5-2014

Factors Influencing the Successful Regeneration of Aspen in Southern Utah, USA

Justin M. Britton
Utah State University

Recommended Citation

Britton, Justin M., "Factors Influencing the Successful Regeneration of Aspen in Southern Utah, USA" (2014). *All Graduate Theses and Dissertations*. 4147.
https://digitalcommons.usu.edu/etd/4147

FACTORS INFLUENCING THE SUCCESSFUL REGENERATION OF ASPEN IN SOUTHERN UTAH, USA

by

Justin M. Britton

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

James N. Long Major Professor	R. Justin DeRose Committee Member
Karen E. Mock Committee Member	Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2014

ABSTRACT

Factors Influencing the Successful Regeneration of Aspen in Southern Utah, USA

by

Justin M. Britton, Master of Science

Utah State University, 2014

Major Professor: Dr. James N. Long
Department: Wildland Resources

There has been recent concern regarding the regeneration and recruitment of aspen (Populus tremuloides) in the western United States. Forest management techniques have been employed in order to promote the regeneration and recruitment of aspen. We quantified aspen regeneration treatments in southern Utah, USA to better understand the factors driving aspen recruitment. Driving factors were identified by addressing two major research themes: (1) identify the primary ecological controls on aspen regeneration success; (2) assess the relative importance and influence of these controls on successful regeneration. Our definition of successful aspen regeneration requires the satisfaction of two criteria relating to height and density, respectively: (1) regeneration that has attained heights above the ungulate browsing threshold (e.g. >2m); and (2) regeneration that is occurring at a density that represents desired conditions for future stocking (e.g. ≥10,000 stems ha^{-1}). The primary ecological controls on regeneration success were identified using nonmetric multidimensional scaling, and Random Forests analysis was used to assess the relative importance and influence of regeneration controls. These analyses identified three primary factors that are responsible for regeneration success. These factors were (1) contemporary herbivory pressure, (2) site preparation technique, and (3) advance reproduction. Herbivory is the leading predictor of regeneration success, and has integral impacts on other primary regeneration drivers. We suggest considerations that can be made regarding regeneration drivers in order to enhance the effectiveness of aspen management in the future.

(41 pages)

PUBLIC ABSTRACT

Factors Influencing the Successful Regeneration of Aspen in Southern Utah, USA

Justin M. Britton

This study addresses critical issues and concerns relating to aspen forest management across the Intermountain West. These concerns have been raised due to the declining condition of aspen forests. As a result, aspen decline has been a topic of interest among academics and popular media outlets alike in recent years due to the economical and ecological value of aspen. Some land managers and management agencies have used forest management techniques as a means to deal with this issue. These management techniques are designed to stimulate the reproduction of aspen in order to provide a bank of seedlings and saplings for the future. This research project focuses on the effectiveness of forest management techniques in the context of many different stand conditions in order to identify what factors are most important for reproduction. Through this research we have identified three factors that are important for reproductive success, and therefore contribute to the effectiveness of forest management techniques. These findings will help land managers and management agencies by providing guidance for future management decisions.

ACKNOWLEDGMENTS

I am appreciative for the consistent guidance and support offered by Justin DeRose, Jim Long, and Karen Mock throughout the course of my graduate program. I am extremely grateful for the educational and professional opportunities granted to me during my time with USU. I would also like to thank the “NIFA Group” for fostering welcoming social and idea-pondering opportunities.

This work was funded by grants from the USU Cedar Mountain Initiative and USDA NIFA Food and Agricultural Sciences National Needs Graduate and Postgraduate Fellowship (NNF) Grants Program. These funding sources allowed me ample opportunity to share this work with the broader scientific community. Patrick Moore (U.S. Forest Service) and Sarah Shaughnessy (Utah Division of Forestry, Fire and State Lands) served as extremely valuable resources, providing great assistance regarding sample site selection. Jerrell “Jerry” Mock was a great technician and friend during the long days in the field during data collection. Lastly, this work could not have been completed without support from the friends, family, and colleagues that provided advice on countless occasions. You all have my sincere gratitude.

Justin Britton

CONTENTS

CHAPTER

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER 1

INTRODUCTION

Aspen (*Populus tremuloides*) has been the focus of ecological research for nearly a century, and has long been recognized as an ecologically and economically important forest species (Baker, 1925, 1918). A prevalent theme in the aspen literature has been concern regarding the regeneration and recruitment of aspen, particularly in the western United States. Recently, this concern has resulted in an impressive number of novel insights concerning the ecology of this species including the identification of: 1) remarkable, and unexpected, genetic diversity (Mitton and Grant, 1996; Mock et al., 2008); 2) continental-scale genetic subdivision (Callahan et al., 2013; Mock et al., 2012); 3) qualitative functional types (Rogers et al., 2014); 4) sensitivity to drought stress associated with climatic variation (Anderegg et al., 2014, 2013; Worrall et al., 2013); and 5) new recommendations for silvicultural systems (Long and Mock, 2012). Despite this large body of work few studies that integrate the regeneration ecology and management of aspen have been conducted.

In accompaniment to this long history of ecological research, recent studies of aspen have posited that it is in decline in western US landscapes, and have offered possible explanations (Bartos and Campbell, 1998; Brodie et al., 2012; Hanna and Kulakowski, 2012; Perrette et al., 2014; Rehfeldt et al., 2009; Rogers and Mittanck, 2013; Seager et al., 2013; Smith et al., 2011; Worrall et al., 2010, 2008). This putative decline, which has been termed as sudden aspen decline (SAD), has been observed throughout much of the western US, and has been attributed, in part, to many factors such as: (1) a combination of successional and demographic processes (Smith et al., 2011); (2)

lack of fire (Shinneman et al., 2013); and (3) long-term overuse by ungulates (Bartos and Campbell, 1998). Conversely, other studies have shown aspen coverage in some western landscapes to have increased over longer time periods (e.g., Kulakowski et al., 2013). These potentially contrasting viewpoints are consistent with a host of environmental drivers thought to influence the growth, mortality, and regeneration of aspen stands.

Aspen is prolific in its sprouting response to overstory removal, capable of producing thousands of shoots per hectare via vegetative suckering. Traditionally, successfully regenerating aspen was a textbook example of the simple coppice regeneration method, having long been used to guide silviculture (Baker, 1918; Long and Mock, 2012; Shepperd, 2001). Shepperd (2001) presented options for managing aspen communities such as, commercial harvest (coppice), prescribed fire, mechanical root stimulation, and the removal of vegetative competition. These management recommendations have recently been expanded to account for potential seeding events (Long and Mock, 2012).

Previously described management strategies tend to mimic ecological processes known to promote aspen regeneration commonly observed under “natural” circumstances. In this sense, the traditional coppice systems are an analog to stand-clearing disturbance (e.g. high-severity fire), which is the primary disturbance agent driving aspen regeneration in the west (Shinneman et al., 2013). Because of its dependence on disturbance for establishment and regeneration, aspen is typically characterized as an early successional or pioneer species. Like many other species that fall into this successional category, aspen is considered to be intolerant of shade (Helms, 1998). The combination of shade-intolerance and its tendency to asexually reproduce via root suckers following disturbance typically results in substantial stocking densities; for example, Smith et al. (2011) documented average sucker densities around 37,000 stems ha^{-1} seven years post-fire. Such profuse suckering has been described in the context of the disruption of important growth hormones in the plant (see Wan et al., 2006).

The ability to sexually reproduce via seed complements the sprouting nature of aspen. Once assumed to be extremely rare in the west, the successful establishment of aspen seedlings has been fairly widely documented and is no longer considered negligible (e.g., Fairweather et al., 2014; Mock et al., 2008). The bimodal regeneration capability expressed by aspen (seeding and suckering) can be compared to the "quantity versus quality" paradigm: asexual reproduction may be prolific, but all the individuals are genetically identical and susceptible to the same damage agents (i.e. disease); sexual reproduction may be intermittent and spotty, but could result in dramatically increased genetic diversity and the opportunity for future adaptation (De Woody et al., 2009; Long and Mock, 2012; Mock et al., 2008).

