THESIS

STATES AND TRANSITIONS IN ASPEN DOMINATED ECOSYSTEMS IN WESTERN

COLORADO

Submitted by

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ABSTRACT

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In Colorado and the southwestern United States, quaking aspen (*Populus tremuloides* Michx.) is a species of high ecological, economic, and aesthetic importance. In response to the interests of several landowners and land managers in my study sites, this thesis describes my efforts to identify differences among aspen stand types in western Colorado and the ecological sites on which they occur; to describe aspen communities on different ecological sites based on species composition, functional traits, and drivers of change; and to synthesize this information in state-and-transition models (STM) applicable to specific ecological sites (ESs).

In Chapter 2, I analyzed the results of aspen inventories and found that three of my four study sites contained aspen stands that are considered stable aspen subtypes. The fourth site contained stands representing a seral aspen type where conifer encroachment has occurred. I found higher frequencies and intensities of browsing in areas with isolated stands compared to areas with large continuous stands and in these areas there was evidence that browsing has affected juvenile aspen stem densities. Clear-felling on one site with large stable stands stimulated new stem growth, while prescribed burns on another site with smaller stable stands did not stimulate new stem growth. In Chapter 3, I classified sites based on soil and other abiotic site characteristics using partitioning around medoids (PAM). I then developed STMs for these sites using agglomerative hierarchical clustering analysis, indicator species analysis, permutational multivariate analysis of variance (PERMANOVA), non-metric multidimensional

scaling (NMS), and the Random Forest algorithm to identify plant species associations and correlated abiotic factors and management treatments. Three of my STMs depict aspen and non-aspen dominated states associated with differences in abiotic site characteristics, and one STM depicts a single aspen dominated state.

My investigation of aspen health and factors contributing to aspen mortality provides land managers in western Colorado with useful information for making informed decisions regarding aspen management. The STMs I have developed for these sites show which abiotic variables can be expected to be correlated with specific vegetation states and will inform future STM development for aspen-dominated systems. My findings suggest that the frequency and intensity of herbivory has played a major role in aspen survival at three of my four study sites. Future work is needed to develop more complete STMs for aspen-dominated systems in western Colorado.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx.) has the widest distribution of any tree

species in North America (Baker 1925, Preston Jr. 1976, DesRochers and Lieffers 2001). Aspen

stands serve as important summer range for livestock and native herbivores, productive

watersheds, habitat for native flora and fauna, and aesthetically pleasing landscape features

(DeByle and Winokur 1985, Mueggler 1985). In Colorado, quaking aspen is widely regarded as

a species of great ecological, economic, and aesthetic importance. In response to needs expressed

by landowners and land managers, I conducted this study to develop a state-and-transition model

(STM) specific to aspen dominated ecosystems in western Colorado and to describe the

ecological dynamics of those systems within the framework of an STM.

In order to manage land effectively and sustainably, it is important for landowners and

land managers to continuously expand their working knowledge of plant community dynamics

and responses to disturbances across the landscapes they work in. One tool for understanding the

compositional components and drivers of change in these systems is the state-and-transition

model (STM). My research project was one part of the larger Learning from the Land (LFL)

project and was conducted to meet that need. A Conservation Innovation Grant (CIG) from the

Natural Resources Conservation Service (NRCS) and a Chevron research grant funded my

research. Project leaders and participants collaborated and continue to collaborate with

landowners and land managers in several counties in Northwestern Colorado to develop STMs

by incorporating existing research and monitoring information, local knowledge, and ecological

field data. My project focused on plant community interactions in ecosystems in western Colorado in which aspen (*Populus tremuloides spp.* Michx*.)* is found.

I met with project stakeholders in May of 2014 to identify candidate ecological sites (ESs) for STM development. Landowners and managers were concerned with the effects of aspen decline on the health of stands in the area and interested in assessing the extent of damage. Aspen decline refers to the loss of many older, even-aged aspen stands and has been attributed to climate variability, fire suppression, and herbivory of suckers in North America over the last two centuries (Mueggler 1989, Hessl 2002). I developed research questions and goals to specifically address the concerns of my stakeholders.

My research addressed four questions:

1) What aspen stand functional types are present in the study area?

   Background: Multiple aspen stand classification systems have been described in the literature (Mueggler 1988, Shepperd et al. 2006, Rogers et al. 2014). I determined the functional type or types of stands present in my study area in order to create an appropriate aspen STM and determine if multiple STMs are necessary.

2) Do aspen stands in the study area occur on one particular ecological site or across multiple ecological sites?

   Background: Aspen prefer wet, nutrient rich soils and often occur on north facing aspects at lower elevations (Mueggler 1988, Rogers et al. 2014). Aspen stands in the study area may occur on one specific ecological site and should constitute one or more states within

a single STM. It is also possible that aspen stands occur on multiple Ecological Sites and represent states within different STMs for each site.

3) Is the severity of aspen die-off correlated with abiotic site characteristics that distinguish specific ecological sites?

Background: The NRCS defines ecological sites as specific types of land characterized by specific soil, landform, climate, hydrology and geological features (Caudle et al. 2013). I hypothesized that stands or portions of stands that have died off could have been growing in ecological sites with sub-optimal abiotic characteristics that lead to more stressed trees.

4) Are herbivory, reduced root density, and reduced suckering correlated with a decrease in relative stand health within the study area that will inevitably result in stand die-off?

Background: I characterized the regeneration and browse levels in stands within the study area. I hypothesized that a reduction in suckering due to root die off or pressure from herbivory may result in a stand crossing a threshold from which it will not be able to recover.

This project had four primary objectives relating to the four research questions identified above. Those objectives were to:

1) Identify the types of aspen stands in the study area based on stem size class distribution, stem mortality, and presence or absence of conifer.

2) Characterize the ecological sites on which different aspen stands occur.

3) Measure and describe characteristics of new aspen growth, root density, browsing pressure, and other types of damage to identify potential drivers of aspen decline, predict potential future states, and determine possible management treatment options.

4) Develop ES-appropriate STMs for aspen dominated ecological sites in western Colorado from existing generalized STMs.

LITERATURE REVIEW

The purpose of this literature review was to establish what is known about aspen dynamics and regeneration on different ecological sites, what knowledge gaps persist, and to justify my research questions and objectives in the context of existing research. The major topics covered in this review are: 1) the definition and development of Ecological Site Descriptions (ESDs), 2) the theory, development, and structure of STMs, 3) limitations of STMs, 4) aspen stand types, 5) aspen community dynamics, and 6) existing aspen STMs.

ECOLOGICAL SITE DESCRIPTIONS

The concept of ESDs began with Korstian's descriptions of forest sites in 1919 (Shiflet 1975). This site concept gave rise to range sites, which were first mentioned by Renner and Johnson in 1942 and further developed by Humphrey in 1947 (Shiflet 1975). The concept was refined over the following decades in publications until 1976, when the Soil Conservation Service (SCS) outlined a "range site" classification model in the National Range and Pasture Handbook (USDA-SCS 1976). In 1982, the Bureau of Land Management (BLM) decided to use the SCS range site model to derive the Ecological Site Inventory (ESI) which was officially adopted as the new standard for vegetation inventory methods (Habich 2001). The Chief of the US Forest Service (FS), Director of the BLM, and Director of the NRCS signed the Interagency

Memorandum of Understanding (MOU) in 2005, agreeing to adopt the ESD concept (Briske et al. 2008).

An ES is defined as a specific type of land characterized by specific soil, landform, climate, hydrology and geological features (Caudle et al. 2013). These abiotic characteristics result in distinctive vegetation assemblages that respond similarly to natural and anthropogenic disturbances (Caudle et al. 2013). The intent of the ESD classification system is to create a useful classification system for assessment, monitoring, and management. The information provided by ESDs allows managers to determine the land's responses to disturbances or management practices, ability to remain productive, and suitability for various land uses. Approved ESDs include descriptions of abiotic site characteristics, ecological trajectories and dynamics, as well as descriptions of current, historic, and potential vegetation assemblages for a given site. Many areas in Colorado and other western states do not have completed ESDs, so individuals and organizations are working with the NRCS to develop new ESDs for those areas. The NRCS is working to standardize the definitions of STM components and is working with research groups such as LFL to establish well-developed, repeatable methods for creating STMs.

STATE-AND-TRANSITION MODELS

State and transition models (STMs) were proposed by Westoby et al. (1989) as a more dynamic and accurate alternative to traditional Clementsian models that suggested linear succession patterns and a predictable successional trajectory of plant communities toward a climax state. STMs incorporate linear successional dynamics that may exist in a given system, while also acknowledging the potential for multiple successional pathways and restoration pathways. STMs consist of five essential components: states, transitions, restoration pathways, community phases, and community pathways (NRCS 2014). States are suites of community

phases, soil properties, and species assemblages that interact with one another. Alternative states

will have at least one key difference in the pathways through which water, nutrients, or energy

are cycled (NRCS 2014). Transitions define the variables or combination of variables that result

in a shift to an alternative state (NRCS 2014). Thresholds are the suite of conditions between two

states that result in the modification of both the structure and function of an ecosystem beyond its

capacity to resist change or to reorganize and recover function following disturbance, i.e., system

resilience (Briske et al. 2008). A threshold represents the transitional moment beyond which an

ecosystem functions under a different set of feedbacks (Tipton 2015). Once a threshold is

crossed, resulting in an alternative state, returning an area to its former condition can be a

prohibitively expensive and time consuming endeavor (Friedel 1991, Bestelmeyer et al. 2003).

Threshold level disturbances may lead to changes in abiotic site characteristics (NRCS 2014).

Transitions may be attributed to small changes through time or sudden, high magnitude

disturbances (Peters et al. 2004, Barnosky et al. 2012), however, the new state that results will

typically persist after removal of the causal disturbance (Westoby et al. 1989, Friedel 1991).

Restoration pathways identify the management practices or environmental conditions necessary

to return a degraded state to a more favorable condition. Community phases are the plant

assemblages that exist within states and the shifts among phases are called community pathways

(NRCS 2014).

Developing accurate and robust STMs involves the integration of multiple types of

information from a variety of sources. These sources can include expert and local knowledge,

historical records, literature, and field observations (Bestelmeyer et al. 2004, Knapp and

Fernandez-Gimenez 2009, Kachergis et al. 2013). STMs consist of conceptual models that

describe system dynamics. These models often do not provide explanations for mechanisms of

change that can be empirically tested (Lockwood and Lockwood 1993, Bestelmeyer et al. 2004, Tipton 2015). Many of these conceptual models are created after changes have occurred and are limited in their ability to predict results of management applied to current conditions (Brown 1994, Tipton 2015). In predictive models, outcomes and ecological responses are assigned probabilities given management practices and starting conditions (Daniel and Frid 2011, Tipton 2015).

LIMITATIONS OF STATE-AND-TRANSITION MODELS

STMs are potentially powerful range management tools. They have been met with several criticisms including: 1) a general lack of model testing and continuous model revision, 2) ambiguity in, or a lack of, standardization of the definitions of model components, and 3) failure to incorporate all factors and drivers into the model. I took steps to address these criticisms while developing my own models.

In practice, the assumptions of STMs are infrequently validated with rigorous scientific observation or revised (Bagchi et al. 2012, Twidwell et al. 2013). It is vital that the plant communities and dynamic processes identified in an STM are supported with empirical data. This type of evidence can be obtained using remote sensing or by collecting field data. Once an STM has been created, it must be updated as more information is gathered and as changes continue to occur in an ecosystem. To address this issue, my project included collection of ecological field data, used in conjunction with local knowledge and existing scientific knowledge, to generate an accurate, data-driven STM.

There has also been a lack of consistency in the definition and application of STM components and thresholds (Stringham et al. 2003, Twidwell et al. 2013). Knapp et al. (2011) interviewed stakeholders and found that individuals had similar understandings of states, but

differed in their understanding of transitions and thresholds. By adopting STMs for use in ESDs, the NRCS has helped address this issue by standardizing STM component definitions. The NRCS is collaborating with a number of US research institutions to improve the STM development process.

It is difficult to observe thresholds in the field because linear disturbance gradients are not common, and it is important to distinguish between reversible and irreversible transitions (Friedel 1991, Stringham et al. 2003). Thresholds have been described as the point that a system transitions from negative reinforcement feedbacks to positive feedbacks that drive vegetation change (Briske et al. 2006). The nature of thresholds makes them inherently difficult for managers to anticipate. Briske et al. (2008) recommend emphasizing the importance of triggers and process-specific indicators as tools to identify at-risk communities. In this proposed project, I used the most current and widely accepted definitions of STM components and thresholds as defined by the NRCS (2014). By meeting with stakeholders and discussing all project components as they are developed, I attempted to avoid any conceptual misunderstandings.

Finally, Bestelmeyer et al. (2004) emphasized the importance of incorporating a wide variety of potential transition drivers. STMs are often criticized for focusing on livestock grazing as the primary driver of change. In actuality, transitions are often driven by a combination of disturbances. Failure to account for combined effects of multiple disturbances can result in mismanagement (Chapin III et al. 2004, Davies et al. 2012, Kachergis et al. 2012, Evers et al. 2013). Conversely, too much complexity can reduce the utility of STMs to stakeholders requiring information that is difficult or impossible to obtain. One of the major weaknesses of STMs is the failure to include anticipated climate change projections and the transitions that may result in the future. It is important to manage with realistic expectations for future climate

conditions and disturbance frequencies in these systems. To address this limitation, I discussed

climate change projections and their predicted effect on aspen species distributions in chapter 4.

