Mean Dead BA ($m^2 ha^{-1}$)	8.2 ± 1.0	13.8 ± 1.6	**<0.01**	*
Stems ha^{-1}	1512 ± 193	1376 ± 318	0.184	
Regeneration (stems ha^{-1})	824 ± 158	650 ± 120	0.507	
Browsing damage (%)	36.4 ± 3.3	52.4 ± 5.4	**0.026**	*
Oldest establishment (yr)	88 ± 7.3	125 ± 8.9	**0.006**	*

Table 7. Results from a fitted generalized linear model with a Gaussian distribution for all the variables selected from the AICc model dredging to predict aspen regeneration densities on the Roan Plateau. Significant variables are indicated with (*) and in bold. The intercept was -27.139.

Global Model for regeneration density predictors			
Variable	Coefficients	*p*-value	
Annual Temperature (∘C)	379.701	**0.0469**	*
East-ness	-325.984	**0.0180**	*
Stand Mortality (%)	-14.274	**0.0085**	**
Browsing Damage (%)	-8.828	0.0857	.

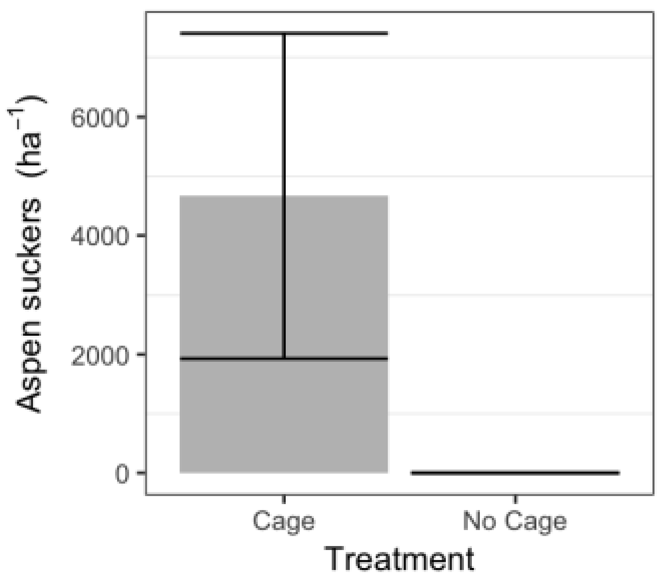


Figure 7. Difference in aspen suckering densities over a year between the caged and no cage browsing exclosure treatments with error bars.

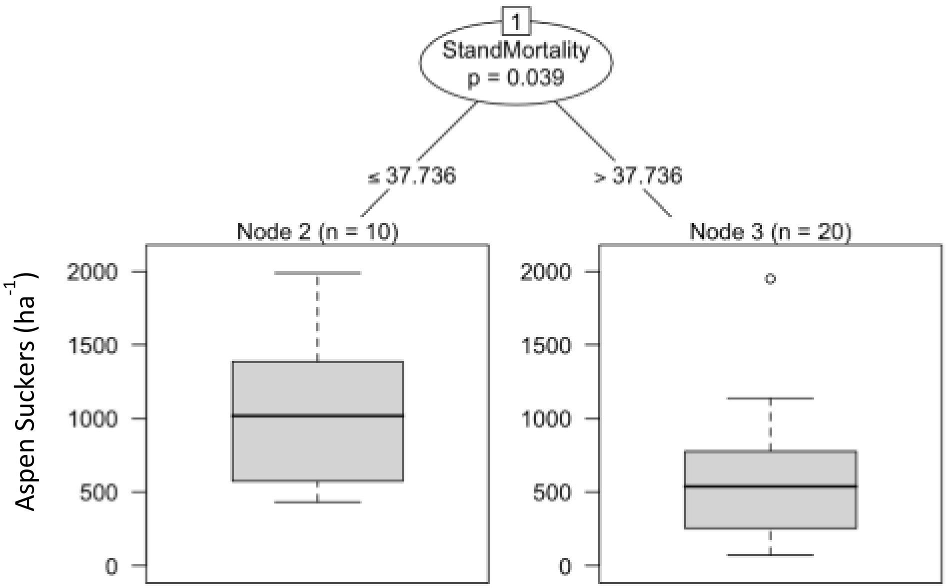


Figure 8. Regression tree illustrating the most important predictor variable (stand mortality (%)) for regeneration density along with ecological threshold (37.7%) for the Roan Plateau, Colorado. The model included all abiotic variables (elevation, annual mean precipitation, annual mean temperature, slope, north-ness, and east-ness) and two biotic variables (percent browsing damage and percent stand mortality) against aspen regeneration densities. Percent stand mortality is the proportion of dead trees in relationship the entire sampled plot. Box-and-whisker diagrams at the terminal nodes depict median (bold line) regeneration densities ha^{-1} for the threshold.