Although the physiology of aspen reproduction is quite well understood, investigation of regeneration drivers is needed in order to better understand their influence on aspen regeneration. In this study we quantified contemporary (i.e., last ten years) aspen regeneration treatments in order to explore factors driving aspen recruitment in southern Utah, USA. We simultaneously explore a multitude of factors that are likely to affect aspen regeneration to address two major research themes: (1) identify the primary ecological controls on aspen regeneration success; (2) assess the relative importance and influence of these controls on successful regeneration. By better understanding the influence of the primary controls on aspen reproduction we can recommend practical and effective regeneration methods.

Regardless of the origin of regeneration, ungulate herbivory is one of the most important factors influencing regeneration and recruitment in western aspen stands. Excessive herbivory from native (deer, elk) and domestic ungulates (cows, sheep) has long been recognized to negatively influence aspen regeneration (Baker, 1925, 1918; Bartos and Campbell, 1998; DeRose and Long, 2010; Kay and Bartos, 2000; Shepperd, 2001). It would be impossible to assess aspen regeneration capacity without explicitly considering the role of herbivores; however, herbivory is not the only issue impacting aspen regeneration in the West.

The overall condition or vigor of aspen stands might also influence its regeneration response. While vigor cannot be measured directly, various quantifiable surrogates can be used as indicators. For example, some landscape-level assessments of aspen have used canopy cover as a proxy to determine stand vigor (Worrall et al., 2010, 2008). Assessments at smaller scales may provide more precise assessments of stand vigor (e.g. contemporary radial increment, sapwood cross-sectional area, abundance of advance reproduction, and overstory species composition). Stand vigor dictates the rate at which regeneration attains heights above the ungulate browsing threshold (e.g., > 2 m) (Johnston, 2001). Bartos et al. (1983) asserted that stem numbers should range from 10,000-20,000 ha^{-1} at this (2m) height threshold. This threshold represents the point at which stems collectively represent recruitment for the future stand (i.e. successful regeneration).

CHAPTER 2

MATERIALS AND METHODS

2.1. Study area

The study area is located on Cedar Mountain and the Cedar City Ranger District (CCRD) of the Dixie National Forest in southwestern Utah (Fig. 1). Cedar Mountain is largely privately owned and encompassing approximately 275 km² of the Kolob Terrace formation of the Markagunt Plateau. The CCRD occupies approximately 1400 km² of the Markagunt Plateau. These physiographic provinces fall within the Colorado Plateau region, encompassing parts of Utah, Colorado, Arizona, and New Mexico. Snowfall delivered primarily by Pacific-origin westerlies comprises most of the precipitation, occurring during the months of October through April. Additionally, the study area receives monsoonal rainfall during the summer months (mid-July through September). Major forest vegetation types in the study site consist of a mosaic of aspen and aspen-conifer mixtures. Common conifer associates include: Douglas-fir (*Pseudotsuga meniesii*); subalpine fir (*Abies lasiocarpa)*; white fir (*Abies concolor*); blue spruce (*Picea pungens*); and Engelmann spruce (*Picea engelmannii*). Higher elevation sites across the Markagunt were historically dominated by Engelmann spruce (DeRose and Long, 2007) but include large areas of aspen-dominated forest. Elevation of the study sites ranged from 2400 to 3100 m a.s.l.

2.2. Study design

We sought to quantify the response of aspen regeneration to a range of silvicultural and harvesting treatment methods. Sample sites were limited to stands where

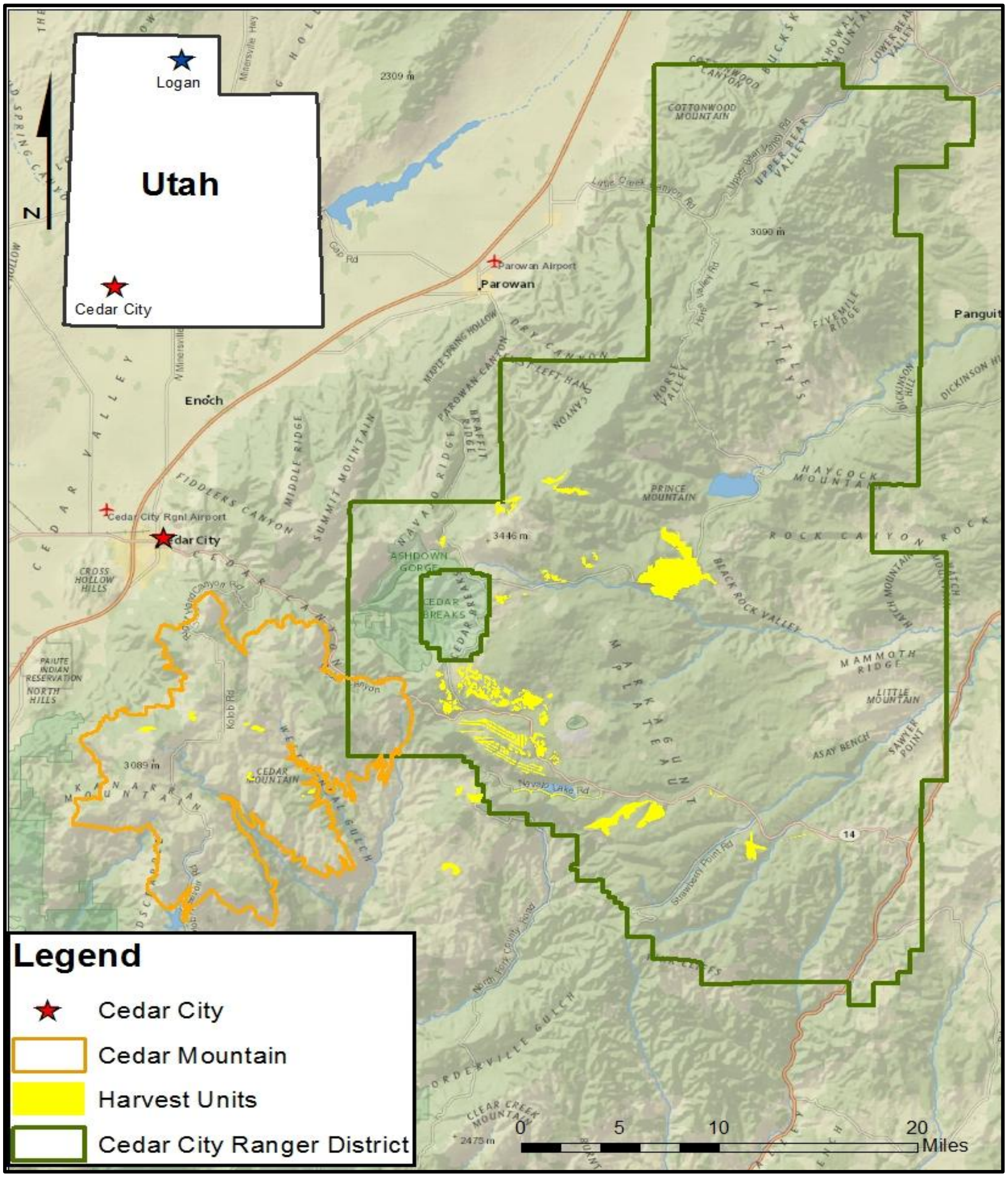


Fig 1. Map of study area. Cedar Mountain and the Cedar City Ranger District Dixie National Forest are located in southwestern Utah east of the town of Cedar City. Aspen harvest units (potential sample sites) are denoted by yellow polygons.

the goal of the treatment was to regenerate aspen. Most sample sites were also subject to silvicultural site preparation techniques. Site preparation is defined as the manipulation of a site (post-harvest), designed to enhance the success of regeneration (Helms, 1998). Aspen regeneration treatments and their associated site preparation, where conducted, occurred between the years 2001 and 2012, and therefore our sampling was retrospective. Due to this retrospective nature, treatments were only sampled if a reasonable portion of the residual stand remained intact, and field reconnaissance determined that conditions in paired plots likely represented pre-treatment conditions (see below and Fig. 2). Regeneration treatments included: prescribed fire (n=4); conifer removal (n=4); removal of declining/dead overstory aspen (n=9); and complete overstory removal or coppice (n=83). Various site preparation techniques were also implemented in the treatment units. Site preparation techniques employed were: (1) broadcast burn (n=25); (2) pile and burn (n=22); (3) relief from domestic animal browsing (n=9); and (4) no site preparation (n=44). A range of edaphic conditions (i.e. slope, aspect, and elevation) were observed across the study site (Tables 1 and 2).