ASPEN STAND TYPES

In order to develop usable STMs for ESs containing aspen stands, it was necessary to first

classify the functional type of aspen stand being observed. Mueggler (1988) set the foundation

for aspen stand classification when he described two functional types of aspen stands: 1) seral

stands that eventually become dominated by conifer forests and 2) stable stands that exist for

periods greater than three hundred years. Alexander's (1988) Clementsian-based habitat

classifications also described seral and stable aspen dominated plant communities. Eventual

colonization of stable stands by conifers may occur (Rogers et al. 2014). Stable stands are

characterized by incremental replacement and gap-phase regeneration, which results in a multi-

layer stand profile (Kurzel et al. 2007, Mueggler 1985, Rogers et al. 2014, Betters and Woods

1981). In an intact stable stand, there are typically three or more distinguishable layers consisting

of similar aged stems, however, single-storied aspen stands are becoming more common

(Shepperd 1990, Kurzel et al. 2007, Rogers et al. 2010, Rogers et al. 2014). Stable stands are

more commonly found in Mollisols that are pachic, argic or boralfic (Mueggler 1988) and are

high in pH and organic matter content. Seral stands are frequently found in typic Alfisolls with

relatively low organic matter and pH (Mueggler 1988).

Shepperd et al. (2006) further separated these seral and stable aspen types into sub-types.

Seral sub-types included meadow fringe, riparian, and upland/conifer communities (Shepperd et

al. 2006). Stable aspen types included upland pure aspen communities, lithic stands, snowpocket

stands, and Krummholz communities. Lithic aspen stands occur on lava, bolder, or talus

(Shepperd et al. 2006). Snowpocket aspen occur mostly at higher elevations on north facing

slopes and are more common in the Great Basin (Shepperd et al. 2006). Trees in snowpocket and Krummholz stands can be stunted because of harsh winters combined with shorter growing seasons (Shepperd et al. 2006). The work of Shepperd et al. (2006) focused on aspen in the Sierra Nevada Mountains of California.

Rogers et al. (2014) focused on all aspen west of the 100th meridian and developed another classification system. This system contained seven categories that deviate from those proposed by Shepperd et al. (2006). The stable aspen type suggested by Rogers et al. (2014) included four subcategories: aspen parklands, elevation and aspect limited, Colorado Plateau or mesa, and terrain isolated stands. Rogers et al. (2014) combined snowpocket, krummholz, lithic, prairie pothole, and avalanche track stands into the terrain isolated category. They also acknowledged that small stable aspen stands surrounded by larger non-forest plant communities could occur that do not fit into any of the other sub-categories of aspen stands (Rogers et al. 2014). Rogers et al. (2014) described two subcategories of seral aspen types: boreal and montane stands. Montane seral aspen are considered to be the most common class of aspen found within the Rocky Mountain region (Mueggler 1989, Rogers 2002, Kashian et al. 2007, Rogers et al. 2014). These montane seral aspen are characterized as even-age stands that reproduce primarily through suckering brought on by stand-replacing disturbance and are eventually overtopped by conifer species (Rogers et al. 2014). Boreal aspen stands occur as mixed wood forests of Canada and Alaska and their composition and distribution is mainly driven by disturbance frequency and intensity (Rogers et al. 2014). The majority of aspen decline over the last century has taken place in montane seral cohorts found in the Rocky Mountains (Bartos and Campbell 1998, Gallant et al. 2003, Strand et al. 2009, Rogers et al. 2014).

In montane areas, stable and seral aspen communities can be found adjacent to one another (Rogers et al. 2014). According to Cryer and Murray (1992), long-term stand stability at these montane sites is likely due to soil conditions that limit encroachment by coniferous species. These elevation and aspect limited aspen stands commonly display a wide variety of stand structures due to a range of disturbance patterns, particularly where aspen stands and conifer forests abut one another (Rogers et al. 2014).

ASPEN STAND DYNAMICS

Aspen stands are considered highly productive forage areas (DeByle 1985) and their decline in recent decades is a major concern to ranchers across the western United States. My project stakeholders expressed concern about the declining health of aspen stands in the study area. I looked at the amount of new growth, browsing levels, and evidence of stand replacing disturbances such as fires. Aspen is a clonal species, and in the western United States aspen was thought to regenerate almost exclusively from root suckers (Schier et al. 1985, Shepperd et al. 2006). Recent research has shown that germination of new clones from seeds is more common than previously believed (Romme et al. 1997, Mittanck et al. 2014, Kay 1993, Mock et al. 2008, Landhausser et al. 2010, Rogers et al. 2014). The individual stems themselves are considered relatively short-lived and shade-intolerant (Schier et al. 1985).

As aspen trees grow, the leaf litter they produce creates a mollic horizon, and if a stand remains healthy, the mollic horizon will continue to thicken (Cryer and Murray 1992). Stand health will deteriorate through time without disturbance, and as leaf fall lessens, the mollic horizon will become thinner and increased water infiltration will result in eluviation (Cryer and Murray 1992). This increased eluviation leads to the formation of an albic horizon that is low in nutrients, has a low water holding capacity, and a low base saturation (Tisdale 1975, Brady

1974). In areas where conifer trees are invading aspen stands, the needle litter can alter soil properties given enough time (Cryer and Murray 1992, Shepperd et al. 2006). After many years, the effects of conifer growth on soil morphology may eventually result in a change to soil classification (Tisdale and Nelson 1975, Cryer and Murray 1992). This would result in a shift to a different ecological site.

Aspen decline refers to the loss of older, even-aged aspen stands attributed to fire suppression, ungulate herbivory, and climate variability in North America over the last two centuries (Mueggler 1988, Hessl 2002). DeByle et al. (1987) estimated that it would take around 12,000 years to complete a fire cycle with current fire occurrence rates (Mueggler 1988). Disturbances such as fire (Bartos and Mueggler 1981) or clear-felling (Crouch 1983) have stopped or reversed this aging process (Birkeland 1974). Fires generally increase soil pH and add to the short-term soil carbon pool (Martin and Dell 1978) which may provide a competitive advantage to aspen (Cryer and Murray 1992). Studies suggest that elevated levels of soil nitrogen can persist for up to 3 years following a fire (Amacher et al. 2001, DesRochers et al. 2003, Shepperd et al. 2006). Increased soil temperatures due to dark ash layers work in tandem with these elevated nutrient levels after fire to favor aspen following fires (Shepperd 2001, Fraser et al. 2002, Shepperd et al. 2006). Results from an experimental burn study conducted by Bartos and Mueggler (1981) in Wyoming indicated that increased temperature and nutrients observed in burned soils led to increased numbers of aspen stems and higher growth rates for up to three years following fires. Another method used by land managers to promote aspen growth is a clear-fell coppice treatment. Normal aspen decline can be observed over decades, however in the early 2000s, land managers observed a large increase in aspen mortality (Worrall et al. 2008).

Sudden Aspen Decline (SAD) refers to the large increase in aspen branch dieback and mortality first observed in Colorado in 2004 (Worrall et al. 2008). Aerial surveys detected SAD on 56,091 ha by 2006 (Worrall et al. 2010). Symptoms of SAD are observed on a landscape scale and include: rapid branch dieback, crown thinning, and mortality without evidence of aggressive pathogen and insect involvement (Worrall et al. 2010). Recent observations taken in southwest Colorado suggest that SAD has slowed or ceased and that stand mortality is still uncommon, even in stands that have experienced a decline (Worrall et al. 2010). Marchetti et al. (2011) found that aspen bark beetles, bronze poplar borer, and cytospora canker were strongly correlated with crown loss and tree damage. These biotic agents may kill trees that are already weakened by drought stress (Marchetti et al. 2011). Ungulate herbivory may also lead to SAD. Aspen ramets are a preferred food source for several large herbivores, and heavy browsing by elk (*Cervus canadensis)*, mule deer (*Odocoileus hemionus*), and domestic livestock can negatively impact aspen regeneration (Bartos et al. 1994; Binkley 2006). In order to save declining aspen stands, it is often necessary to prevent ungulate browsing on new suckers (Ripple and Larsen 2001; Kota and Bartos 2010). Aspen suckers are at the highest risk of being browsed by wild ungulates before they reach heights of at least 4 meters (DeByle 1985; Kota and Bartos 2010). Repeated browsing can be detrimental to aspen sucker survival (Bartos et al. 1994, Kota and Bartos 2010) and can result in an irreversible shrubby growth form (Keigley and Frisina 1998, Kota and Bartos 2010). The near extirpation of elk in Colorado in the early 1900s may have allowed aspen to thrive in the absence of browsing pressure and the subsequent increase in the elk population over the last century could be a major contributor to aspen decline observed in recent decades. Forest Service estimates place the number of elk in the state of Colorado in 1910 at between 500 and 1,000 (Swift 1945). By 1943 the population of elk in Colorado was estimated

to be around 24,000 (Swift 1945). The Colorado elk population has continued to climb since then reaching an estimated 105,000 in 1975 and 203,000 in 1995 (Bunnell 1997). Larger populations and increased access to surface water could be allowing more elk to spend more time in stands, reducing aspen suckering to unsustainable levels. An example of herbivore overpopulation negatively affecting aspen populations can be found in the reexamination of Aldo Leopold's story of deer on the Kaibab plateau in Arizona by Binkely et al. (2006), which found an absence of a normal cohort of aspen from the 1920s and from the 1950s that coincided with increases in mule deer (*Odocoileus hemionus*) populations.

ASPEN STMS

STMs have been developed for rangeland ecological sites across most of the western United States. However, my review of existing aspen and STM literature found that few STMs have been developed for aspen dominated woodlands. Strand et al. (2011) developed an STM for aspen forests using field data and modeled fire return intervals to predict aspen succession in Idaho. That model focused mostly in the role of conifer and fire on aspen succession. Bork et al. (1997) developed a preliminary STM for forest succession in Alberta, Canada that included aspen parklands and vegetation community interactions. The NRCS-USFS-USU (2009) developed conceptual models using the knowledge of resource management professionals and academic professionals for seral and stable aspen types in Utah. I used these STMs for aspen ecosystems to assess the usefulness and accuracy of STMs I developed and determine if my models were consistent or compatible with the models developed by other researchers. In Chapter 3, I compare my STMs aspen and woodland STMs and use them to assess the strengths and weaknesses of my models.

SYNOPSIS

The review of existing research on ESDs and STMs, and specifically their application to aspen-dominated ecological sites, highlights the need for data-driven STMs for aspen-dominated ecological sites in western Colorado. In Chapters 2 and 3, I report on the results of a study in which I collected and analyzed field data from four sites across western Colorado to describe aspen stand types, the ecological sites on which they occur, and factors influencing stand regeneration and transitions, to inform the development of STMs and described the vegetation states and community phases present in ESs in my study areas. These results contribute to improved understanding of distinct aspen stand types, their dynamics, and potential management options.

CHAPTER 2

ASPEN STAND TYPES AND ASPEN MORTALITY IN WESTERN COLORADO

SUMMARY

The objectives of this study were to characterize the aspen stand types in four study areas in western Colorado; assess aspen (*Populus tremuloides spp.* Michx) stem mortality and regeneration; and analyze the roles of factors including conifer encroachment, herbivory, pathogens, and disease, that may be contributing to aspen mortality. Stands at one of my four sites were seral while stands at the other three sites were stable stands. A high proportion of juvenile aspen stems present at the Douglas Pass and DeBeque sites showed evidence of intense browsing. It appears that this heavy browsing is contributing to low densities of juvenile and intermediate sized aspen stems.

INTRODUCTION

The study described in this chapter was a necessary precursor to later work focused on developing STMs for aspen-dominated ecological sites in western Colorado. Existing aspen STMs include different potential states and transitions depending on the type of aspen stand present. Mueggler (1988) described two functional types of aspen stands with different successional trajectories: 1) seral stands that cannot persist for extended periods of time without some sort of stand replacing disturbance, and 2) stable stands that exist for periods greater than three hundred years. Seral aspen stands are characterized as even-age stands that reproduce primarily through suckering brought on by stand-replacing disturbance, and in the absence of such disturbance, these stands are eventually overtopped by conifer species (Rogers et al. 2014). Stable stands do not contain conifer and are characterized by incremental replacement and gap-phase regeneration, which results in a mix of ages within a stand (Rogers et al. 2014, Betters and

Woods 1981). In order to identify potential states, I first needed to understand the types of stands that were present at my study sites.

It is impossible to discuss aspen succession without acknowledging the two types of aspen decline that have been observed in North America: aspen decline and sudden aspen decline (SAD). Aspen decline refers to the loss of older, even-aged aspen stands associated with fire suppression in North America over the last two centuries coupled with conifer conversion (Jones et al. 2005, Kulakowski et al. 2004, Smith and Smith 2005), or extremely high browsing pressure from elk and deer resulting in stand loss (Romme et al. 1995, Kay 2003, Ripple and Larsen 2000). Treatments such as prescribed burns (Shepperd et al. 2006), clear-felling (Shepperd et al. 2015), and herbivore exclusion fencing (Shepperd et al. 2006) have proven effective at stopping or reversing this process of decline in some cases. The majority of aspen decline that has occurred in the United States over the last century has taken place in seral cohorts found in the Rocky Mountains (Bartos and Campbell 1998, Gallant et al. 2003, Strand et al. 2009, Rogers et al. 2014). Since the year 2000, the death of over 3.2 million ha of aspen has been observed in North America (Worrall et al. 2013, Shepperd et al. 2015). This mortality has occurred more quickly than the decades long trend of aspen decline and has been called sudden aspen decline (SAD) (Worrall et al. 2013, Shepperd et al. 2015). SAD has been attributed to severe drought in the early 2000s (Worrall et al. 2013). Low precipitation and high temperatures resulted in water stress and in severe cases, cavitation that resulted in tree mortality (Anderegg et al. 2012). SAD is characterized by rapid aspen canopy mortality and reduced aspen regeneration (Shepperd et al. 2015). Although research has shown that aspen stands contain more genetic diversity than previously thought due to seedlings proliferation (Long and Mock 2012, Fairweather et al. 2014), healthy aspen normally reproduce asexually through intense root suckering after mature trees

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die. Reduced regeneration densities have been observed in SAD affected stands after natural or anthropogenic disturbance and have been attributed to SAD induced root mortality (Worrall et al. 2010, Shepperd et al. 2015). In order to assess the effects of aspen decline and SAD within my study sites, I measured and compared live and dead aspen stem densities and basal areas, and measured and compared counts of aspen roots and root surface areas.