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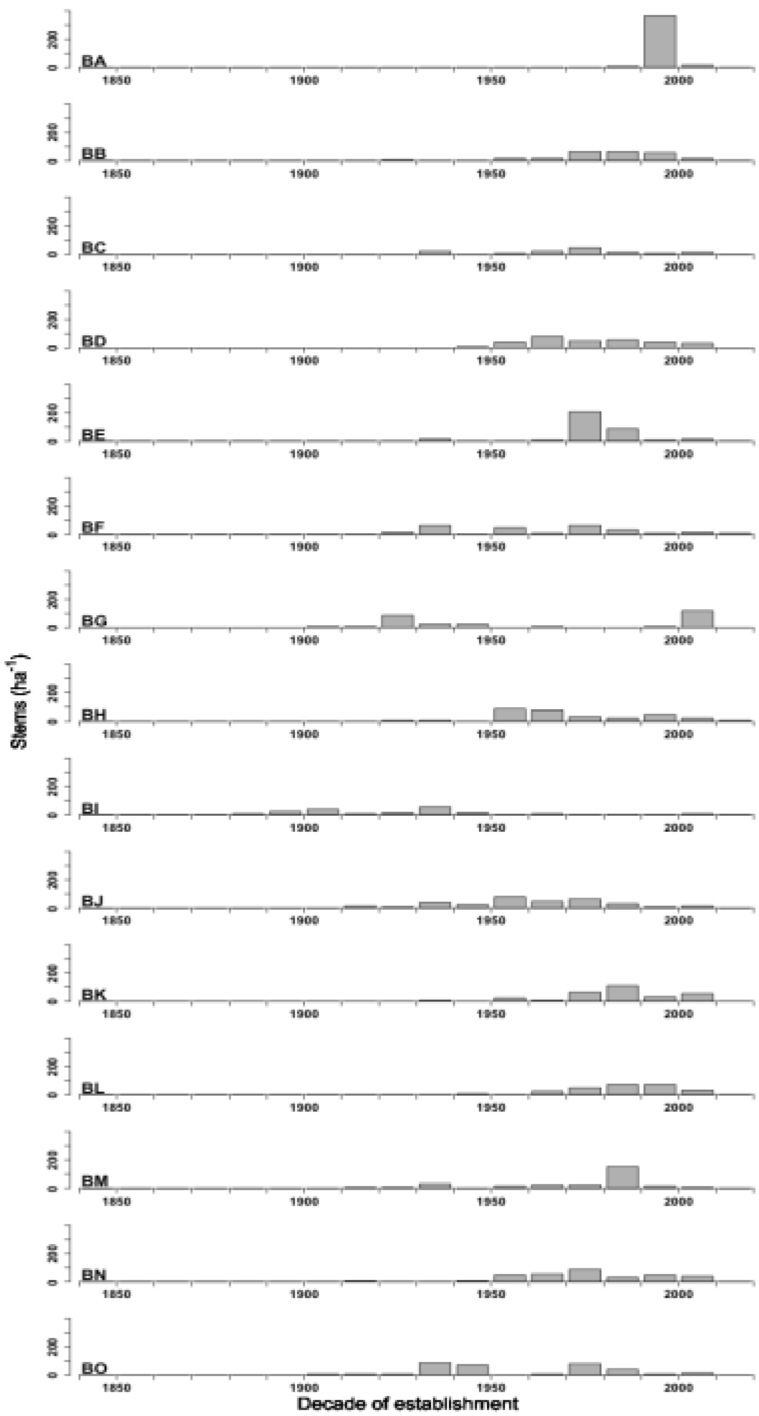