2.3. Site selection and background

Site selection was guided through a collaborative effort with the USFS, the Utah Department of Forestry, Fire, and State Lands, as well as private landowners. This collaboration involved communication with land managers involved in the implementation of aspen treatments on Cedar Mountain and the CCRD. Cedar Mountain landowners are particularly interested in regenerating aspen for aesthetic purposes, and are willing to implement a variety of measures to encourage regeneration. Sheep grazing

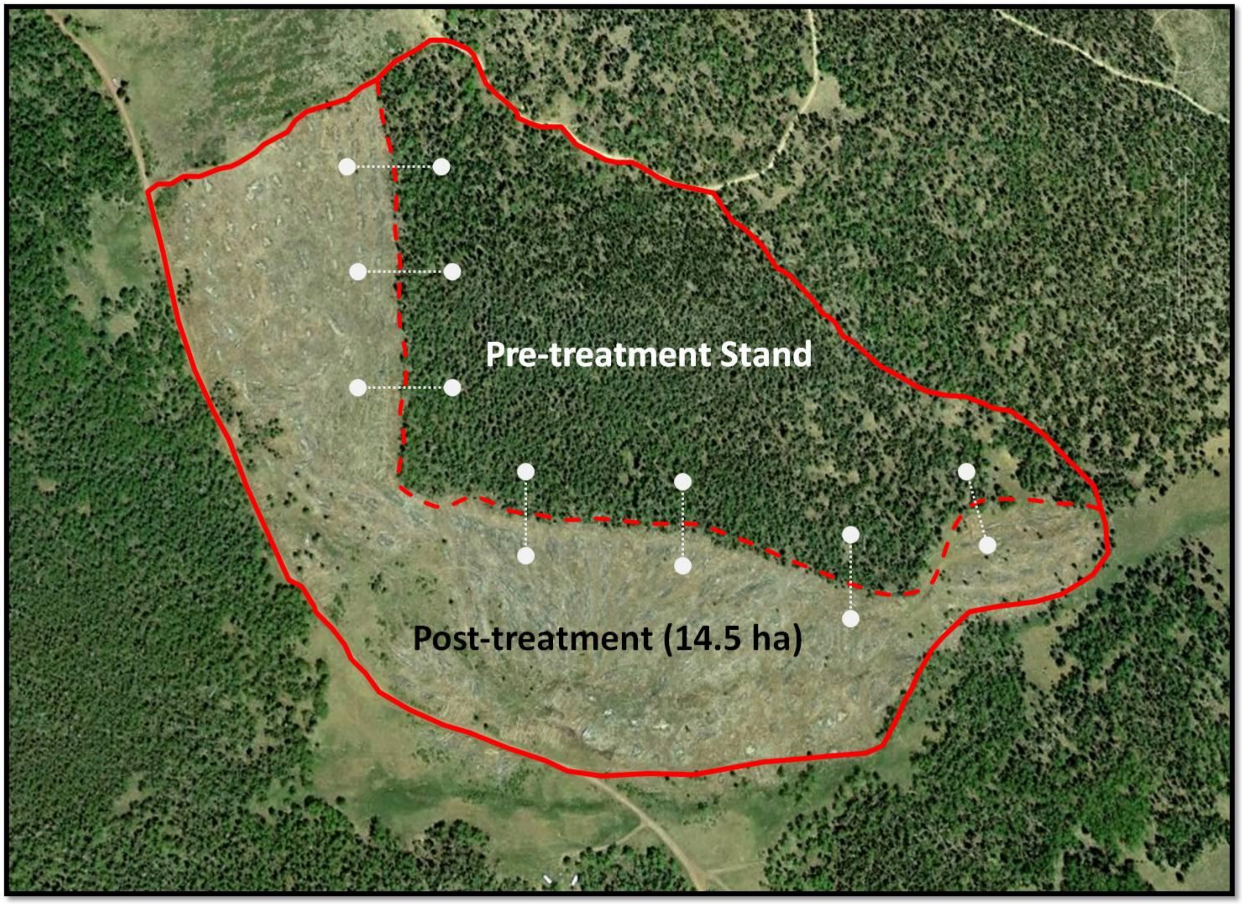


Figure 2. Example of an aspen regeneration study site with n=7 sample plot pairs (denoted by the white dots). The red outline represents the original aspen stand. A portion of that stand was removed via coppice (post-treatment), while pre-treatment representative vegetation remains. Site preparation in this case was broadcast burn. Measurements were taken in the pre-treatment plot and paired with the post-treatment response.

Table 1

Summary statistics of quantitative predictors.

*6 pre-treatment overstory plots contained no live overstory trees.

Variable	Plot Type	Minimum	Maximum	Mean	Standard Deviation
10 Year Average Radial Increment (mm)	Pre	2.73	16.21	7.85	3.89
Site Index	n/a	35.20	66.2	49.97	8.36
Cohorts of Aspen	Pre	1	2	1.32	0.47
Elevation (m)	n/a	2429	3082	2809	204.86
Slope (degrees)	slope	0.0	45.0	6.4	9.21
Percent Canopy Closure	Pre	18.75	100.0	80.06	18.19
Quadratic Mean Diameter (cm)	Pre	0.0*	47.5	22.55	9.53
Aspen Quadratic Mean Diameter (cm)	Pre	0.0*	47.5	18.48	10.72
Basal Area (m^2 ha^{-1})	Pre	0.0*	102.8	35.61	21.47
Aspen Basal Area (m^2 ha^{-1})	Pre	0.0*	83.89	24.94	19.38
Aspen Sapwood Cross-sectional Area (m^2 ha^{-1})	Pre	0.0*	46.68	12.85	10.23
Advance reproduction	Pre	0.0	45860.0	4096.0	6233.61
Non-aspen Regeneration	Pre	0.0	16300.0	2038.0	2830.58
	Post	0.0	4586.0	565.5	1090.84
Herbivory Index	Pre	0.0	1.0	0.60	0.38
	Post	0.0	1.0	0.42	0.39
Treatment Unit Size (ha)	Size	5.0	200.0	66.91	49.30
Successful Regeneration	Post	0.0	103900.0	7454.0	14574.0
Total Sapwood Cross-sectional Area (m^2 ha^{-1})	Pre	0.0*	50.69	17.11	10.95

Table 2

Qualitative predictors of aspen regeneration.

Variable	Description
Management	The silvicultural treatment that was implemented; i.e. prescribed fire (n=4), conifer removal (n=4), removal of declining/dead overstory (n=9), complete overstory removal (n=83).
Treatment Year	Calendar year in which silvicultural treatment was implemented; 2001-2012
Site Preparation	Site preparation implemented to encourage aspen regeneration after initial management (i.e. broadcast burn (n=25), pile and burn (n=22), domestic animal relief (n=9), no site preparation (n=44)
Ownership	Private (n=43) or public ownership (n=57).
Aspect	Compass direction that a topographic slope faces, measured in degrees from north.
Stand Condition	Evaluation of the stand condition regarding overstory composition; i.e. pure (n=7), pure declining (n=16), mixed (n=48), and mixed declining (n=29). Stands were deemed declining if > 50 % of aspen overstory was dead.

is also prevalent on Cedar Mountain stemming from multi-generational family tradition (Bowns and Bagley, 1986). Aspen management on the CCRD was motivated by the previous decade's spruce beetle (*Dendroctonus rufipennis*) epidemic, which has fostered interest in promoting aspen on the landscape (Patrick Moore, USFS, personal communication).

2.4. Ungulate pressure

Ungulate pressure within the study area has been well documented (Bowns and Bagley, 1986; DeRose and Long, 2010; Kay and Bartos, 2000). Both wild and domestic ungulates contribute to herbivory on aspen. Wild ungulate species include deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*), while sheep (*Ovis aries*) and cattle (*Bos spp*.) constitute the domestic ungulates. It has been suggested that this congregation of ungulate species, at high densities, may increase herbivory on aspen (DeRose and Long, 2010). Landscape level assessments of the study site indicate problems with successful aspen recruitment due, at least in part, to herbivory (DeRose and Long, 2010; Rogers et al., 2010). Further, past research suggests that Cedar Mountain has been subjected to long-term grazing, primarily from domestic sheep, which has altered herbaceous understory communities (Bowns and Bagley 1986). Although Bowns and Bagley (1986) focus on the herbaceous component of the understory, regeneration within aspen stands would also have been subject to browsing.