Prior to developing data-driven STMs for my study sites, I first sought to characterize the aspen stand types in the study areas as seral or stable; measure aspen stem mortality and new growth within stands in order to assess stand health and the extent of SAD; and analyze the roles of factors, such as herbivory, pathogens and disease, that may be contributing to aspen mortality. These steps were necessary to distinguish different stand types with potentially distinct dynamics, and to identify factors that could potentially cause transitions between states in the STMs.

METHODS

SAMPLING DESIGN

I sampled aspen stands at four sites in western Colorado to address the objectives of this study. Two sites were in northwestern Garfield County, one near Douglas Pass and another north of DeBeque. Another site was located in Gunnison National Forest, just north of Paonia, Colorado. The fourth site was in the northwestern corner of Moffat County, Colorado. In order to assess the impact of different management treatments and potential resulting transitions to alternative states, I sampled four sites with different management histories. Evidence of herbivory by cattle and/or wild ungulates was present at all four sites, but the degree of herbivory at the Garfield County sites was obviously greater. Clear-felling occurred in aspen stands at the

Gunnison study site in 2008 and 2009. The Little Snake Field Office of the Bureau of Land Management conducted prescribed burns on stands in the Moffat study area in 2008.

At the Douglas Pass and DeBeque sites, where no management treatments occurred other than summer cattle grazing, I selected sample plot center points in aspen. At the Moffat and Gunnison sites, I selected points in both untreated and treated aspen stands. Within the Douglas Pass and DeBeque sites, I designed my sampling to capture aspen stands on different ecological sites. I used 2014 National Agriculture Imagery Program (NAIP) satellite imagery to identify aspen stands within each of my study areas. I digitized all observed aspen stands in each study area using in ArcMap version 10.1 (ESRI 2014) and generated a centroid point in the center of each aspen stand polygon. This centroid point would later serve as a plot center during my stand inventory. I moved centroid points at least 50 m if they re located on a fence line, road of any kind, or water source (stream or catch basin) and allowed for no more than 2 plots to be located within 400 m of each other. Gunnison plots were generated in clear-felled and adjacent untreated aspen stands. Moffat plots were generated in burned and adjacent unburned aspen stands.

DATA COLLECTION

Plots consisted of a 50 x 50 meter square centered on my aspen centroid point coordinates. I sampled vegetation along three parallel 50 meter transect tapes placed 25 meters apart, parallel to the hill aspect (i.e. perpendicular to contours). I measured foliar and basal cover by species, bare ground, and litter cover at 1 meter intervals along each transect using the line point intercept (LPI) method (Herrick et al. 2005). Canopy foliar cover was measured at each LPI point using a GRS densiometer. I recorded metadata in the form of slope, aspect, and elevation as well as observed evidence of past vegetation treatments or disturbances.

In order to assess aspen stand structure and mortality, I estimated basal area and measured densities of stems in different size classes. I used a prism gauge with an English Basal Area Factor (BAF) of 2.294 m^2/ha. to estimate stand basal area within each plot (Oderwald 1990). Prism gauge measurements were taken at 12.5 and 37.5 meters along the center transect. Borderline trees were not included in counts. I observed and recorded the number and size classes of aspen trees within a 2-meter wide belt transect adjacent to each LPI transect. I used size classes outlined by Strong et al. (2010): class one stems are those less than 0.46 meters tall, class two stems are those between 0.46 meters and 1.37 meters tall, class three stems are those greater than 1.37 meters tall and less than 5.08 centimeters in diameter at breast height, class 4 stems are those greater than 1.37 meters tall and greater than 5.08 centimeters in diameter at breast height, and class five stems are those considered canopy height. The occurrence of any factors known to be correlated with aspen mortality was recorded, including evidence of browsing, disease, insect damage, or physical damage from large mammals. Ungulate herbivory typically removes the terminal bud and leaves resulting in bare stems or stems that appear to have been roughly shorn off, and repeated browsing results in gnarled, and stunted stems (Strong et al. 2010). I recorded whether or not stems had been browsed and ranked the intensity of browsing using protocols outlined by Strong et al. (2010).

Stand root measurements were taken by excavating a trench to a depth of 0.2 m using methods outlined by Shepperd and Smith (1993). Trenches started at plot centers extended to a length of 2 meters. I split the soil surface with two parallel mattock lines and excavated the soil between them. Roots along a single wall of the trench were then sampled using a plane intercept method employed in studies of aspen roots (Shepperd and Smith 1993). I counted and measured cross-sectional diameters of all aspen roots larger than 4 mm along one wall of each trench.

ANALYSIS

For the purpose of this analysis, treated and untreated Moffat and Gunnison plots were separated into distinct groups. I used Levene's test to assess the equality of variances of distributions of each variable across all 6 of my sites and treatment combinations. Variables that did not have significant differences in variance were then checked for normality using a Shapiro-Wilk test and quantile–quantile plots. Due to differences in variance for some of the data distributions, the small size of Moffat and Gunnison treated and untreated samples, and the non-normality of other distributions, I used non-parametric tests in this analysis.

I compared distributions of conifer foliar cover, aspen stem size classes, live and dead aspen basal area, aspen foliar cover, observed browsing, and root counts and surface areas between study sites and treatments. I used non-parametric Kruskal-Wallis rank sum tests to determine whether or not distributions were significantly different. If the null hypothesis of a Kruskal-Wallis rank sum test was rejected, I used a post-hoc Bonferroni corrected Dunn's test to conduct pairwise comparisons of sites and treatments.

Presence of conifer within a plot along with lower numbers of intermediate-sized aspen stems indicated that the plot was within a seral stand. Live and dead aspen basal area and live and dead aspen stem counts were used to gauge aspen mortality. Browsing and other observed damages were measured to try to identify factors contributing to aspen mortality. Root counts and root surface area measurements were used to track the progression of aspen decline and attempt to gauge the potential for stand recovery following a treatment. I used Pearson product-moment correlation to identify linear relationships between measured variables. Prior to running correlations, all variables were standardized. All analyses were performed using R version 3.1.3 (R Development Core Team 2015).

RESULTS

CONIFER COVER

Douglas fir (*Pseudotsuga* menziesii (Mirb.) Franco) was found in 80% of plots at the Douglas Pass site. Rocky mountain juniper (*Juniperus scopulorum* Sarg.) was found in 40% of burned plots and 50% of unburned plots in Moffat County. Lodgepole pine (*Pinus contorta* ex Loudon) was found in 20% of burned plots in Moffat County. Conifer foliar cover distributions for all sites and treatments are displayed in Figure 2.1. Median conifer tree foliar cover in plots near Douglas Pass was the highest (median =10%, IQR = 13.4) and a Kruskal-Wallis test did not find significant differences (p=0.59) in unburned plots (median = 1%, IQR = 3.675) and burned plots (median = 0%, IQR= 1.3) in Moffat County. I rejected the null hypothesis of that conifer foliar cover measurements came from populations with identical distributions (p=0.000037). No conifer was found on any plot at the DeBeque or Gunnison sites.

STEM SIZE CLASS DISTRIBUTIONS

Distributions for all size classes in all study area and treatment combinations are displayed in Figure 2.2. Kruskal-Wallis tests revealed that there were no significant differences in class 1 stem density distributions across sites (p = 0.074), however there were significant differences among sites for distributions of all other live aspen stem classes (Class 2, p = 0.009; Class 3, p = 0.000039; Class 4, p = 0.00094; Class 5, p=0.015). The use of Bonferroni corrected Dunn's tests allowed pairwise comparisons for each size class. Mean rank sums of class 2 stem densities were higher in clear-felled Gunnison plots than in DeBeque plots (p=0.022). Mean rank sums of class 3 stem densities at Douglas Pass were lower than clear-felled Gunnison plots (p=0.0002) and untreated Gunnison plots (p=0.01). Mean rank sums of class 3 stems in burned Moffat plots were also lower than clear-felled (p=0.001) and untreated (p=0.02) Gunnison plots. Mean rank sums of class 4 stem densities at DeBeque were higher than at Douglas Pass

(p=0.042) and lower than in clear-felled Gunnison plots (p=0.023). I detected differences between DeBeque and clear-felled Gunnison plots for mean rank sums of class 5 stem densities (p=0.0059).

ASPEN COVER, ASPEN MORTALITY, BROWSING, AND OTHER DAMAGE

Distributions of live aspen foliar cover and live and dead aspen basal area distributions for each site are displayed in Figure 2.3. Distributions of aspen foliar cover (p=0.003), live aspen basal area (p=0.003), and dead aspen basal area (p=0.0001) differed significantly across sites. The highest median levels of aspen foliar cover occurred in clear-felled Gunnison plots (median = 64%, IQR = 36.65), because I did not differentiate between adult and juvenile trees when measuring foliar cover. Live and dead basal area values were zero for all clear cut plots because larger diameter stems were no longer present and my prism gauge measurements did not pick up trees with a very small diameter. Dead aspen basal area values were generally highest in untreated Gunnison plots (Figure 2.3). The ratios of median live to dead standing class 4 and 5 aspen stems for each site can be found in Table 2.1.

I compared observed densities of live and dead class 4 and 5 stems to provide an indication of aspen mortality (Tables 2.1 and 2.2). Clear-felled Gunnison plots contained no live class 4 or 5 aspen stems as a result cutting. Comparing median values across untreated plots, I saw a much higher ratio of standing live to standing dead stems in Gunnison plots (median = 4.5) and the lowest ratio in Douglas Pass plots, (median =1) where the median number of live stems was equal to the median number of dead stems per hectare. The median ratio of live to dead mature stems was only marginally higher in untreated Moffat plots (median = 1.32).

The proportion of class 1, 2, and 3 stems with browsing damage differed significantly across sites (p = 0.001), as did the proportion of browsed class 1, 2, and 3 stems considered

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browsed at low (p=0.003) and high (p=0.0006) intensities. The proportion of browsed stems was significantly lower in clear-felled Gunnison plots than in Douglas Pass plots (p=0.005) and DeBeque plots (p=0.008); the proportion of browsed class 1, 2, and 3 stems browsed at low intensity was significantly lower in Douglas Pass plots than DeBeque plots (p=0.02); and the proportion of browsed class 1, 2, and 3 stems browsed at high intensity was significantly higher in Douglas Pass plots than clear-felled Gunnison plots (p=0.03) and DeBeque plots (p=0.007). The median proportion of all aspen stems that showed evidence of other types of damage did not exceed 5% for any study site or treatment (Figure 2.4).

ASPEN ROOTS

I found no significant differences in the number of aspen roots counted (Kruskal-Wallis p=0.16) or the aspen root surface area (Kruskal-Wallis p=0.169) between sites and treatments. I did not find any aspen roots in unburned Moffat plots. Distributions of aspen roots counted per 2-meter trench and total root surface area per trench are displayed in Figure 2.5.

LINEAR CORRELATIONS

Percent of aspen browsed was significantly negatively correlated with the number of live class 3 aspen stems per hectare (PPMCC = -0.60, p = 0.00012). Percent of aspen stems browsed at low intensity was positively correlated with live class 4 aspen stems (PPMCC = 0.48, p= 0.0009). A plot of Pearson product-moment correlation coefficients is displayed in Figure 2.6

DISCUSSION

ASPEN STAND TYPES

In 1976 Mueggler stated that while conifer presence or absence is the most valid indicator of stand type, it is not a perfect indicator, as some stands with a small conifer component are capable of persisting as an aspen dominated climax state. Mueggler (1985) later clarified that

conifer must not only be present in a stand, but it must be prominent. More recently, authors have further identified distinct aspen functional types within the seral and stable stand types based on responses to different disturbances, moisture regimes, and geographical locations (Shepperd et al. 2006; Rogers et al. 2014). Despite those efforts, conifer cover remains the most commonly used metric to determine whether an aspen stand is considered seral or stable (Rogers et al. 2014). Rogers et al. (2014) defined seral stands as those containing more than 10% conifer canopy cover, or if stand-replacing disturbance had occurred within the past thirty years, the potential to exceed 10% conifer canopy cover and noted that in many cases an aspen forest either contains no conifer trees or many and a determination of stand type can be made based on visual assessment. I measured conifer cover in terms of absolute conifer foliar cover which yielded lower values than canopy cover measurements, however I used the conifer cover metrics outlined by Rogers et al. (2014), juvenile growth metrics outlined by Kurzel et al. (2007), and other indicators of aspen stand subtypes identified by Shepperd et al. (2006) and Rogers et al. (2014) as my indicators of aspen stand type.

I found no conifer species in or near plots at the Gunnison or DeBeque study sites. This alone indicates that stands in these sites are likely stable stands. Comparing the characteristics of the areas in which these stands occur to descriptions of seral and stable stand subtypes further supports this conclusion. Rogers and others (2014) describe a "Colorado Plateau highlands and mesas" subtype of stable aspen stands as large and nearly homogenous stands that occur in western Colorado and southern Utah. The Gunnison site matches this description, which leads me to conclude that aspen stands there are Colorado Plateau highland and mesa seral stands. Rogers et al. (2014) also describe a "terrain isolated" stable stand subtype surrounded by non-forest communities displaying stunted aspen growth forms indicating abiotic site limitations that

limit conifer invasion. The photo in 2.7 is an example of a typical stand encountered at the DeBeque site and clearly shows a stunted growth form as well as the surrounding shrub dominated community. This description of terrain isolated stable aspen stands by Rogers and others (2014) accurately describes the stands occurring at the DeBeque site, which can be classified as the terrain isolated stable aspen subtype.