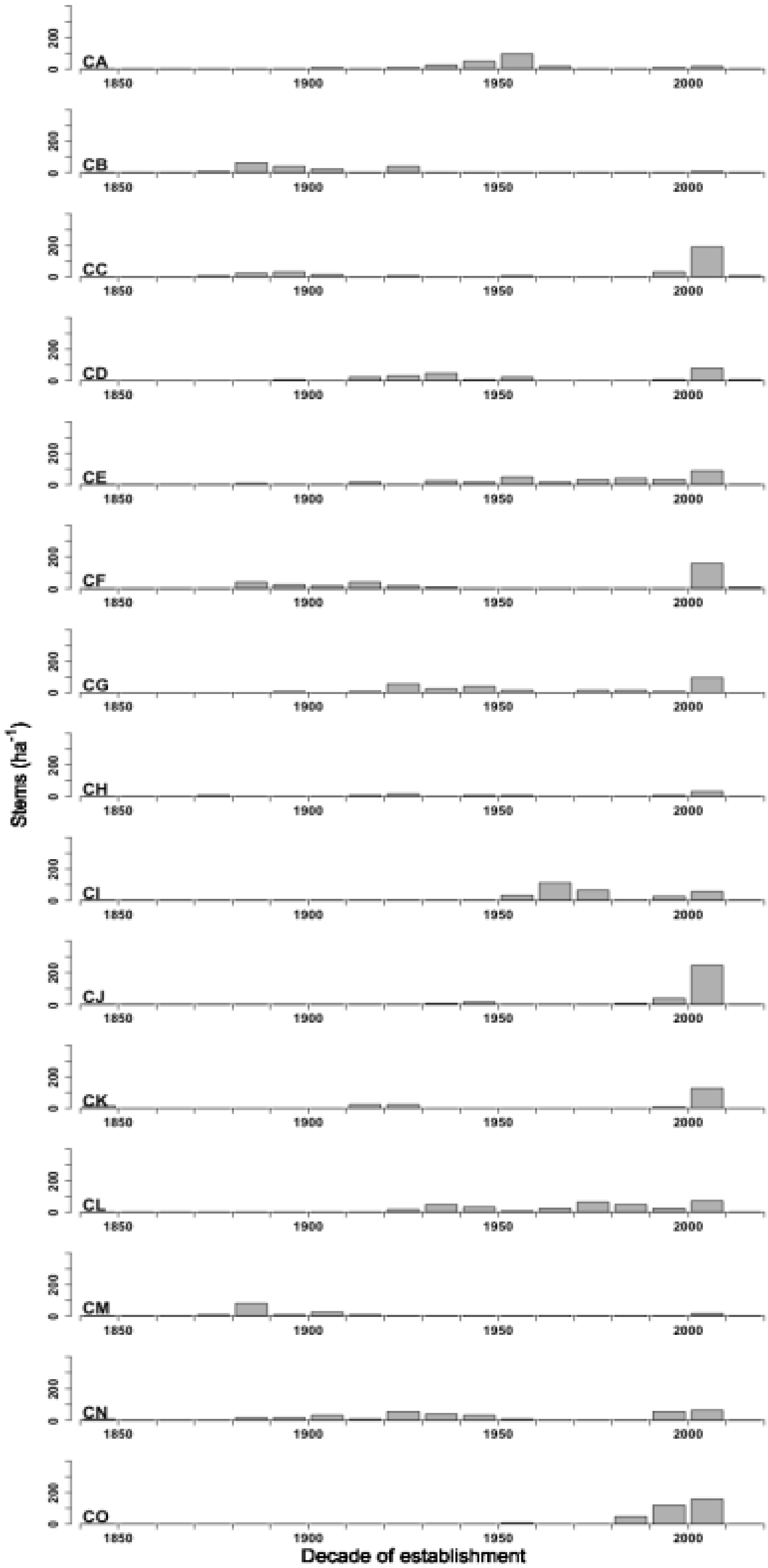
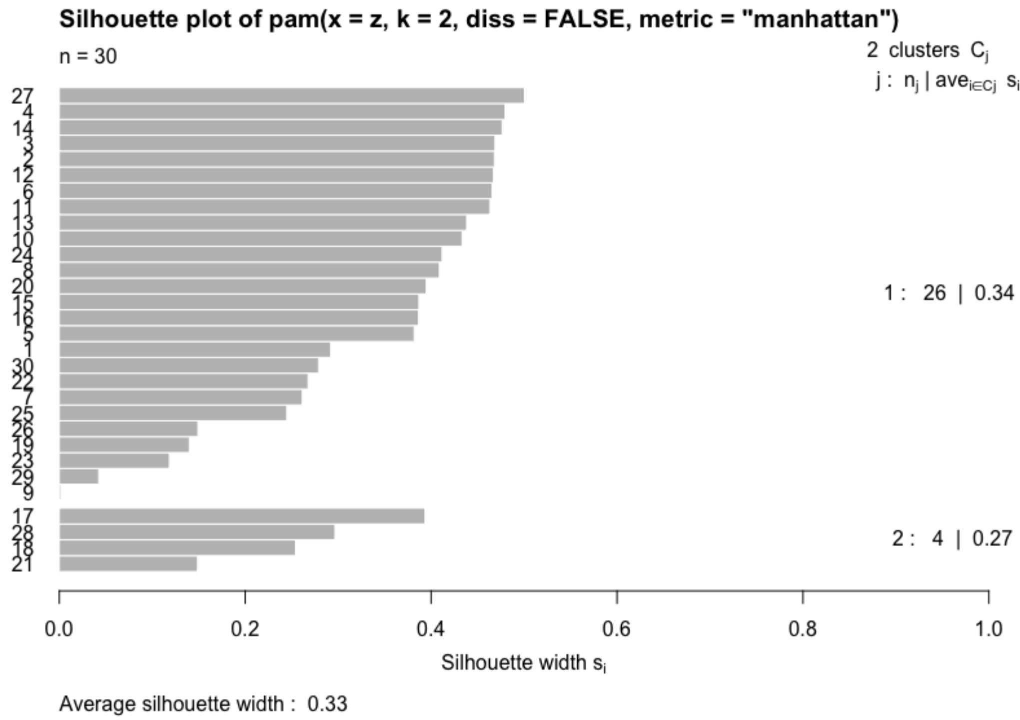
APPENDIX