2.5.Sampling

Seventeen geographically distinct aspen regeneration treatments were measured, yielding a total of 100 paired sample plots. The number of plots measured at each treatment varied (3 to 12 treatment^{-1}) according to the area remaining in the residual stand (1 to 20+ ha). Due to observed inherent stand heterogeneity, each plot pair was considered an individual sample. A plot pair consists of two primary plots; (1) a pre-treatment plot (representing a reference condition), and (2) a post-treatment plot (representing the response to treatment) (Fig. 2). Each primary plot consisted of two sub-plots: (1) an overstory plot and (2) a regeneration plot. Plot pairs were at least 50 meters apart in order to minimize spatial autocorrelation. Pre-treatment overstory plots were located randomly within the adjacent unharvested (reference) aspen stand, and care was taken to avoid any obvious inconsistencies with the surrounding stand conditions. Post-treatment plots were selected by entering the treatment unit a minimum of 50 m while holding edaphic attributes (i.e., slope, aspect, and elevation) constant with those of the pre-treatment pair. Sub-plots consisted of a 5 m fixed-radius overstory plot in combination with a nested 2.5 m fixed radius regeneration plot for regeneration quantification (trees < 10 cm DBH). Within overstory plots, each tree greater than 10 cm diameter at breast height (DBH) and height(s) (total and base of the live crown) were measured, and species, and status (dead or alive) were noted. Post-treatment overstory plots were only measured when treatment did not completely remove the overstory (n=17).

From the overstory plot-level data we calculated metrics for use as potential predictors of aspen regeneration. Quadratic mean diameter (QMD) is a measure of central tendency which is considered more appropriate than arithmetic mean diameter for characterizing stand data due to its practical advantage of being directly related to basal area (Curtis and Marshall, 2000). Species-specific and total basal area were also calculated from the tree-level data, and provided a basis of comparison for productivity and growth rate. A spherical densiometer was used to obtain a general measure of canopy closure and overall condition. Two increment cores were extracted from each live tree at breast height. Increment cores were used to determine stand ages, site index, radial increment, and sapwood cross-sectional area; all measures that could describe stand vigor. Aspen sapwood was reliably discerned and marked in the field by holding the extracted core to the sky, orienting the cells such that sunlight passed through, allowing the sapwood boundary to be easily distinguished from the heartwood (Table 1) . Qualitative plot characteristics were also noted (Table 2).

Regeneration plots were used to quantify the focal dependent variable for this study. The focal dependent variable in this study was “successful” aspen regeneration, more specifically, regeneration that has attained heights above the browsing threshold and occurring at densities conducive to desired future stocking (i.e. 10,000 stems ha^{-1}). Regeneration was recorded and classified according to three height classes designed to represent critical stages in the regeneration process, respectively: 1) aspen stems <1m in height (i.e. aspen stems that are wholly susceptible to damage by all ungulates), 2) aspen stems 1-2m in height (i.e. stems that have partially exceeded the browsing threshold height for sheep and deer), and 3) >2m in height (i.e. stems that have fully escaped browsing threat of all ungulates and thereby represent ‘successful’ recruitment). The browse status of the terminal bud (browsed, unbrowsed) was also ascertained, and used to develop an herbivory index. This index is a ratio of browsed stems to total stems within the plot. This metric provided strong indication of contemporary browsing pressure. All aspen stems less than 10 cm DBH and > 2 m in HT were considered successful regeneration, i.e. the dependent variable in our analyses. This upper diameter limit served as a standard cutoff for sampling regeneration. Because our sampling design resulted in aspen regeneration data from treatments that had occurred over the last decade, we expected the data to provide inference specifically relating to how aspen regeneration responds to varying management conditions over time, thus allowing us to suggest management prescriptions suitable for projected future circumstances.

2.6. Analytical methods

2.6.1. Nonmetric multidimensional scaling

To explore ecological controls on aspen regeneration success (Theme 1) we used nonmetric multidimensional scaling (NMS). NMS is an ordination technique that is used to find structure in complex, non-parametric data, and is particularly well suited for ecological data (Clarke, 1993). We used NMS to explore potential controls on aspen regeneration across our study area. Twenty-five plot-level variables (Tables 1 and 2) measured on the 100 sample plots constituted the primary matrix in our NMS analysis. We used the PC-ORD software to conduct NMS and produce related graphical outputs. Sorensen distance measure was used for a total of 500 runs, and stability was assessed by plotting a graph of stress vs. number of iterations. Highly correlated variables were overlain on an ordination joint plot showing the results of the NMS.

2.6.2. Random forests

We tested the predictability of successful regeneration as well as the relative influence/importance of the identified ecological controls (Theme 2) using Random Forests (RF) analysis. Random forests is a powerful statistical classifier that has been successfully implemented in ecological applications (Cutler et al., 2007). Advantages of this classifier include (1) very high classification accuracy; (2) a novel method of determining variable importance; (3) ability to model complex interactions among predictor variables; (4) flexibility to perform several types of statistical data analysis, including regression, classification, survival analysis, and unsupervised learning; and (5) an algorithm for imputing missing values as discussed by Cutler et al. (2007). RF analysis was performed using the randomForest package in R (R Development Core Team). 10-fold cross-validation was used to evaluate model accuracy. Five-classification accuracy parameters are reported (Table 3). These include: (1) Percent correctly classified (PCC) denoting the percentage of observations correctly classified; (2) Specificity is the percentage of regeneration failures correctly classified; (3) Sensitivity is the percentage of sites with successful regeneration that were correctly classified; (4) Kappa (K) is a measure of agreement between predicted presences and absences with actual presences and absences corrected for agreement that might be due to chance alone; and (5) Area under the curve (AUC) is the area under the receiver operating characteristic (ROC) curve.

We used this analytical tool to determine the predictability of regeneration controls, using successful aspen regeneration as the dependent variable. High predictability pointed us in the direction of “important” determinants of aspen regeneration, and their general influence on regeneration success. A variable importance plot and partial dependence plots were constructed to aid in the visualization of these relationships. The variable importance plots show the relative importance of a given variable in predicting successful regeneration by way of that variable's effect on prediction accuracy (Cutler et al., 2007).

Table 3
10-fold cross-validated accuracy of the random forests model. PCC denotes the percentage of observations correctly classified, and AUC is the area under the ROC curve. Specificity is the percentage of regeneration failures correctly classified. Sensitivity is the percentage of sites with successful regeneration that were correctly classified.

PCC	Specificity	Sensitivity	Kappa	AUC
85.00	93.30	60.00	0.64	0.9

CHAPTER 3

RESULTS

3.1. Ecological controls on aspen regeneration

The NMS ordination produced a two-dimensional (i.e. axes) solution with a final stress of 13.35 (instability < 0.001). Seventy-one iterations (maximum = 500) were required to reach stability. Monte Carlo test results indicated that the two-axis solution using real data was significant ($P = 0.004$). Two axes explained the majority of the variability in our data set (Axis 1: $r^2 = 0.68$, Axis 2: $r^2 = 0.21$; total $r^2 = 0.89$, orthogonality = 97.0%, Fig. 3). Successful regeneration and the herbivory index were nearly diametrically opposed on the first NMS axis, which suggested a strong negative influence of herbivory on recruitment. Pre-treatment advance reproduction (hereafter referred to as advance reproduction) was less strongly related to axis 1; however, was positively aligned with successful regeneration (Table 4). Axis two represented elevational trends among sample sites particularly related to ownership, and thus, species composition (Table 4). For example, low elevation sites were characterized by pure aspen stands and private ownership, whereas mixed stands were common among higher, publicly managed sites (Table 4).

3.2. Relative importance of ecological variables

RF consistently identified three variables as being most important for predicting regeneration success: (1) post-treatment herbivory index; (2) site preparation technique; and (3) aspen advance reproduction (Fig. 4, Table 4). Partial dependence plots revealed the nature of the relationship among important variables and successful regeneration.