I found Douglas fir in 80% of my Douglas Pass plots with foliar cover values ranging from 2% to 26%. Three of these plots had a Douglas fir foliar cover value greater or equal to 10%. Canopy cover values for these plots would be greater than my measured foliar cover values, so Douglas fir canopy cover measurements would be greater than 10% in these three plots. These levels of conifer cover, the high proportion of stands containing Douglas fir, and the abundance of conifer seed sources in the area indicate that conversion to a conifer dominated state is possible and leads me to conclude that Douglas Pass aspen stands are seral stands.

I observed Rocky Mountain juniper and lodgepole pine in two (40% of burned plots) burned and two (50% of unburned plots) unburned Moffat County plots. Conifer tree foliar cover values in the two unburned Moffat plots were 2% and 8.7%. Conifer tree foliar cover values in the two burned Moffat plots were 2.3% and 5.3%. Stands in this area were surrounded by non-forest plant communities and displayed a stunted growth form similar to trees at the DeBeque site. The lower proportion of stands containing conifer, the low amount of conifer foliar cover, the difference in the type of conifer species present, and the similarities to stands at the DeBeque site indicate that these stands were at least historically stable stands.

Determining the type of aspen stands occurring at a specific site allows me to make predictions about STMs for these sites. First, I expect that the differences in potential successional trajectories between sites likely necessitate the development of separate models for

each site. Second, I predict that STMs developed for the Gunnison and DeBeque sites will not have the potential to transition to a conifer-dominated state, however Douglas Pass and Moffat may. Thus, these findings will inform the development of STMs for these sites.

MORTALITY, NEW GROWTH, AND DAMAGE

Mueggler 1989 stated that aspen stands with fewer than 500 juvenile stems (classes 1, 2, and 3) per acre are not capable of self-replacement. I observed median juvenile stem densities of over 500 stems per acre in untreated Moffat plots, and treated and untreated Gunnison plots. I also observed higher proportions of standing live mature stems in untreated Gunnison plots and DeBeque plots relative to other sites (Figure 2.2). The high proportion of standing dead stems and low juvenile stem densities in Douglas Pass and burned Moffat plots indicate that these stands are at risk of completely disappearing from these sites.

In the western United States, over-browsing by elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), cattle (*Bos* spp.), and sheep (*Ovis* spp.) can inhibit new stand growth and prevent a stand from producing enough juvenile stems to replace itself (DeByle 1985; DeRose & Long 2010; Rogers et al. 2010). Rogers et al. (2014) stated that in areas where elk populations are thought to be higher than the "historical range of variation" due to reintroduction (Bailey et al. 2007; Stritar et al. 2010) and elimination of predators (Beschta and Ripple 2009) this problem can be more severe. The high frequency and intensity of browsing observed in Douglas Pass and burned Moffat aspen stands are likely contributing to the low class 3 and 4 stem densities recorded in these areas. Large numbers of elk and other herbivores that remain in these areas for extended periods of time have the potential to have a long-term negative impact on stand resilience (Beck et al. 2006; Martin and Maron 2012; Rogers et al. 2014).

MANAGEMENT IMPLICATIONS AND FUTURE DIRECTIONS

Land managers interested in preserving aspen stands on the landscape can treat stands to initiate new growth. Prescribed burning (Bartos et al. 1994), clear-felling (Frey 2003), and spraying herbicide (Bartos and Lester 1984) are methods that have shown success in initiating suckering. In aspen rich areas such as the Gunnison site, the impact of herbivory is more widely distributed across the area. At the Douglas Pass, DeBeque and Moffat sites, where stands are in isolated patches surrounded by other, less palatable vegetation types, protecting juvenile stems from predation by herbivores is necessary (Baker et al. 1997; Seager et al. 2013). In Douglas Pass stands, where conifer cover levels are higher, conifer removal can be used to prevent potential transitions into a Douglas fir dominated state. Further work is needed to develop separate state-and-transition models for these systems in order to accurately describe plant associations at these sites and the abiotic and anthropogenic variables affecting these associations.

Table 2.1: Median live, standing dead, and fallen dead class 4 and 5 stems per hectare by site and treatment. The column on the far right displays the ratio of median live to median standing dead class 4 and 5 stems per hectare by site.

Site	Median Values by Site (Stems Per Hectare)			Ratio of Live to Standing Dead Class 4 and 5 Stems
	Live Class 4 and 5 Stems	Standing Dead Class 4 and 5 Stems	Fallen Dead Class 4 and 5 Stems	
DeBeque	466.67	166.67	66.67	2.34
Douglas Pass	100.00	100.00	33.33	1.00
Moffat Burned	33.33	100.00	66.67	0.67
Moffat Untreated	416.67	316.67	150.00	1.32
Gunnison Clear Cut	0.00	0.00	0.00	-
Gunnison Untreated	300.00	66.67	66.67	4.50

Table 2.2: Live, standing dead, and fallen dead class 4 and 5 stems per hectare by plot. Ratios of live to standing dead class 4 and 5 stems are presented in the far right column.

Plot	Stems Per Hectare			Ratio of Live to Standing Dead Class 4 and 5 Stems
	Live Class 4 and 5 Stems	Standing Dead Class 4 and 5 Stems	Fallen Dead Class 4 and 5 Stems	
DB11A	700.00	100.00	66.67	7.0
DB12A	100.00	0.00	100.00	-
DB13A	366.67	66.67	66.67	5.5
DB14A	333.33	233.33	33.33	1.4
DB15A	500.00	266.67	166.67	1.9
DB17A	66.67	66.67	66.67	1.0
DB1A	333.33	266.67	66.67	1.3
DB2A	466.67	266.67	100.00	1.8
DB3A	466.67	166.67	66.67	2.8
DB4A	300.00	100.00	66.67	3.0
DB5A	1000.00	100.00	33.33	10.0
DB6A	466.67	166.67	66.67	2.8
DB7A	533.33	400.00	33.33	1.3
DP10AA	133.33	66.67	0.00	2.0
DP11A	200.00	300.00	0.00	0.7
DP14A	66.67	200.00	33.33	0.3
DP19A	66.67	233.33	0.00	0.3
DP1A	433.33	166.67	33.33	2.6
DP20A	0.00	200.00	133.33	0.0
DP22A	100.00	0.00	33.33	-
DP22P	33.33	0.00	0.00	-
DP2A	133.33	100.00	66.67	1.3
DP3A	100.00	0.00	66.67	-
DP5A	33.33	66.67	166.67	0.5
DP6AB	233.33	100.00	0.00	2.3
DP6P	66.67	33.33	0.00	2.0
MCSMB1	0.00	33.33	133.33	0.0
MCSMB1F	66.67	100.00	0.00	0.7
MCSMP1	666.67	400.00	200.00	1.7
MCSMB2	0.00	200.00	566.67	0.0
MCSMB3	33.33	33.33	66.67	1.0
MCSMP2	433.33	333.33	100.00	1.3
MCSMP3	66.67	100.00	0.00	0.7
MDPB1	200.00	466.67	500.00	0.4
MDPP1	400.00	300.00	600.00	1.3
NF1AT	0.00	0.00	0.00	-

NF1AU	233.33	166.67	33.33	1.4
NF2AT	0.00	0.00	0.00	-
NF2AU	500.00	66.67	66.67	7.5
NF4AT	0.00	0.00	0.00	-
NF4AU	300.00	66.67	100.00	4.5
NF6AT	0.00	0.00	0.00	-
NF6AU	533.33	66.67	66.67	8.0
NF7AT	0.00	0.00	0.00	-
NF7AU	166.67	100.00	100.00	1.7
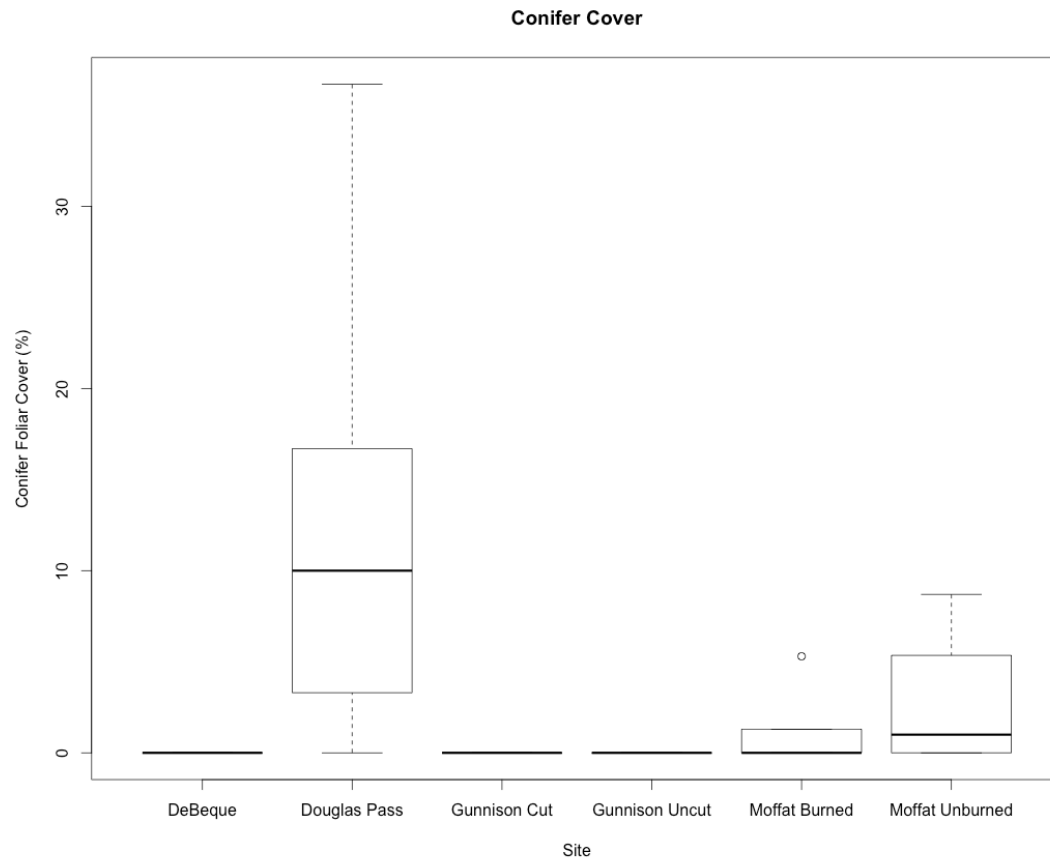
Conifer Cover