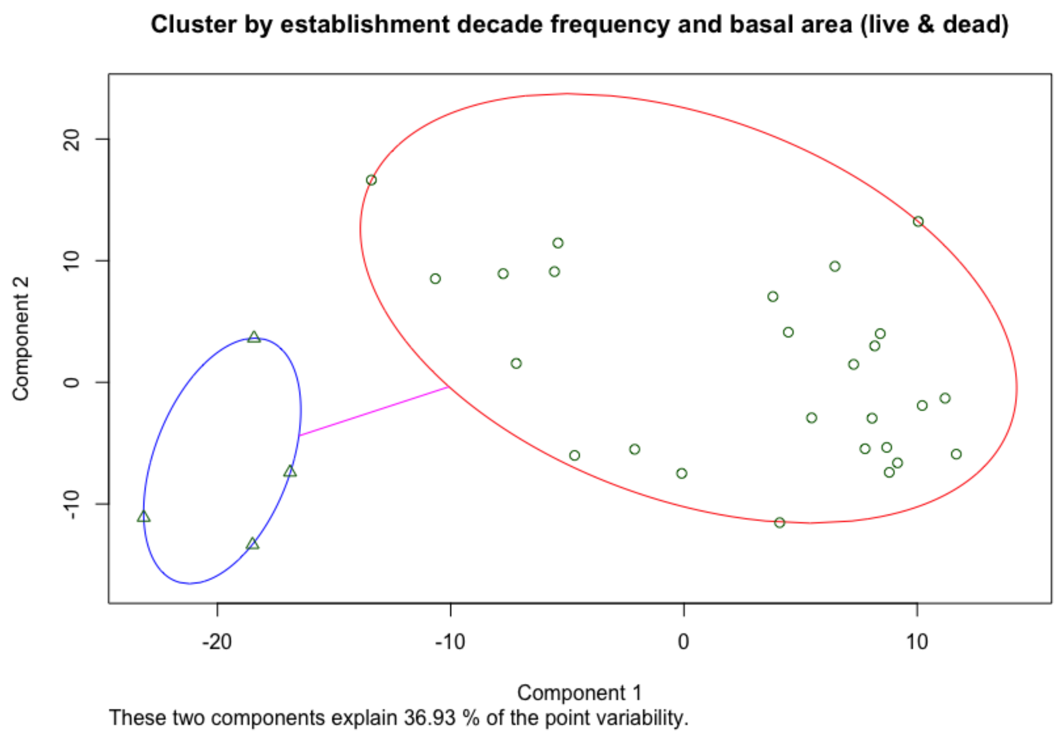


Appendix 1. Aspen age distribution (by decade) for plots sampled across the Roan Plateau, Colorado. 2015.



Appendix 1. *Continued* Aspen age distribution (by decade) for plots sampled across the Roan Plateau, Colorado. 2015





Appendix 2. Cluster analysis output