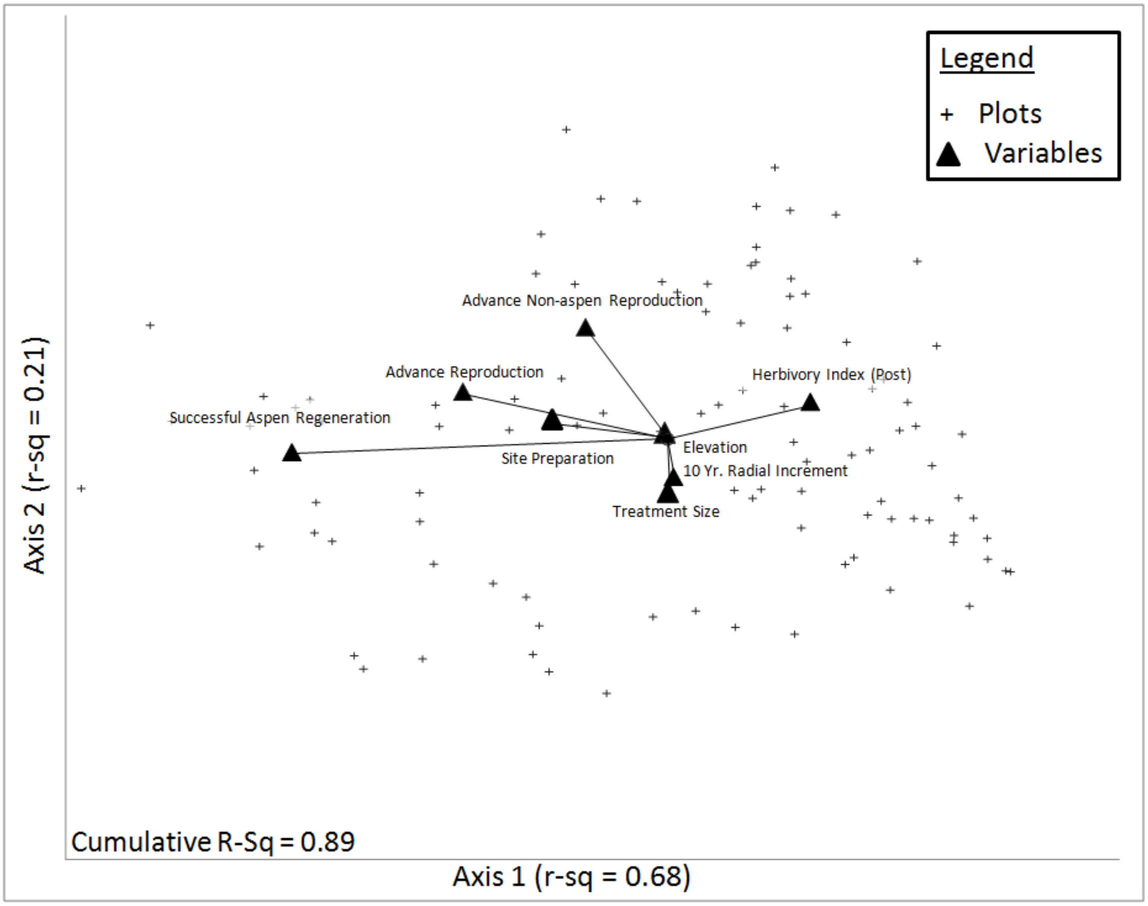


Fig. 3. Nonmetric multidimensional scaling results. Results are shown in a joint plot that highlights aspen regeneration drivers within our data set. Vectors with > 0.5 or < - 0.5 Pearson coefficient (r) value (Table 4) are showed in relation to plot space. Axis 1 explains variation in regeneration response where ungulate herbivory and “successful” regeneration occupy the opposing extremes of the axis. Axis 2 displays trends related to elevation among sample plots.

Table 4
Pearson coefficients (r) between variables and ordination axes. Strong response variables are in bold, r > 0.5 or r < - 0.5.

Variable	*r-Value* **Axis 1**	 **Axis 2**
Successful Regeneration (Post)	**- 0.798**	- 0.266
10 Year Radial Increment	0.094	**- 0.538**
Site Index	0.331	- 0.448
Treatment Size	0.043	**- 0.538**
Treatment Year	0.114	0.211
Aspen Cohorts (Pre)	0.062	- 0.362
Elevation	- 0.220	**0.627**
Slope	0.015	- 0.191
Azimuth	0.092	- 0.077
Aspen QMD (Pre)	- 0.136	- 0.200
QMD (Pre)	- 0.066	- 0.046
Aspen Basal Area	- 0.121	- 0.011
Aspen Sapwood Cross-sectional Area	- 0.194	- 0.116
Total Trees ha^{-1} (Pre)	- 0.159	0.274
Aspen Trees ha^{-1} (Pre)	- 0.180	- 0.098
Total Basal Area	- 0.019	0.217
Total Sapwood Cross-sectional Area	- 0.188	0.096
Advance Aspen Reproduction	**- 0.608**	0.102
Advance Non-aspen Reproduction	- 0.286	**0.553**
Herbivory Index (Pre)	0.340	- 0.085
Canopy Density (Pre)	- 0.182	0.316
Herbivory Index (Post)	**0.607**	0.425

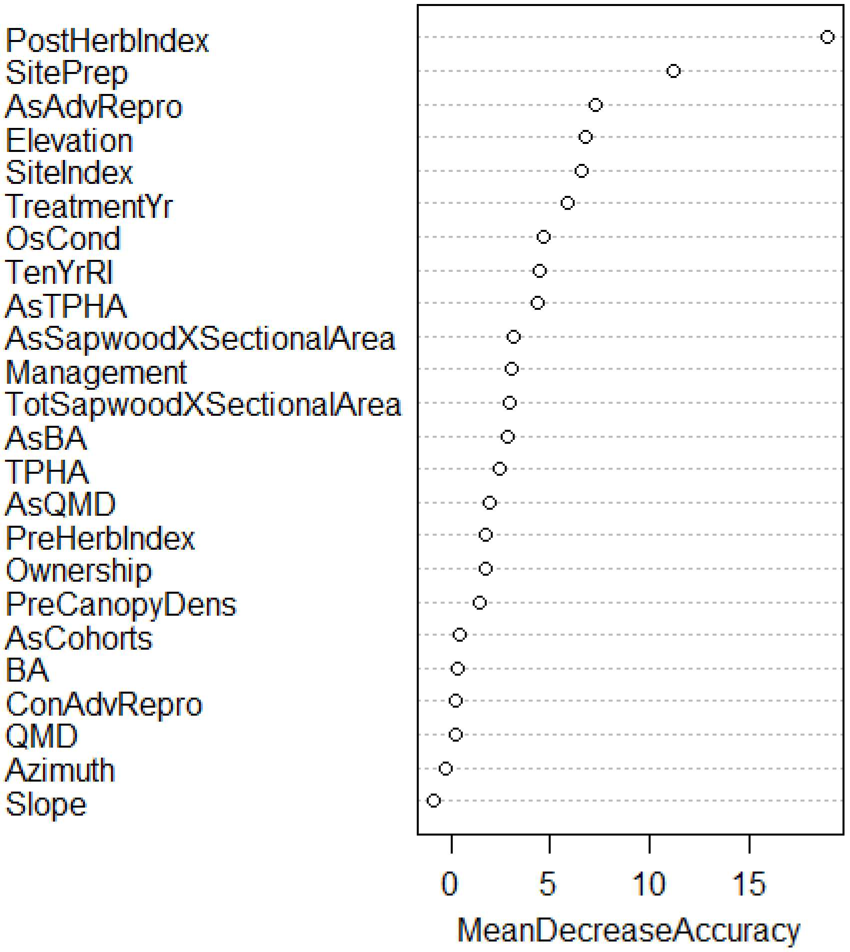
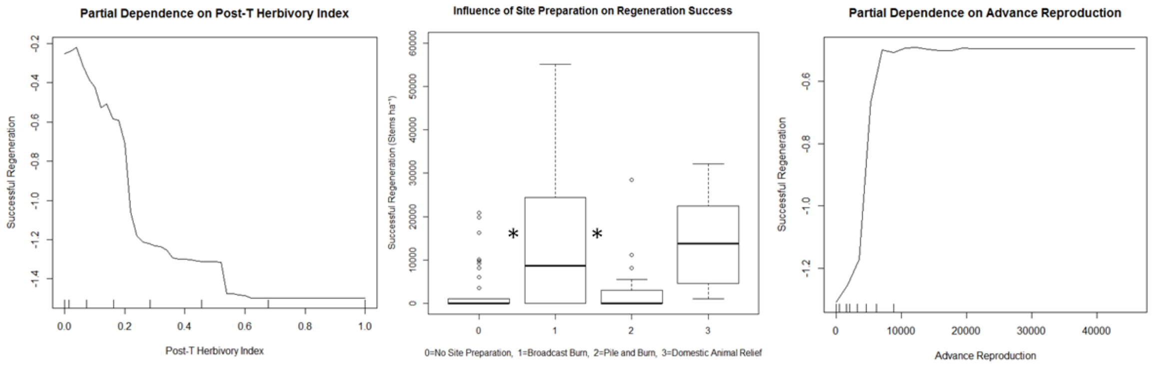


Fig. 4. Variable importance plot from random forests (RF) classification. Variables are used for predicting the successful regeneration of aspen. Higher values of mean decrease in accuracy indicate variables that are more important to the classification.