Figure 2.1: Distributions of percent conifer tree foliar cover for each site and treatment. No conifer trees were present in any DeBeque or Gunnison plots. Species observed included: Douglas-fir (*Pseudotsuga* menziesii (Mirb.) Franco) at Douglas Pass and juniper (*Juniperus scopulorum* Sarg.) and lodgepole pine (*Pinus contorta* ex Loudon) in burned and unburned Moffat plots. Median conifer tree foliar cover in plots near Douglas Pass was the highest (median =10%, IQR = 13.4). Significant differences were found between Douglas Pass and Moffat conifer cover distributions (Kruskal-Wallis p=0.000037). No significant differences (Kruskal-Wallis p=0.59) were found between unburned plots (median = 1%, IQR = 3.675) and burned plots (median = 0%, IQR= 1.3) in Moffat County.
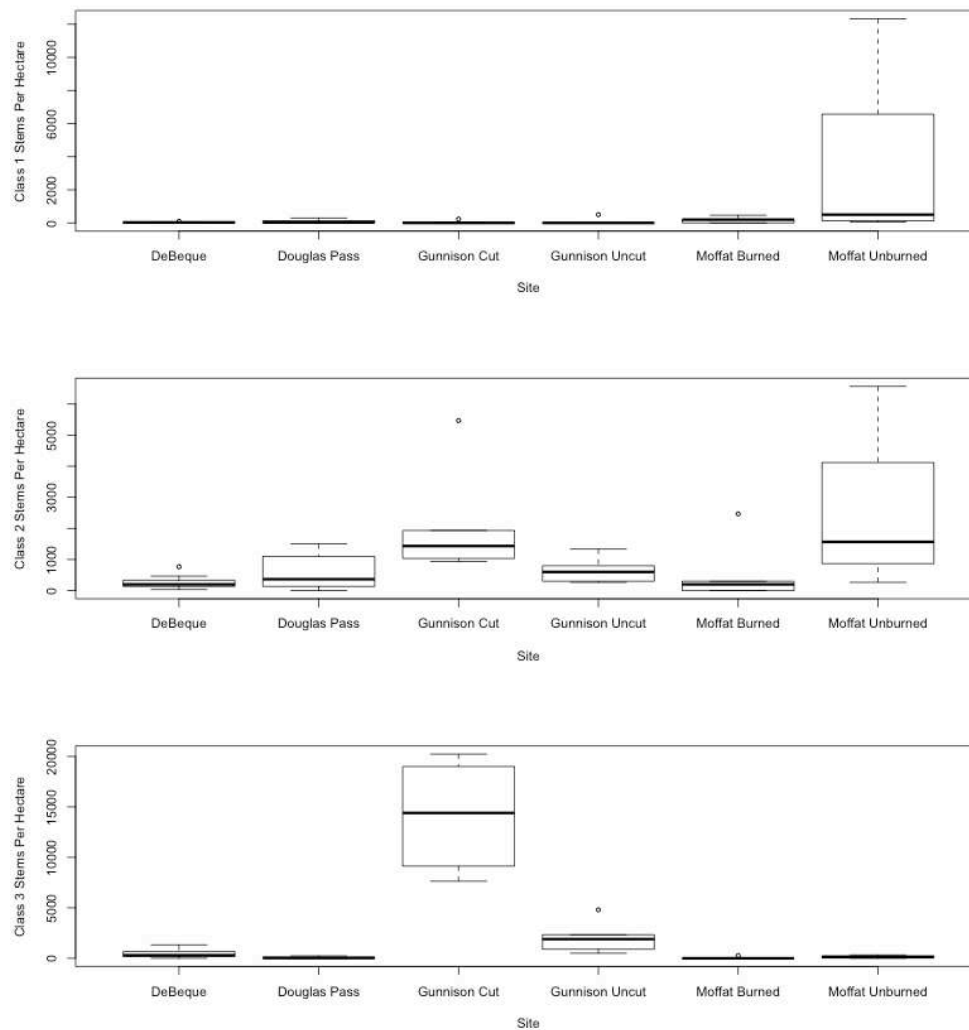
Figure 2.2: Distributions of aspen stem counts (stems/hectare) by size class for each site and treatment. I used size classes outlined by Strong et al. (2010): class one stems are those less than 0.46 meters tall, class two stems are those between 0.46 meters and 1.37 meters tall, class three stems are those greater than 1.37 meters tall and less than 5.08 centimeters in diameter at breast height, class 4 stems are those greater than 1.37 meters tall and greater than 5.08 centimeters in diameter at breast height, and class five stems are those considered canopy height. There were no significant differences in class 1 stem density distributions across sites (Kruskal-Wallis $p = 0.074$), however Kruskal-Wallis tests found significant differences among sites for distributions of all other live aspen stem classes (Class 2, $p = 0.009$; Class 3, $p = 0.000039$; Class 4, $p = 0.00094$; Class 5, $p=0.015$). Mean rank sums of class 2 stem densities were higher in clear-felled Gunnison plots than in DeBeque plots (Dunn's test $p=0.022$). Mean rank sums of class 3 stem densities at Douglas Pass were lower than clear-felled Gunnison plots (Dunn's test $p=0.0002$) and untreated Gunnison plots ($p=0.01$). Mean rank sums of class 3 stems in burned Moffat plots were lower than clear-felled (Dunn's test $p=0.001$) and untreated (Dunn's test $p=0.02$) Gunnison plots.
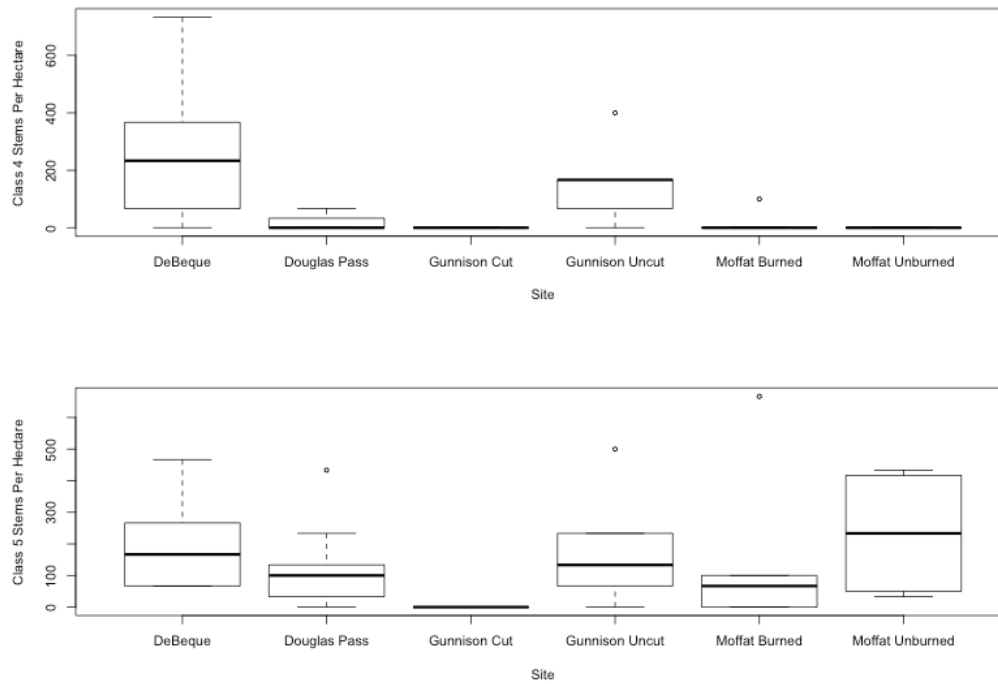
Figure 2.2 Continued: Mean rank sums of class 4 stem densities at DeBeque were higher than at Douglas Pass (Dunn's test p=0.042) and lower than in clear-felled Gunnison plots (Dunn's test p=0.023). Significant differences were found between DeBeque and clear-felled Gunnison plots for mean rank sums of class 5 stem densities (Dunn's test p=0.0059).
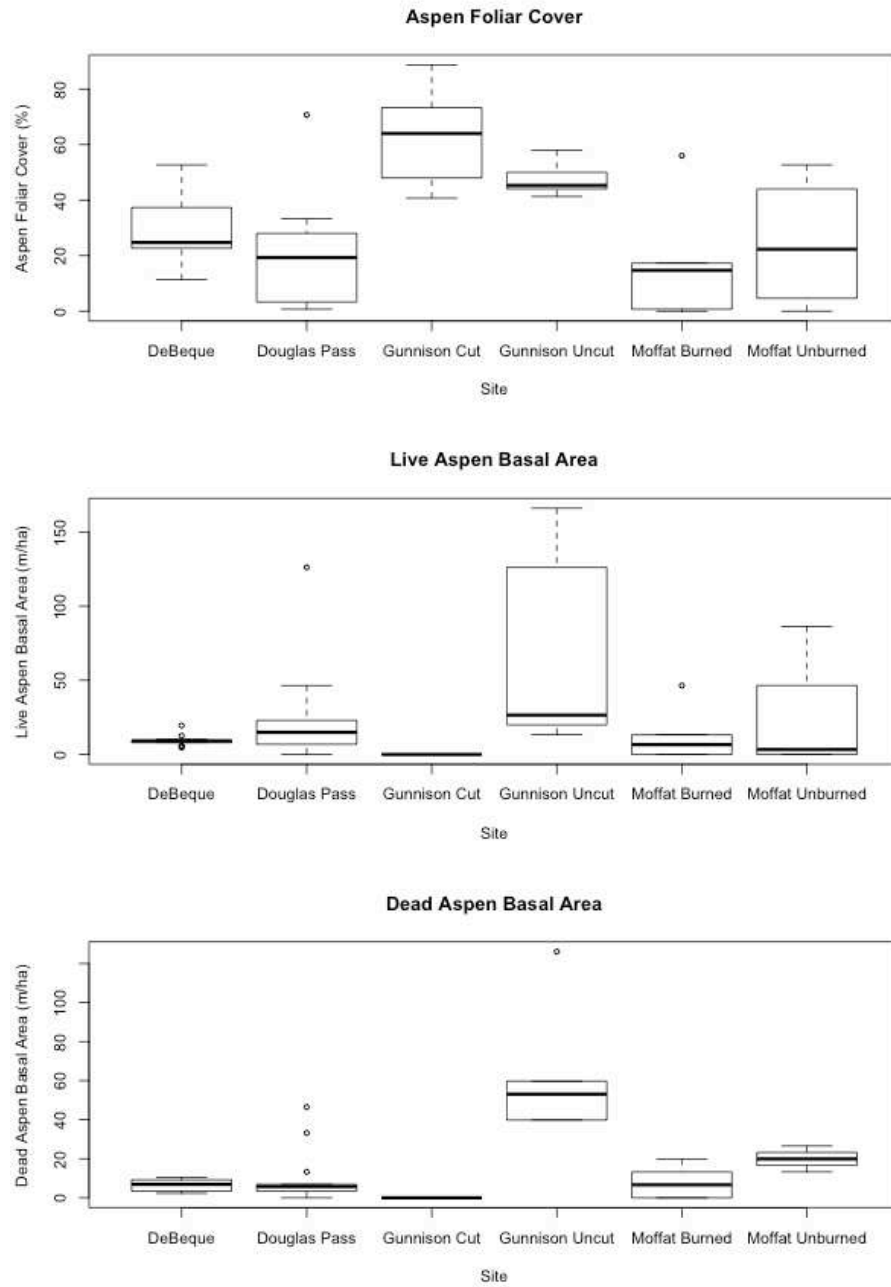
Figure 2.3: Distributions of live aspen foliar cover, live aspen basal area estimates, and dead aspen basal area estimates by site and treatment. Distributions of aspen foliar cover (Dunn's test p=0.003), live aspen basal area (Dunn's test p=0.003), and dead aspen basal area (Dunn's test p=0.0001) differed significantly across sites. The highest median level of aspen foliar cover occurred in clear-felled Gunnison plots (median = 64%, IQR = 36.65).
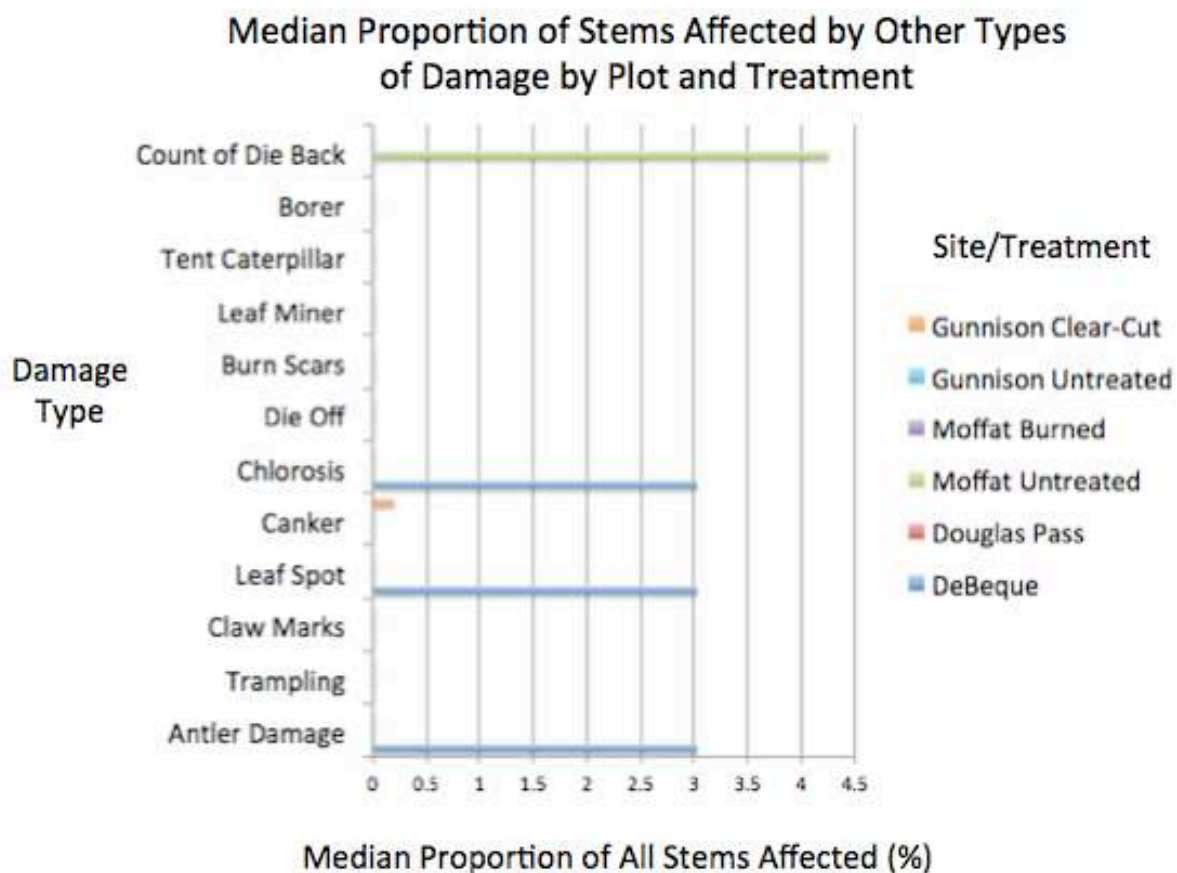
Figure 2.4: Median proportion all stems observed to show damage of any form other than browsing by site and treatment. Damage observed includes: antler damage, trampling, claw marks, leaf spot, canker, chlorosis, stem die off, burn scars, leaf miner, tent caterpillar, or any borer.
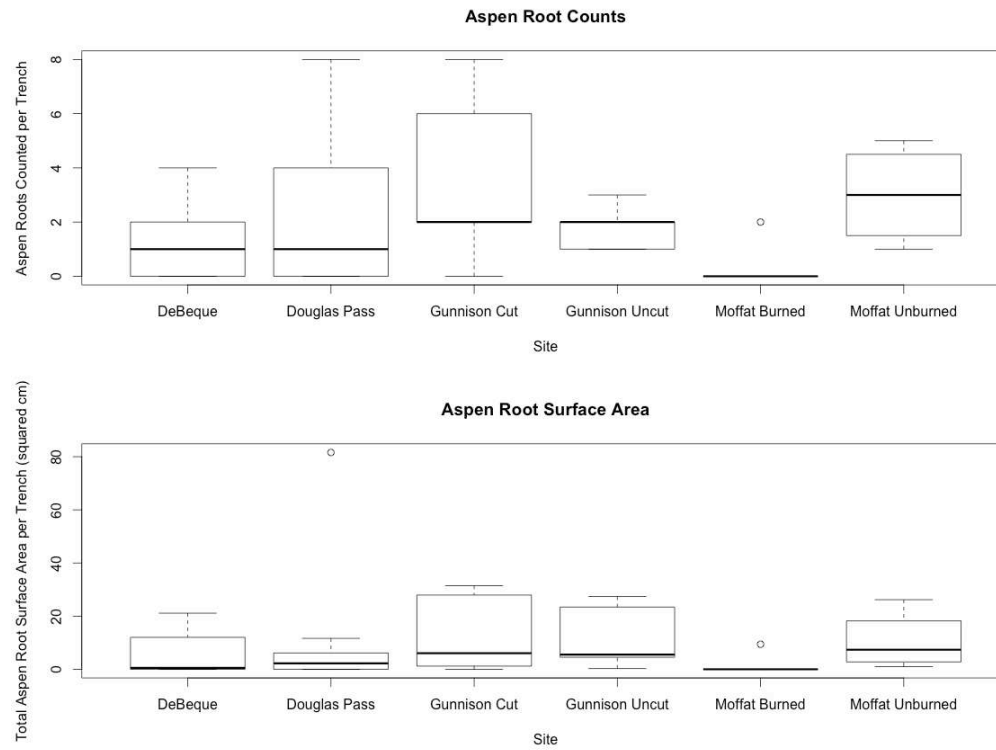
Figure 2.5: Distributions of aspen root counts and calculated root surface area by plot and treatment.