Post-treatment herbivory index had the most influence on successful regeneration response and demonstrated a strong negative relationship (Figure 5A). Site preparation techniques also influenced regeneration response where broadcast-burned plots had significantly more aspen stems per hectare (Figure 5B). Lastly, the presence of advance reproduction of aspen was identified as a prominent predictor of regeneration success indicated by the positive relationship (Figure 5C).

Pre-treatment aspen trees ha^{-1} (AsTPHA), sapwood cross-sectional area (ASWA), overstory condition (OSCOND), and live basal (ALBA) were weakly negatively correlated with the primary NMS axis (Table 3), and contributed moderately as a predictor of successful regeneration (Figure 4).



a. b. c.

Fig. 5. Partial dependence plots for important variables. These variables are consistently identified as important for random forests (RF) predictions of successful regeneration. Partial dependence is the dependence of the probability of regeneration success on one predictor variable after averaging out the effects of the other predictor variables in the model (Cutler et al., 2007). Raw data shown for Site Preparation; significant differences between site preparation techniques are denoted by an asterisk ($P < 0.05$).

CHAPTER 4

DISCUSSION

The exploration of ecological controls on aspen regeneration in response to management in southern Utah resulted in a meaningful characterization of relatively simple factors that might be highly applicable to aspen stand management. Additionally, this study provides an integrative evaluation of contemporary silviculture in aspen systems that improved our understanding of the factors governing successful aspen regeneration. Specifically, our results indicate that relatively few factors are responsible for driving post-treatment recruitment of aspen. In stands subject to contemporary silviculture (1) the presence of advance reproduction is a prominent indicator of regeneration potential, (2) broadcast burning as a site preparation technique greatly increases the likelihood of successful regeneration, and (3) post-treatment herbivory exhibits substantial influence on successful regeneration. Thoughtful consideration of these factors in the context of silvicultural activity should increase the successful regeneration of aspen in the region.

The importance of advance reproduction on successful aspen regeneration was an unexpected result. We are unaware of any accounts in the aspen literature relating the presence of advance reproduction to future regeneration potential. While the presence of advance reproduction prior to treatment could, in part, directly contribute to future stand stocking, this metric likely also represents an integration of factors that contribute to successful suckering response. Primarily, advance reproduction may be an indicator of stand vigor and regeneration potential, as well as relatively contemporary browsing pressure from herbivores. Aspen stands that have experienced long disturbance-free intervals have been documented to demonstrate continuous regeneration, which in our data represent stands with advance reproduction (Kurzel et al., 2007). Indeed, our data show that stands characterized by abundant advance reproduction tend to be predictive of vigorous regeneration response to treatment (Figs. 4 and 5c). However, regardless of response, herbivory has severe negative consequences on regeneration (Figs. 4 and 5a), and identifying this potential risk of damage prior to treatment is extremely important. Specifically, advance reproduction heights below the ungulate browsing threshold (~2 meters) should elicit concern for the immediate future (i.e., post-treatment). Similarly, in stands where advance reproduction has already attained heights above this threshold, the concern of browsing pressure could be relaxed.

This is not the first study to offer ecological explanations regarding the condition of aspen within the larger region, and in the presence of considerable browsing pressure (e.g. DeRose and Long, 2010; Mittanck, 2012; Oukrop et al., 2011; Rogers et al., 2010; Tshireletso et al., 2010). For example, Cedar Mountain, Utah has been the subject of research over the past two decades, some of which concluded that the current aspen decline was a permanent shift (Worrall et al., 2013). For example, a recent evaluation suggested that the amount of recruiting stems present on Cedar Mountain were not capable of perpetuating the aspen type (Rogers et al., 2010). Our study clearly identified herbivory as the strongest deterrent to the establishment of successful aspen regeneration (Fig. 3, Table 4). Previous research has suggested browsing issues based on experiments that involved a comparison of sites with protected aspen regeneration versus those without protection (Brodie et al., 2012; Kay and Bartos, 2000; Mueggler and Bartos, 1977). DeRose and Long (2010) observed ample successful aspen regeneration on the

Markagunt Plateau centered in lava flow substrate that effectively serves as a natural refugium from herbivores. Deliberate ungulate exclosure experiments have reported complimentary findings (Brodie et al., 2012; Kay and Bartos, 2000; Kota and Bartos, 2010; Mueggler and Bartos, 1977). Rogers et al. (2010) did not identify herbivory as a definitive cause of reproductive failure in aspen on Cedar Mountain, although the possibility was acknowledged. In contrast, our results suggest that herbivory could be the leading proximate cause of reproductive failure in study area, including Cedar Mountain.

Rogers and Mittanck (2013) also reported strong effects of herbivory in the Book Cliffs region of eastern Utah and Western Colorado, a more remote area that has a climate similar to our study area. Among the host of potential environmental variables assessed, herbivore use of aspen habitat was identified as the primary factor limiting aspen recruitment in the Book Cliffs region. The authors asserted that pre- and post-treatment monitoring is necessary to evaluate management effectiveness in restoring appropriate levels of aspen regeneration to a site (Rogers and Mittanck, 2013). Though retrospective, the present study satisfied this recommendation, and provides additional support with respect to identifying the onset and amount of herbivory pressure (herbivory index).

Our data show that site preparation techniques influence regeneration response (Figs 3 and 5b). Shepperd (2001) suggested that the combination of site preparation, particularly prescribed fire (broadcast burning), and manipulation treatments (e.g. harvesting), greatly benefited regeneration response. Data from this study suggested broadcast burning is particularly effective at bolstering successful regeneration. Broadcast burning can result in many possible benefits to suckering aspen, particularly, the interruption of auxin flow among root segments, removal of competing vegetation, nutrient release, increased soil temperatures, and the creation seedbed conditions suitable for seedling establishment (Fairweather et al., 2014; Romme et al., 2005; Shepperd, 2001). Whether this is a result of burn chemistry, or could be replicated without fire, is a question that warrants further study. Domestic animal relief encouraged successful regeneration on seven of nine (78%) sites where this non-traditional site preparation technique was employed, likely due to decreased herbivory pressure, at least in the short-term, which is sufficient to reach the 2m threshold. All site preparation techniques, including the no-treatment alternative, yielded successful regeneration in some cases (Fig. 5b). The combined results from the no site preparation alternative and pile-and-burn resulted in successful regeneration in only seven of 66 (~10%) sites. This was likely due to a lack of stimulation of root suckering. Pile-and-burned sites may have been subjected to excessive root damage from machinery and the burning of slash piles.

In addition to advance reproduction, our analyses identified less important, albeit interpretable proxies for stand vigor that warrant mention as they relate to regeneration success. The pre-treatment metrics of aspen stand vigor that were at least partially predictive of regeneration potential were: aspen sapwood cross-sectional area (ASWA), condition of overstory aspen (OSCOND), aspen trees ha^{-1} (AsTPHA), and aspen live basal area (ALBA). Kaufmann and Treondle (1981) demonstrated a positive relationship between ASWA and leaf area, a prominent indicator of forest productivity, suggesting a positive relationship between ASWA and reproductive potential. Previously, poor OSCOND was linked to ‘SAD’, as characterized by the lack of regeneration, among other factors (Frey et al., 2004; Worrall et al., 2008), with the inherent implication that healthy OSCOND should relate to favorable regeneration conditions. Lastly, AsTPHA and ALBA have also been found to be potentially indicative of regeneration potential (Perrette et al., 2014; Worrall et al., 2010). While these ancillary indicators of stand vigor could be taken into account when evaluating the regeneration potential of an aspen stand, our research indicates they would be secondary to herbivory pressure, advance reproduction, and site preparation.

This study elucidates the utility of characterizing advance reproduction as indication for future regeneration potential. There are few management scenarios that carry present advance reproduction over as a component of the future stand. This suggests that advance reproduction serves as an indicator of future regeneration potential versus the argument that advance reproduction imparts direct contribution to future stocking. For instance, a majority of the stands in this study were subject to overstory removal where logging equipment and slash likely damaged most, if not all, of the advance reproduction during the harvest. Studies from species with similarly intense silvicultural systems, such as clearcuts in lodgepole pine, report extensive damage to their understory seedling bank from harvesting operations (e.g. Lewis Murphy et al., 1999). Further, many treatments were subject to site preparation techniques such as broadcast burning and pile-and-burn, which would have effectively killed the advance reproduction.

Comprehensive studies regarding herbivory have been conducted, and provide inference regarding long term impacts on system resilience (Seager et al., 2013). The present study provides an objective evaluation of silvicultural treatment success, identifying herbivory as the leading predictor of regeneration success or failure. We offer interpretation on this matter by identifying the primary contributors to aspen regeneration success, all of which pivot on the complications of herbivory. The quality (i.e. height) and quantity of advance reproduction is inherently dependent on antecedent herbivory conditions and indicative of its present impacts. The effective site preparation techniques (i.e. broadcast burning, domestic animal relief) have implications for herbivory as well. Domestic animal relief has obvious and direct impacts on herbivory pressure where less manageable native ungulate populations are not excessive. Broadcast burning may dissuade herbivore pressure within treatment areas by removing vegetation, thus redirecting herbivores to the diverse understories of adjacent aspen stands (Coop et al., 2014).

Unfortunately, effective options for mitigating the detrimental impacts of herbivory are relatively few. Kota and Bartos (2010) demonstrated that herbivore damage on aspen can be significantly reduced through the use of constructed(e.g. livestock fencing, wildlife exclosures) and natural barriers (e.g. slash debris, tree hinging) in the Black Hills of South Dakota. In practice, however, these measures can be limited by high fencing costs, and lack of slash materials in scant aspen stands. Alleviation from domestic ungulates may also be effective when viable. Lastly, if protection from herbivory is equivocal one might consider storing the regeneration potential ‘on the stump’ until conditions become amiable for successful regeneration (Bartos and Campbell, 1998).

CHAPTER 5

CONCLUSION

Inferences drawn from our study are generally limited to management in mixed and pure aspen types in the Colorado Plateau Region. Rogers et al. (2010) affirm this assertion. The recommendations presented here should be considered during the management process and prior to aspen treatments across the region of inference. In summary:

- Advance reproduction is an important indicator of regeneration potential as well as current levels of herbivory. An evaluation of the quantity and quality of advance reproduction augments the ability to forecast regeneration response, and also identifies extant herbivory. Consider promoting advance reproduction in stands where advance reproduction is lacking in order to ensure reproductive potential. This may be achieved by opening small gaps in the overstory (Long and Mock, 2012).
- Broadcast burning and relief from domestic animal browsing serve as the best site preparation techniques where successful regeneration is desired.
- It is imperative that the browse condition of regeneration be regularly monitored post-treatment. In the event the herbivory is observed to be increasing, stems must be protected in order to avoid regeneration failure. (Fig. 6).

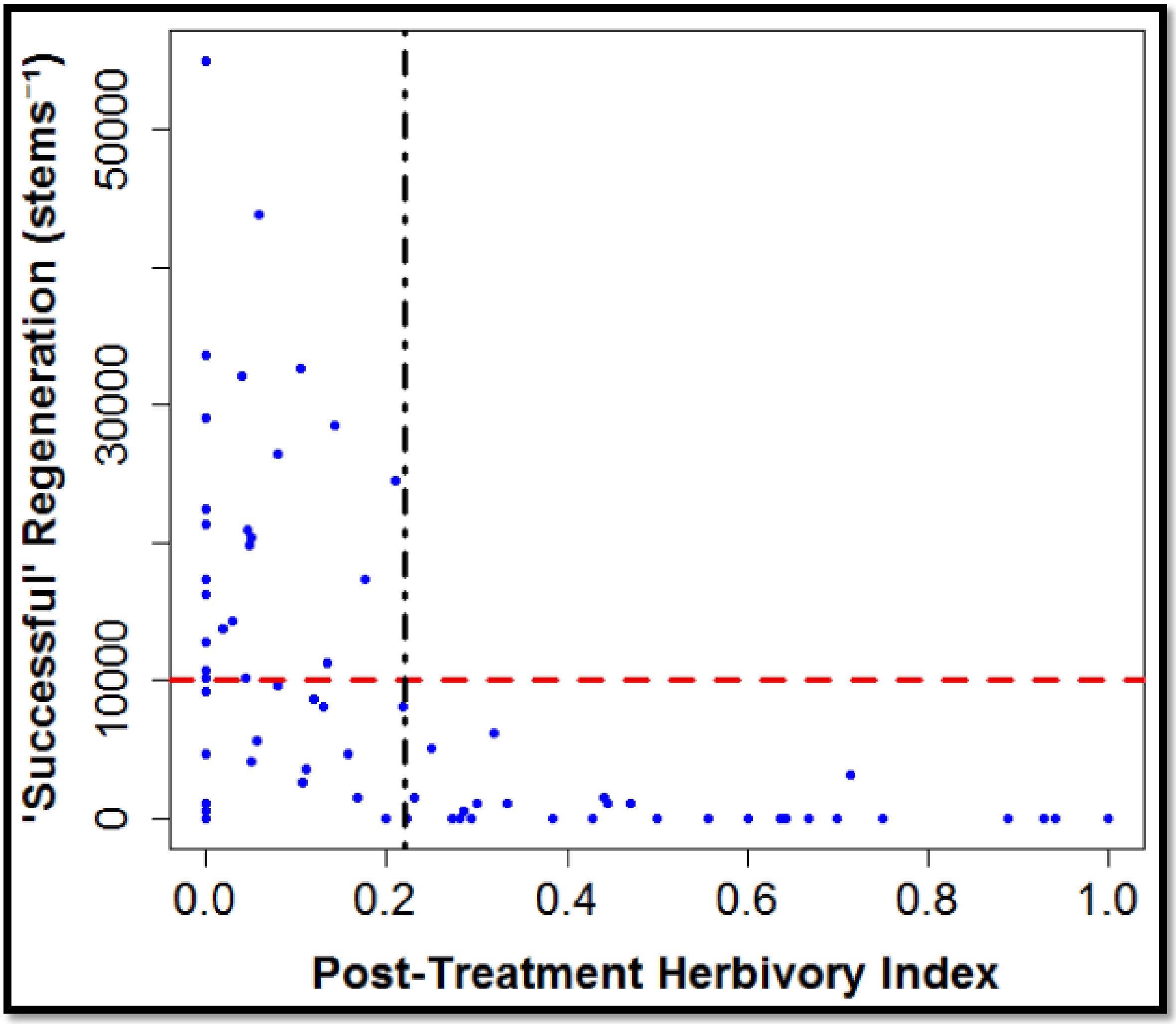


Figure 6. Plot of raw data showing distinct thresholds in regeneration success related to post-treatment herbivory. Herbivory indices ≥ 0.21 result in regeneration treatment failure. Herbivory index is a ratio of terminally browsed stems to total stems. Jones et al. (2005) attest similar findings.

REFERENCES

Anderegg, W.R.L., Anderegg, L.D.L., Berry, J.A., Field, C.B., 2014. Loss of whole-tree hydraulic conductance during severe drought and multi-year forest die-off. Oecologia 175, 11–23.

Anderegg, W.R.L., Plavcová, L., Anderegg, L.D.L., Hacke, U.G., Berry, J.A., Field, C.B., 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. Glob. Chang. Biol. 19, 1188–96.

Baker, F.S., 1918. Aspen reproduction in relation to management. J. For. 16, 389–398.

Baker, F.S., 1925. Aspen in the central Rocky Mountain region. U.S. Dept. Agric. Bull. No. 1291.

Bartos, D.L., Campbell, R.B., 1998. Decline of quaking aspen in the Interior West-examples from Utah. Rangelands 20, 17–24.

Bartos, D.L., Ward, F.R., Innis, G.S., 1983. Aspen succession in the Intermountain West : a deterministic model. USDA For. Serv. Gen. Tech. Rep. INT-153.