|	Aspen	Conifer	Class.1.Stems.Hectare	Class.2.Stems.Hectare	Class.3.Stems.Hectare	Class.4.Stems.Hectare	Class.5.Stems.Hectare	LiveAspBA	DeadAspBA	Percent.Browsed	Percent.Browsed.Low	Percent.Browsed.Medium	Percent.Browsed.High	RootsPerTrench	Total.Root.Surface.Area	TotSD	TotDF
Aspen	100	-29	16	48	63		21	38	10	-35	13	-15	-12	50	50	31	
Conifer	-29	100	10		-19	-24	-19		-13	21	-34	19	33	-7	-11	-21	-11
Class.1.Stems.Hectare	16	10	100	70	-6	-11	29	30	8				4	25	21		6
Class.2.Stems.Hectare	48		70	100	43	-21	11	24		-22	-14	-13	8	52	35	20	10
Class.3.Stems.Hectare	63	-19	-6	43	100	-12	-32	-18	-7	-60		-25	-27	37	20	47	-22
Class.4.Stems.Hectare		-24	-11	-21	-12	100		-12	9		48		-29		-6		-8
Class.5.Stems.Hectare	21	-19	29	11	-32		100	47		31	8	19	11	8	22		17
LiveAspBA	38		30	24	-18	-12	47	100	31		5	15	4	33	52		7
DeadAspBA	10	-13	8		-7	9		31	100	-34	37	-12	-19	5	21		9
Percent.Browsed	-35	21		-22	-60		31		-34	100	-17	49	47	-18	-18	-15	21
Percent.Browsed.Low	13	-34		-14		48	8	5	37	-17	100	-15	-54	-16	-7	12	
Percent.Browsed.Medium	-15	19		-13	-25		19	15	-12	49	-15	100	-17	-6			-11
Percent.Browsed.High	-12	33	4	8	-27	-29	11	4	-19	47	-54	-17	100		-4		26
RootsPerTrench	50	-7	25	52	37		8	33	5	-18	-16	-6		100	77		-21
Total.Root.Surface.Area	50	-11	21	35	20	-6	22	52	21	-18	-7		-4	77	100	6	-11
TotSD	31	-21		20	47					-15	12					100	28
TotDF		-11	6	10	-22	-8	17	7	9	21		-11	26	-21	-11	28	100

Correlation coefficients are represented as percentages and only significant values are shown ($p < 0.05$).

Figure 2.6: Pearson product-moment correlation values (as %) for all measured variables. Percent of aspen browsed (Percent.Browsed) was significantly negatively correlated with the number of live class 3 aspen stems per hectare (Class.3.Stems.Hectare) (PPMCC = -0.60, $p = 0.00012$). Percent of aspen stems browsed at low intensity (Percent.Browsed.Low) was positively correlated with live class 4 aspen stems (Class.4.Stems.Hectare) (PPMCC = 0.48, $p = 0.0009$).

Figure 2.7: Photograph of DeBeque plot . This stand was representative of the isolated stands in this area and shows that the vegetation covering the surrounding landscape was shrub-dominated.

CHAPTER 3

ASPEN STATE-AND-TRANSITION MODEL DEVELOPMENT

SUMMARY

This chapter addresses the following research objectives: 1) characterize the ecological

sites on which aspen stands occur in four study sites in western Colorado, and 2) develop ES-

specific data-driven STMs for aspen dominated ecological sites in western Colorado using

ecological field data. Using multivariate cluster analyses, ordination, and PERMANOVA, I

identified four distinct ecological sites corresponding with the four different study sites. I

identified aspen and non-aspen dominated states at the Douglas Pass, DeBeque, and Gunnison

sites and a single aspen–dominated state at the Moffat site. Abiotic factors seemed to explain

differences between states, while presence or absence of burning or clear-felling did not.

Potential vegetation states were described for each of the ecological sites. I presented my models

and compared them to existing aspen STMs in order to assess the completeness of my models.

INTRODUCTION

Westoby et al. (1989) introduced the state-and-transition model (STM) as an alternative

to traditional linear Clementsian successional models of plant communities toward a climax

state. STMs are conceptual diagrams used to present what I know about the dynamics of an

ecosystem. Unlike linear Clementsian models, STMs recognize the potential for multiple

successional pathways and restoration pathways (Briske et al. 2008). In 2005 the US Forest

Service (USFS), Bureau of Land Management (BLM), and Natural Resources Conservation

Service (NRCS) formally adopted the Ecological Site (ES) concept and the creation of STMs for

approved Ecological Site Descriptions (ESDs) by signing the Interagency Memorandum of

Understanding (Briske et al. 2008). An ecological site is defined as a specific type of land

characterized by specific abiotic characteristics, including: soil, landform, climate, hydrology, and geological features (Caudle et al. 2013). These abiotic characteristics result in distinctive vegetation assemblages that respond similarly to natural and anthropogenic disturbances (Caudle et al. 2013). Approved ESDs include descriptions of abiotic site characteristics as well as an STM that describes current, historic, and potential vegetation assemblages for a given site and ecological trajectories and dynamics. The information provided by ESDs allows managers to predict the land's responses to disturbances or management practices, its resilience, and suitability for various uses. Many areas in the western United States do not currently have approved ESDs, so individuals and organizations are partnering with the NRCS to develop new ESDs for these areas. The NRCS is working to standardize the definitions of STM components and collaborating with research groups such as LFL to create well-tested, repeatable methods for creating STMs.

STMs can be used as tools by land managers to understand plant community dynamics and can offer insight into the types of management practices that can help a site transition toward a preferable state. STMs consist of five components: states, transitions, restoration pathways, community phases, and community pathways (NRCS 2014). Box and arrow diagrams are used to visually represent STMs. Within STMs, community phases refer to plant associations that differ in terms of species composition, but are functionally similar (NRCS 2014). Suites of communities that differ in species composition and functionality are collectively referred to as states (Briske et al. 2006; NRCS 2014). In alternative states, there will be at least one key difference in the pathways through which water, nutrients, or energy are cycled (NRCS 2014). In an STM diagram, a box can be used to represent a state or a community. Shifts from one community phase to another within a state are called community pathways and may be reversible

(Briske et al. 2006). Transitions are the shifts that occur between states when state structure, function, or both structure and function are significantly altered by a natural or anthropogenic external factor or disturbance (Briske et al. 2006). Transitions may be caused by multiple small changes over a period of time or sudden, high magnitude disturbances (Peters et al. 2004; Barnosky et al. 2012). The moment within a transition that results in the modification of both the structure and function of an ecosystem beyond its resistance and resilience capacity, and a shift from negative reinforcement feedbacks to positive reinforcement feedbacks is referred to as a threshold (Briske et al. 2006; Briske et al. 2008). Once a threshold is crossed, the result is a transition to an alternative state (Briske et al. 2008). Restoration pathways identify the management practices or environmental conditions needed to return a degraded state to a more favorable state. However, returning a site to its former condition can be a prohibitively expensive and time consuming endeavor (Friedel 1991; Bestelmeyer et al. 2003). The new alternative state that results from a transition will typically persist after the causal disturbance has ceased or been removed (Westoby et al. 1989; Friedel 1991).

STMs can rely on professional knowledge like many of the models developed by the NRCS for ESDs; they can be purely data-driven such as those developed by Allen-Diaz and Bartolome (1998), and Kachergis et al. (2011). STMs can also be based on local knowledge (Knapp and Fernandez-Gimenez 2009) or can integrate a combination of expert and local knowledge, literature, and field observations (Kachergis et al. 2013). STMs are potentially powerful land management tools that should be, but often are not, tested using empirical data (Bagchi et al. 2012, Twidwell et al. 2013, Tipton 2015). I used ecological field data to generate data-driven STMs. I record and report the methods used and ensure that they are repeatable so

that more information can be gathered in the future to enable future updates and improvements to the model.

Ecological site descriptions (ESDs) and the STMs they contain are currently being developed to describe rangeland vegetation dynamics across the western United States. Many of the STMs currently being incorporated into these ESDs are entirely conceptual (Tidwell et al. 2013). ESDs have been used to describe rangelands, and as a result many conceptual STMs exist for rangelands in the western United States (Tidwell et al. 2013). A number of STMs have also been used to describe woodland systems: Creutzburg et al. (2012) addressed juniper invasion in Oregon; George and Alonso 2008 created models for oak woodlands in California; Klenner et al. (2000) modeled forests in British Colombia; Klenner and Walton (2009) created a model for dry forest ecosystems in British Colombia; and Price et al. (2012) looked at impacts of climate change in forests in Michigan. Generalized conceptual STMs have been developed for aspen dominated systems in Utah and Colorado (NRCS-USFS-USU, 2009). Very few data-driven STMs have been developed for aspen dominated systems, such as the model developed by Strand et al. (2009) for aspen systems in Idaho or the draft STM for forest succession in Alberta, Canada developed by Bork et al. (1997) that included aspen parklands and vegetation community interactions. There is a need for data-driven STMs for aspen woodlands in Colorado and other western states. My research objectives for this chapter were to characterize the ecological sites on which aspen stands occur in four study sites in western Colorado and to develop ES-specific data-driven STMs for aspen dominated ecological sites in western Colorado using ecological field data.

METHODS

STUDY SITES

Two sites were in northwestern Garfield County, one near Douglas Pass and another north of DeBeque. Landowners at these sites were concerned with the health of aspen stands on their properties. To assess the impact of different management treatments and potential resulting transitions to alternative states, aspen stands were also sampled at sites in Gunnison National Forest just north of Paonia, Colorado and northwestern Moffat County. Clear-felling occurred in aspen stands at the Gunnison study site in 2008 and 2009. The Little Snake Field Office of the Bureau of Land Management conducted prescribed burns on stands in the Moffat study area in 2008. Sites were selected to represent a variety of potential aspen-supporting ecological sites, stand types and management treatments that I expected to influence stand dynamics. The Douglas Pass and DeBeque sites are both private ranches. DeBeque plots are between 2398 and 2620 meters in elevation and receive between 512 and 518 centimeters in precipitation annually (PRISM Climate Group 2012). DeBeque plot soils were loams, clay loams, and sandy clay loams. Douglas Pass plots were between 2560 and 2676 meters in elevation and receive between 546 and 597 centimeters in precipitation annually (PRISM Climate Group 2012). Douglas Pass soils were loams, clay loams, sandy clay loams, sandy clays, and clays. The sites in Gunnison National Forest and in Moffat County were on public land. Gunnison plots are between 2636 and 2864 meters in elevation and receive between 656 and 749 centimeters in precipitation annually (PRISM Climate Group 2012). Gunnison soils were a combination of clay loams, loams, sandy clays, and clays. Moffat plots are between 2440 and 2672 meters in elevation and receive between 409 and 479 centimeters in precipitation annually (PRISM Climate Group 2012). Moffat soil textures were loams, sandy loams, clays, sandy clays, and silty loams. In 2008 and

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2009, the National Forest Service clear-felled portions of aspen stands in Gunnison National Forest. The Bureau of Land Management conducted prescribed burns on stands in my Moffat study area in 2008 and 2009. I included treated stands at both sites in my sample design.

SAMPLING DESIGN

In order to determine whether aspen stands occurred on different ecological sites and be able to identify different states and communities within ecological sites, I designed my sampling to capture potential alternative vegetation states within the same soil or ecological site. At the DeBeque and Douglas Pass sites, I did this by selecting paired plots on the same soil map unit within and adjacent to aspen stands. At the Gunnison site, I sampled paired plots in treated and untreated aspen stands. I was only able to sample one non-aspen plot that occurred within the same soil map unit as one of my paired treated and untreated aspen stands at the Gunnison site because aspen stands completely covered the soil map units in which the treated stands were found. At the Moffat site, I sampled paired plots in treated and untreated aspen stands.

To select plot locations at the Douglas Pass and DeBeque sites, I digitized aspen stands in each study area using 2014 National Agriculture Imagery Program (NAIP) satellite imagery in ArcMap version 10.1. I generated a centroid point in the center of each aspen stand polygon. I moved plot points at least 50 m if they were located on a fence line, road of any kind, or water source (stream or catch basin) and allowed for no more than 2 plots to be located within 400 m of each other. I then created a map layer of slope ranges in 10% increments using shuttle radar topography mission digital elevation data (USGS 2004). I overlaid a soil survey geographic (SSURGO) data base soil map (Soil Survey Staff 2014). I placed one new paired plot point within the same soil map unit and slope range as each aspen centroid point, outside of the aspen stand polygon. At the Gunnison and Moffat sites I used maps provided by the U.S. Forest

Service and the Bureau of Land Management to locate treated and untreated stands in Gunnison National Forest and on Cold Springs Mountain and Diamond Peak. Treated stands were digitized and centroids were generated for each treatment. Paired points were then placed within adjacent untreated stands. I was only able to generate one non-aspen point within the same soil map unit as one of the clear-felled and uncut aspen plot pairs at the Gunnison site using the same methods described for paired plot point generation at Douglas Pass and DeBeque.