Bowns, J.E., Bagley, C.F., 1986. Vegetation responses to long-term sheep grazing on mountain ranges. J. Range Manage. 39, 431–434.

Brodie, J., Post, E., Watson, F., Berger, J., 2012. Climate change intensification of herbivore impacts on tree recruitment. Proc. R. Soc. Biol. Sci. 279, 1366–137070.

Callahan, C.M., Rowe, C. a., Ryel, R.J., Shaw, J.D., Madritch, M.D., Mock, K.E., 2013. Continental-scale assessment of genetic diversity and population structure in quaking aspen (*Populus tremuloides*). J. Biogeogr. 40, 1780–1791.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Coop, J.D., Barker, K.J., Knight, A.D., Pecharich, J.S., 2014. Aspen (*Populus tremuloides*) stand dynamics and understory plant community changes over 46 years near Crested Butte, Colorado, USA. For. Ecol. Manage. 318, 1–12.

Curtis, R.O., Marshall, D.D., 2000. Why quadratic mean diameter? West. J. Appl. For. 15, 137–139.

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. Ecology 88, 2783–92.

De Woody, J., Rickman, T.H., Jones, B.E., Hipkins, V.D., 2009. Allozyme and microsatellite data reveal small clone size and high genetic diversity in aspen in the southern Cascade Mountains. For. Ecol. Manage. 258, 687–696.

DeRose, R.J., Long, J.N., 2007. Disturbance, structure, and composition: spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah. For. Ecol. Manage. 244, 16–23.

DeRose, R.J., Long, J.N., 2010. Regeneration response and seedling bank dynamics on a Dendroctonus rufipennis-killed *Picea engelmannii* landscape. J. Veg. Sci. 21, 377–387.

Fairweather, M.L., Rokala, E.A., Mock, K.E., 2014. Aspen seedling establishment and growth after wildfire in central Arizona: An instructive case history. For. Sci. 60, 1–10.

Frey, B.R., Lieffers, V.J., Hogg, E.H.T., Landhäusser, S.M., 2004. Predicting landscape patterns of aspen dieback : mechanisms and knowledge gaps. Can. J. For. Res. 34, 1379–1390.

Hanna, P., Kulakowski, D., 2012. The influences of climate on aspen dieback. For. Ecol. Manage. 274, 91–98.

Helms, J., 1998. The dictionary of forestry. Society of American Foresters. Bethesda, MD.

Johnston, B.C., 2001. Multiple factors affect aspen regeneration on the Uncompahgre Plateau, west-central Colorado. In: Sustaining Aspen in Western Landscapes: Symposium Proceedings. pp. 395–414.

Jones, B.E., Burton, D., Tate, K.W., 2005. Effectiveness monitoring of aspen regeneration on managed rangelands. USDA For. Serv. R5-EM-TP-004.

Kaufmann, M.R., Troendle, C.A., 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. For. Sci. 27, 477–482.

Kay, C.E., Bartos, D.L., 2000. Ungulate herbivory on Utah aspen: assessment of long-term exclosures. J. Range Manag. 53, 145–153.

Kota, A.M., Bartos, D.L., 2010. Evaluation of techniques to protect aspen suckers from ungulate browsing in the Black Hills. West. J. Appl. For. 25, 161–168.

Kulakowski, D., Matthews, C., Jarvis, D., Veblen, T.T., 2013. Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). J. Veg. Sci. 24, 168–176.

Kurzel, B.P., Veblen, T.T., Kulakowski, D., 2007. A typology of stand structure and dynamics of quaking aspen in northwestern Colorado. For. Ecol. Manage. 252, 176–190.

Lewis Murphy, T.E., Adams, D.L., Ferguson, D.E., 1999. Response of advance lodgepole pine regeneration to overstory removal in eastern Idaho. For. Ecol. Manage. 120, 235–244.

Long, J.N., Mock, K., 2012. Changing perspectives on regeneration ecology and genetic diversity in western quaking aspen: implications for silviculture. Can. J. For. Res. 42, 521–524.

Mittanck, C.M., 2012. Exploring a stable aspen niche within aspen-conifer forests of Utah. Master's Thesis. Utah State University, Logan, Utah.

Mitton, J.B., Grant, M.C., 1996. Genetic variation and the natural history of quaking aspen. Bioscience 46, 25–31.

Mock, K.E., Callahan, C.M., Islam-Faridi, M.N., Shaw, J.D., Rai, H.S., Sanderson, S.C., Rowe, C. A, Ryel, R.J., Madritch, M.D., Gardner, R.S., Wolf, P.G., 2012. Widespread triploidy in western North American aspen (*Populus tremuloides*). PLoS One 7, 10.

Mock, K.E., Rowe, C.A., Hooten, M.B., Dewoody, J., Hipkins, V.D., 2008. Clonal dynamics in western North American aspen (*Populus tremuloides*). Mol. Ecol. 17, 4827–4844.

Mueggler, W.F., Bartos, D.L., 1977. Grindstone Flat and Big Flat exclosures: a 41-year record of changes in clearcut aspen communities. USDA For. Serv. Res. Pap. INT-195.

Oukrop, C.M., Evans, D.M., Bartos, D.L., Ramsey, R.D., Ryel, R.J., 2011. Moderate-scale mapping methods of aspen stand types: a case study for Cedar Mountain in southern Utah. USDA For. Serv. Rocky Mt. Res. Station. Gen. Tech. Rep. RMRS-GTR-259.

Perrette, G., Lorenzetti, F., Moulinier, J., Bergeron, Y., 2014. Site factors contribute to aspen decline and stand vulnerability following a forest tent caterpillar outbreak in the Canadian Clay Belt. For. Ecol. Manage. 323, 126-137.

R Development Core Team, 2004. R: A Language and Environment for Statistical Computing. R Foundatation for Statistical Computing.

Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. For. Ecol. Manage. 258, 2353–2364.

Rogers, P.C., Landhausser, S.M., Pinno, B.D., Ryel, R.J., 2014. A functional framework for improved management of western North American aspen. For. Sci. 60, 345–359.

Rogers, P.C., Leffler, A.J., Ryel, R.J., 2010. Landscape assessment of a stable aspen community in southern Utah, USA. For. Ecol. Manage. 259, 487–495.

Rogers, P.C., Mittanck, C.M., 2013. Herbivory strains resilience in drought-prone aspen landscapes of the western United States. J. Veg. Sci. 25, 457–469.

Romme, W.H., Turner, M.G., Tuskan, G.A., Reed, R.A., 2005. Establishment, persistence , and growth of aspen (*Populus tremuloides*) seedlings in Yellowstone National Park. Ecology 86, 404–418.

Seager, S.T., Eisenberg, C., St. Clair, S.B., 2013. Patterns and consequences of ungulate herbivory on aspen in western North America. For. Ecol. Manage. 1–10.

Shepperd, W.D., 2001. Manipulations to regenerate aspen ecosystems. In: Sustaining Aspen in Western Landscapes: Symposium Proceedings. pp. 355–365.

Shinneman, D.J., Baker, W.L., Rogers, P.C., Kulakowski, D., 2013. Fire regimes of quaking aspen in the Mountain West. For. Ecol. Manage. 299, 22-34.

Smith, E. A., O'Loughlin, D., Buck, J.R., St. Clair, S.B., 2011. The influences of conifer succession, physiographic conditions and herbivory on quaking aspen regeneration after fire. For. Ecol. Manage. 262, 325–330.

Tshireletso, K., Malechek, J.C., Bartos, D.L., 2010. Basal area growth for aspen suckers under simulated browsing on Cedar Mountain, southern Utah, western United States of America. Botswana J. Agric. Appl. Sci. 6, 71–76.

Wan, X., Landhäusser, S.M., Lieffers, V.J., Zwiazek, J.J., 2006. Signals controlling root suckering and adventitious shoot formation in aspen (*Populus tremuloides*). Tree Physiol. 26, 681–7.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P. A., Shepperd, W.D., 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. For. Ecol. Manage. 255, 686–696.

Worrall, J.J., Marchetti, S.B., Egeland, L., Mask, R.A., Eager, T., Howell, B., 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. For. Ecol. Manage. 26, 638–648.

Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M., Gray, L.K., 2013. Recent declines of *Populus tremuloides* in North America linked to climate. For. Ecol. Manage. 299, 35-51.