DATA COLLECTION

We collected soil and vegetation data within 50 meter x 50 meter square plots, centered on one of my generated aspen centroid or paired points. In each plot, I collected data along 3, 50 meter transect tapes, located 25 meters apart, parallel to the hill aspect (perpendicular to contours) and parallel to one another. I used the line point intercept (LPI) method (Herrick et al. 2005) to record each vertical species hit to estimate foliar and basal cover by species, bare ground, and litter cover. I recorded measurements at 1 m intervals along each of the three 50m transects. Tree canopy foliar cover observations were made using a GRS densiometer at each LPI point. I did not record multiple hits for a single species at a given point unless one of the hits was in the basal layer (Herrick et al. 2005). I observed and recorded the slope, aspect, and elevation from plot center. I measured utilization for a selected representative grass species at each plot and calculated utilization using species utilization curves.

A soil pit was excavated at the center of each plot to a depth of 100cm or until bedrock layer is encountered. I assessed and recorded soil color, structure, texture, effervescence, type of parent material, and rock fragment content for each soil horizon following protocols set forth by the NRCS (Schoeneberger et al. 2002). Climate variables included: 30 year mean annual and monthly precipitation; 30 mean temperature; 30 mean high temperature; 30 mean low

temperature; and a measure of isothermality, and were obtained from a USGS data set created using PRISM data (O'Donnell and Ignizio 2012; PRISM Climate Group 2012). Surface geology data were obtained from USGS preliminary data set (USGS 2005).

DATA ANALYSIS

My objectives in this chapter were to 1) identify potentially distinct ecological sites based on environmental and soil characteristics, 2) identify potential vegetation states based on plant species composition, 3) determine if states are functionally as well as compositionally distinct, and 4) examine the relationships between abiotic variables, management or disturbance history, and potential states and communities. I then synthesized the results of these analyses into draft STMs. Below, I have described the multivariate analysis methods used to achieve each of these objectives in detail. Data were entered onto a shared working drive using either Excel or the MS Access Database for Inventory, Monitoring, and Assessment (Courtright and Van Zee 2011). All entered data were later checked for errors.

First, I classified all plots according to their abiotic characteristics in order to separate potentially distinct ecological sites with different ecological potentials. I performed linear correlations of all climate and soil variables and where Pearson's correlation absolute value was greater than 0.75, the variable with the largest mean absolute correlation was removed. I clustered plots based on soil and climate characteristics using partitioning around medoids (PAM) (van der Laan et al. 2003). Potential ecological sites were selected based on average the silhouette width of clusters. I used pairwise permutational multivariate analysis of variance (PERMANOVA) to determine if these abiotic associations were significantly different than random.

Second, to identify community phases and alternative states, I analyzed the vegetation foliar cover of plots within each potential ecological site identified using PAM clustering. To prepare vegetation foliar cover data for analysis, I removed species that occurred in fewer than 5% of plots from the compositional data so that community composition was defined by more common species (McCune and Grace 2002). Foliar cover data were then square root transformed to reduce the impact of the most common species (McCune and Grace 2002). Plot foliar cover dissimilarities were calculated using Bray-Curtis distance measures based on per plot species composition.

Plant associations were determined by performing agglomerative hierarchical cluster analysis on species composition data within my PAM clusters (potential ecological sites). This method groups plots into branches on a cluster dendrogram based on similarities in species composition. I then used indicator species analysis (ISA) and a randomization test (1000 iterations) on the resulting clusters. This allowed me to select an appropriate number of potential community phases and states by pruning the dendrogram using the number of clusters that resulted in the greatest number of significant indicator species (Kachergis et al. 2012; McCune and Grace 2002).

Third, I performed pairwise permutational multivariate analysis of variance (PERMANOVA) to determine if these plant associations were significantly different than random based on species composition and a suite of functional indicators. Functional indicators included percent bare ground, basal plant cover, litter cover, duff cover, graminoid foliar cover, forb foliar cover, shrub foliar cover, tree foliar cover, and total plant foliar cover. Plant clusters that are significantly different according to species composition comparisons are considered different plant communities. Communities that do not differentiate significantly based on

functional traits are considered community phases within the same state. Significant differences in species composition and functional indicators indicated functionally and compositionally distinct states.

Fourth, relationships between species associations, treatments, and abiotic variables were assessed using non-metric multidimensional scaling (NMS) and the random forest algorithm that is capable of assessing variable importance within a clustering classification (McCune and Grace 2002). These analyses were used to inform the transitions between states.

Fifth and finally, I integrated the results of the findings of the above analyses with the results of chapter 2 and existing STMs to develop draft STMs for each study site.

RESULTS

SOIL AND ABIOTIC SITE CHARACTERISTICS: POTENTIAL ECOLOGICAL SITES

I identified 4 clusters based on abiotic site characteristics, which corresponded with my 4 sampling sites, with one exception. One plot from the DeBeque site was more closely associated with the plots in Gunnison National Forest. The mean PAM silhouette width was 0.27, indicating weak abiotic associations across my sites. PAM clustering revealed weaker abiotic cluster associations within sites with the exception of Moffat plots which had a mean silhouette width of 0.39 (Figure 2). Mean silhouette widths between 0.26 and 0.5 indicate weak or artificial cluster structure (Struyf et al. 1997). Pairwise PERMANOVA revealed significant differences between all abiotic clusters (p=0.006). The abiotic differences among my 4 sites likely indicate different ecological sites. Based on the reasoning that the four sites represent for distinct ecological sites, I conducted analyses of plant communities separately for each site.

POTENTIAL VEGETATION STATES AND PLANT COMMUNITIES

In the following sections, I describe the plant communities and potential vegetation states separately for each of the four study sites.

DEBEQUE SITE

The 26 plots in abiotic group 1 clustered into two groups based on hierarchical cluster analysis of species cover and indicator species analysis. Two groups had the lowest average indicator species analysis P-value (ISA; P=0.181). Indicator species codes for each cluster are listed in Table 3.1 4. Dominant species in cluster 1 included: snowberry (*Symphoricarpos albus* (L.) S. F. Blake) (median foliar cover = 48.7%), Kentucky bluegrass (*Poa pratensis* L.) (median foliar cover = 36%), and quaking aspen (*Populus tremuloides* Michx.) (median foliar cover = 23.3%). Dominant species in cluster 2 included: Kentucky bluegrass (*Poa pratensis* L.) (median foliar cover = 40%), snowberry (*Symphoricarpos albus* (L.) S. F. Blake) (median foliar cover = 36.6%), and serviceberry (*Amelanchier alnifolia* Nutt.) (median foliar cover = 20%), and no aspen were found in these plots. The variation in species composition between groups 1 and 2 that can be explained by group membership was 22.9% (PERMANOVA; R-squared =0.229; Bonferonni P-Value = 0.001). Groups 1 and 2 were also significantly different when compared using pair-wise PERMANOVA on my matrix of functional traits (Table 3.1). I therefore concluded that these two plant associations represent two distinct states, which differ in both species composition and functional attributes.

NMS identified associations among species composition and certain environmental variables. A solution was found after 10 tries. The final stress for the 3 axis NMS solution was 0.086 on 25 plots and 55 species (Axis 1 r^2 = 0.20, Axis 2 r^2 = 0.12, Axis 3 r^2 = 0.09). The non-metric fit R-squared = 0.993, the linear fit R-squared = 0.951. The random forest model found an

out-of-bag error rate of 32% and found the highest mean decrease in accuracy values for my

horizon 2 thickness, horizon 1clay content, aspect, and depth variables (Figure 3.3).

These results indicate that there are two potential alternative states at the DeBeque site,

an aspen-dominated state and a shrub-dominated state (Figure 3.4). The aspen state was

associated with a deeper pedon and thicker horizons 1 and 2 (Figure 3.5). The shrub-dominated

state was associated with more clay, a higher hillslope position and higher horizon 2 values and

chromas (Figure 3.5).

GUNNISON SITE

I removed the DeBeque plot, which was an outlier and was disproportionately affecting

my classification, then performed hierarchical cluster analysis, indicator species analysis, and a

randomization test on the 11 Gunnison National Forest plots. I selected 5 groups based on the

result of my randomization test, which found that these 5 groups had the lowest average indicator

species analysis P-value (ISA; P=0.0.322). Significant indicator species for each state are listed

in Table 3.2.

One of the five resulting potential states, group 4, was comprised of a single non-aspen

dominated plot. Group 3 consisted of a single untreated aspen-dominated plot, and groups 1, 2,

and 5 were made up of treated and untreated plots (Table 3.2). One hundred percent of the

variation in species composition between groups 3 and 4 can be explained by group membership

(PERMANOVA; R-squared =1). None of the remaining groups were significantly different

when compared using pair-wise PERMANOVA on my matrix of species composition or on my

matrix of functional traits (Table 3.1). I determined that cluster 4 was one non-aspen dominated

state and the remaining clusters made up another separate aspen dominated state (Figure 3.6).

Dominant species in the non-aspen state included: snowberry (median foliar cover = 58.7),

Kentucky bluegrass (median foliar cover = 38.7), and Gambel oak (*Quercus gambelii* Nutt.) (median foliar cover = 25.3%). Dominant species in the aspen-dominated state included: quaking aspen (median foliar cover = 49%), snowberry (median foliar cover = 40.65), and Kentucky bluegrass (median foliar cover = 30%).

Using NMS, a solution was reached after 4 tries. The final stress for my three axis NMS solution was 0.037 on 11 plots and 51 species (Axis 1 r^2 = 0.22, Axis 2 r^2 = 0.094, Axis 3 r^2 = 0.037). The non-metric fit R-squared = 0.991, the linear fit R-squared = 0.952. The random forest model found an out-of-bag error rate of 0% and found the highest mean decrease in accuracy values for my horizon 3 clay content, horizon 2 clay content, horizon 2 thickness, and horizon 1 clay variables (Figure 3.7). The aspen-dominated state was associated with higher elevation and lower clay content in the top 3 horizons. Clear felling treatments were not found to be associated with separate states or communities.

DOUGLAS PASS SITE

After conducting hierarchical cluster analysis and indicator species analysis to identify different potential alternative states among the 26 Douglas Pass plots included in my third abiotic PAM cluster, I selected 5 groups based on the result of my randomization test, which found that these 5 groups had the lowest average indicator species analysis P-value (ISA; P=0.289). Indicator species for each state are listed in Table 3.2.

The variation in species composition between groups 1 and 2 and groups 1 and 4 were significant (Table 3.1). Groups 1 and 2 were also significantly different when compared using pair-wise PERMANOVA on my matrix of functional traits (Table 3.1). These findings indicate that group 1 is an aspen-dominated state and groups 2 and 4 make up one non-aspen dominated state (Figure 3.9), however groups 3 and 5 were not compositionally or functionally different

from either state and may indicate that these plots are in the process of transitioning from one state to the other.

Dominant species in my aspen-dominated state included: blue wildrye (*Elymus glaucus* Buckley) (median foliar cover = 25%); mountain brome (*Bromus marginatus* Nees ex Steud.) (median foliar cover = 22%); quaking aspen (median foliar cover = 22%); and Kentucky bluegrass (median foliar cover = 17%). Dominant species in my non-aspen state included: snowberry (median foliar cover = 29.3%); Kentucky bluegrass (median foliar cover = 17.4%); and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (median foliar cover = 16%).

Using NMS, a solution was reached after 1 try. The final stress for the 3 axis NMS solution was 0.15 on 22 plots and 61 species (Axis 1 r^2 = 0.25, Axis 2 r^2 = 0.15, Axis 3 r^2 = 0.095). The non-metric fit R-squared = 0.978, the linear fit R-squared = 0.909 (Figure 3.10). The random forest model found an out-of-bag error rate of 54.54% and found the highest mean decrease in accuracy values for my horizon 3 thickness and horizon 1 thickness variables (Figure 3.11). Membership in the aspen dominated state was correlated with deeper soils and thicker horizons 1 and 3 (Figure 3.9).

MOFFAT SITE

Among the 9 Moffat plots included in my fourth abiotic PAM cluster, I selected 4 groups based on the result of my randomization test, which found that these 4 groups had the lowest average indicator species analysis P-value (ISA; P=0.435). Plant codes for all significant indicator species for each potential state are listed in Table 3.2. Pairwise comparisons of species composition and functional traits between groups using pair-wise PERMANOVA revealed no significant differences (Table 3.1). I was not able to identify separate plant communities or states at my Moffat County site. This led me to conclude that all plots occurred within a single aspen-

dominated state (Figure 3.12). Dominant plant species included: smallwing sedge (*Carex*

microptera Mack.) (median foliar cover = 14.7%), quaking aspen (median foliar cover = 14.7%),

and Kentucky bluegrass (median foliar cover = 12.7%).

A solution was found using NMS after 1 try. The final stress for the 3 axis NMS solution

was 0.11 on 9 plots and 31 species (Axis 1 r^2 = 0.33, Axis 2 r^2 = 0.11, Axis 3 r^2 = 0.042) (Figure

3.13). The non-metric fit R-squared = 0.987, the linear fit R-squared = 0.9. The random forest

model resulted in an out-of-bag error rate of 88.89% and found the highest mean decrease in

accuracy values for my elevation and depth variables (Figure 3.14). I identified 1 state and did

not find different communities within this state. Prescribed burning did not result in an alternate

state.

DISCUSSION

STATES, COMMUNITIES AND POTENTIAL TRANSITIONS IN ASPEN WOODLAND
DOMINATED ECOLOGICAL SITES

Soil and other abiotic characteristics differed significantly among the four study sites,

indicating that each site should be treated as a distinct ecological site. At each of these sites,

when multiple vegetation states were present, soil properties and other abiotic site characteristics

were correlated with observed differences in compositional and functional attributes of species

associations, indicating that the observed states may be occurring across environmental gradients

within ecological sites, or on alternative ecological sites. These findings support the work of

others (Bestelmeyer et al. 2009; Kachergis et al. 2012; Tipton 2015), who concluded that even

though management history may drive plant community dynamics, environmental heterogeneity

can play a significant role in influencing plant community dynamics within a single ecological

site.

I did not find evidence that clear-felling, burn treatments, or management practices drove significant differences in plant community composition at any of the four study sites. NMS analyses did not show significant correlation between species associations within sites and management history. Results from chapter 2 showed high levels of juvenile aspen growth in Gunnison stands that had been clear-felled; however, these plots were not compositionally different from untreated aspen plots and did not separate out in my cluster analysis.

I identified aspen and non-aspen states at the DeBeque, Douglas Pass, and Gunnison sites. The Moffat site comprised a single aspen-dominated state. Differences in abiotic site characteristics and the presence of conifer species on plots in the Douglas Pass and Moffat sites prevented combining these models into a single generalized STM. The STM developed by Strand et al. (2011) for seral aspen forests in Idaho, depicts transitions to a conifer-dominated state in the absence of fire. The conceptual STM developed by NRCS-USFS-USU (2009) also included a shift from seral aspen stands to a conifer-dominated state in the absence of fire. Findings in chapter 2 indicated that seral Douglas Pass aspen stands contain enough conifer tree cover that a transition to a conifer-dominated state may be possible in the future, which would align with the predictions in the Strand (2011) and NRCS-USFS-USU (2009) models. Although I did not sample plots that consisted of a conifer state at my sites, it may be appropriate to include a potential Douglas-fir state in the STM for Douglas Pass and a transition from an aspen state to a Douglas-fir state in the absence of fire or conifer removal.

Results of the analysis of browsing in chapter 2 indicated that high levels of browsing are likely driving low juvenile stem densities in stands in Douglas Pass and DeBeque aspen stands. Isolated stands like those that occur at the Douglas Pass, DeBeque, and Moffat sites may be subject to higher browsing intensities, because they provide cover and relatively high quality

browse compared to surrounding shrub-dominated vegetation types. Repeated heavy browsing can lead to stand loss over time as canopy trees die off and root energy reserves become exhausted (Schier et al. 1975). Overbrowsing may be driving a transition to a shrub-dominated state at the Douglas Pass site, where browsing frequency and intensity are high.

IMPLICATIONS

This study sampled a limited number of plots within several small areas across western Colorado. My data-driven models contain states similar to those found in existing generalized seral and stable aspen STMs (NRCS-USFS-USU, 2009), however my states do not contain different community phases or all of the alternate states included in these models. Additional work is needed to observe the full range of abiotic and biotic variation within these study areas and on other ecological sites in western Colorado. Experimental treatments followed by long-term observation are needed to accurately assess the long and short-term effects of browsing, burning, clear cutting, and other management treatments and disturbances and to fully inform data-driven STMs for aspen woodland sites.

Table 3.1: PERMANOVA results for all abiotic clusters. Results for comparisons of species composition and functional traits are shown in separate columns.

Abiotic Cluster	Biotic Clusters Compared	Comparing Species Composition			Comparing Functional Traits		
		R - Squared	P-Value	Bonferonnii Corrected P-Value	R - Squared	P-Value	Bonferonni i Corrected P-Value
1	1 vs. 2	0.229	0.001	0.001	0.255	0.001	0.001
2	1 vs. 2	0.340	0.024	0.216	0.112	0.760	1.000
2	1 vs. 3	0.397	0.214	1.000	0.207	0.609	1.000
2	1 vs. 4	0.539	0.246	1.000	0.529	0.214	1.000
2	1 vs. 5	0.368	0.075	0.675	0.333	0.062	0.558
2	2 vs. 3	0.483	0.258	1.000	0.265	1.000	1.000
2	2 vs. 4	0.596	0.236	1.000	0.471	0.238	1.000
2	2 vs. 5	0.338	0.169	1.000	0.354	0.210	1.000
2	3 vs. 4	1.000	NA	NA	1.000	NA	NA
2	3 vs. 5	0.715	0.332	1.000	0.513	0.674	1.000
2	4 vs. 5	0.819	0.334	1.000	0.805	0.338	1.000
3	1 vs. 2	0.235	0.001	0.010	0.297	0.001	0.010
3	1 vs. 3	0.256	0.021	0.210	0.196	0.023	0.230
3	1 vs. 4	0.239	0.002	0.020	0.271	0.001	0.010
3	1 vs. 5	0.153	0.083	0.830	0.231	0.083	0.830
3	2 vs. 3	0.424	0.053	0.530	0.467	0.046	0.460
3	2 vs. 4	0.187	0.010	0.100	0.238	0.055	0.550
3	2 vs. 5	0.164	0.829	1.000	0.300	0.348	1.000
3	3 vs. 4	0.406	0.073	0.730	0.442	0.067	0.670
3	3 vs. 5	0.608	0.352	1.000	0.705	0.342	1.000
3	4 vs. 5	0.262	0.611	1.000	0.399	0.228	1.000
4	1 vs. 2	0.481	0.317	1.000	0.391	0.366	1.000
4	1 vs. 3	0.538	0.335	1.000	0.600	0.340	1.000
4	1 vs. 4	0.366	0.097	0.582	0.529	0.112	0.672
4	2 vs. 3	0.507	0.330	1.000	0.467	0.342	1.000
4	2 vs. 4	0.434	0.104	0.624	0.312	0.207	1.000
4	3 vs. 4	0.410	0.194	1.000	0.305	0.298	1.000

Table 3.2: Abiotic cluster characteristics, significant indicator species, and management history.

Site	Potential State or Community	No. of Plots	Indicator Species Codes (P ≤ 0.05)	Management History
DeBeque	Group 1, (Aspen Dominated)	13	THFE, BRPO2, POTR5, ELGL, ROAC, ANPI2, CYOF, OSBE, URDI, PRVI, TAOF, SYRO, VICA13, PEPA14, RIIN2, AGCO, LAOC3	Summer Cattle Grazing and Oil Field
DeBeque	Group 2 (Non-Aspen)	12	ARTRV, CHVI8, PASM, LUSE4, ELTR3, AMAL, POPR, BRMA4, HEMU3, ERUM, NAVI4	Summer Cattle Grazing and Oil Field
Gunnison	Group 1	4	WYAM, ANPI2, AGUR, ACMI2, SYRO	2 clear cut, 2 untreated
Gunnison	Group 2	3	Carex spp 1., ARTRV, CHVI8, PASM	2 clear cut, 1 untreated
Gunnison	Group 3	1	VICA13, POTR5, RIIN2, PRVI, ELGL, OSBE, THFE, BRPO4, ROAC	1 untreated
Gunnison	Group 4 (Non-aspen)	1	GABO2	1 untreated
Gunnison	Group 5	5	None	1 clear cut, 1 untreated
Douglas Pass	Group 1	10	DECA18, SIEN2, LALA6, BRMA4	Summer Cattle Grazing
Douglas Pass	Group 2	5	None	Summer Cattle Grazing
Douglas Pass	Group 3	2	HEMA2, ACRU2, UTDI, PODO, AQCO, ACGL, MEAR15, THFE, POTR5, OSBE, PSJA2, ELGL	Summer Cattle Grazing
Douglas Pass	Group 4	4	ELTR7	Summer Cattle Grazing
Douglas Pass	Group 5	1	None	Summer Cattle Grazing
Moffat	Group 1	2	POPR	2 burned, and Summer Cattle Grazing
Moffat	Group 2	2	POSE	2 burned and Summer Cattle Grazing
Moffat	Group 3	2	JUCO, POTR5, CAMI7	3 unburned and Summer Cattle Grazing
Moffat	Group 4	3	BERE, ARTRV, PSJA2	1 burned, 1 unburned, all used for summer cattle grazing

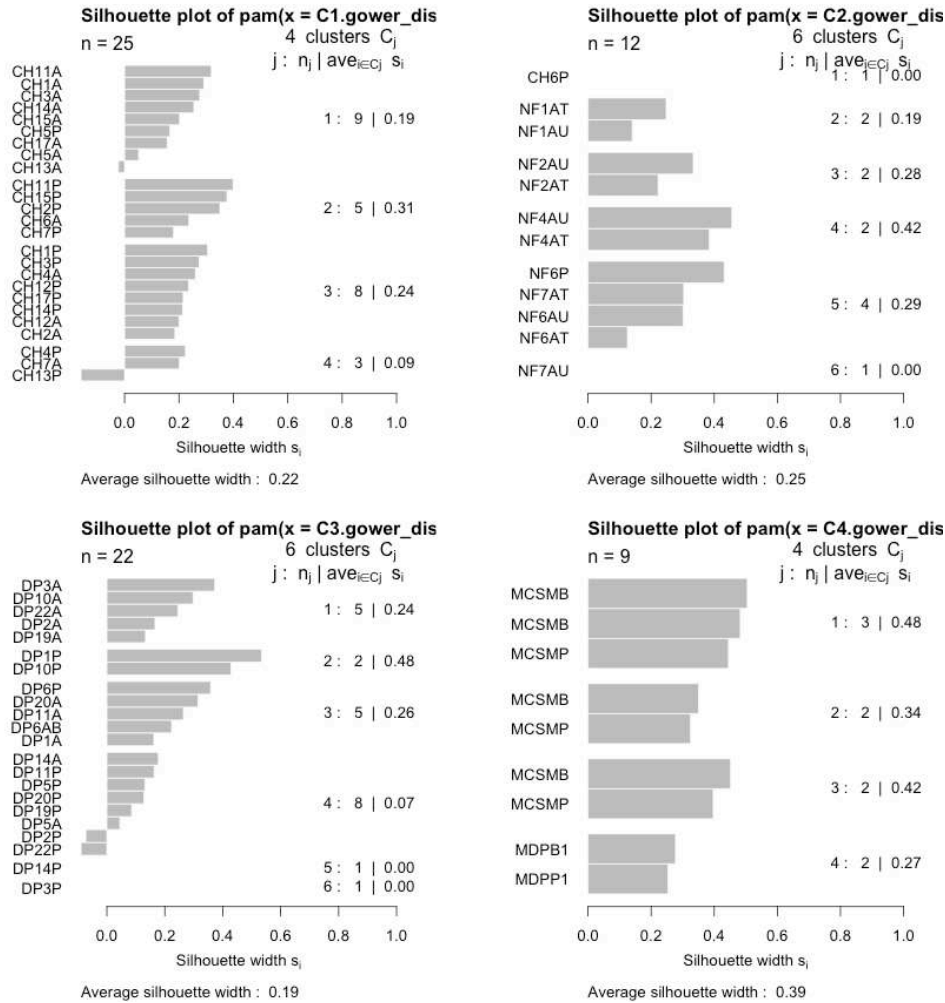Figure 3.1: Map of Colorado showing study site locations (ESRI 2014).

Figure 3.2: Plots displaying partitioning around medoids silhouette width values for each research site based on abiotic variables. Top left: DeBeque. Top right: Gunnison. Bottom left: Douglas Pass. Bottom right: Moffat.
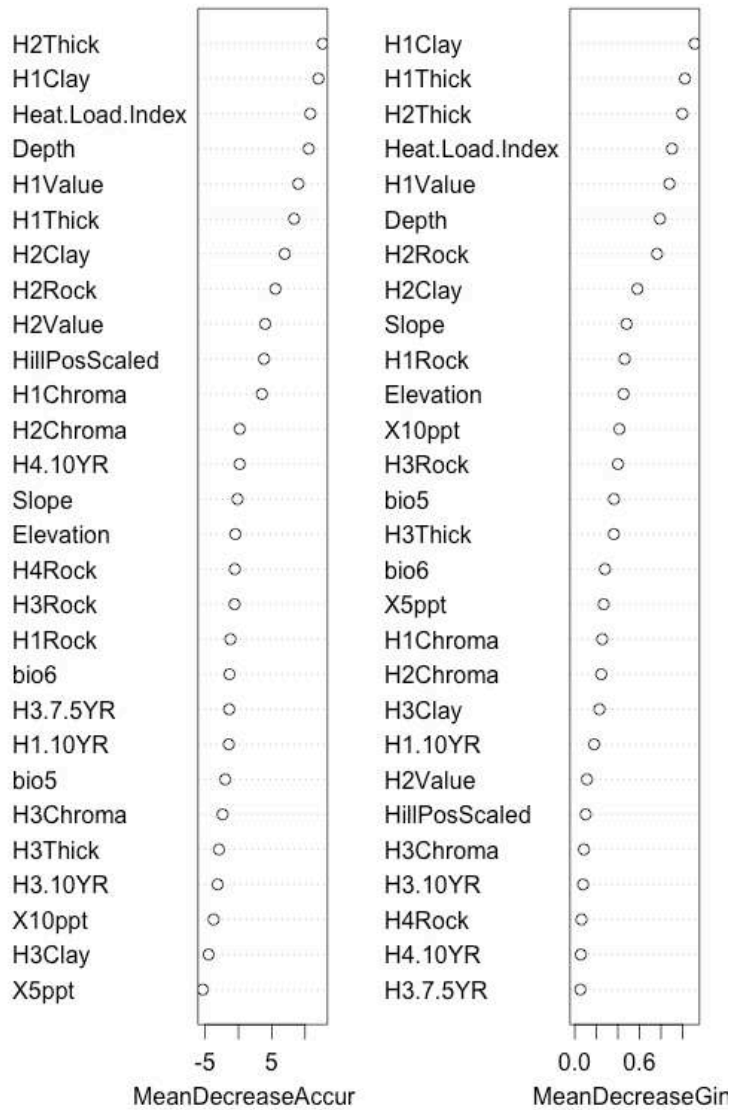
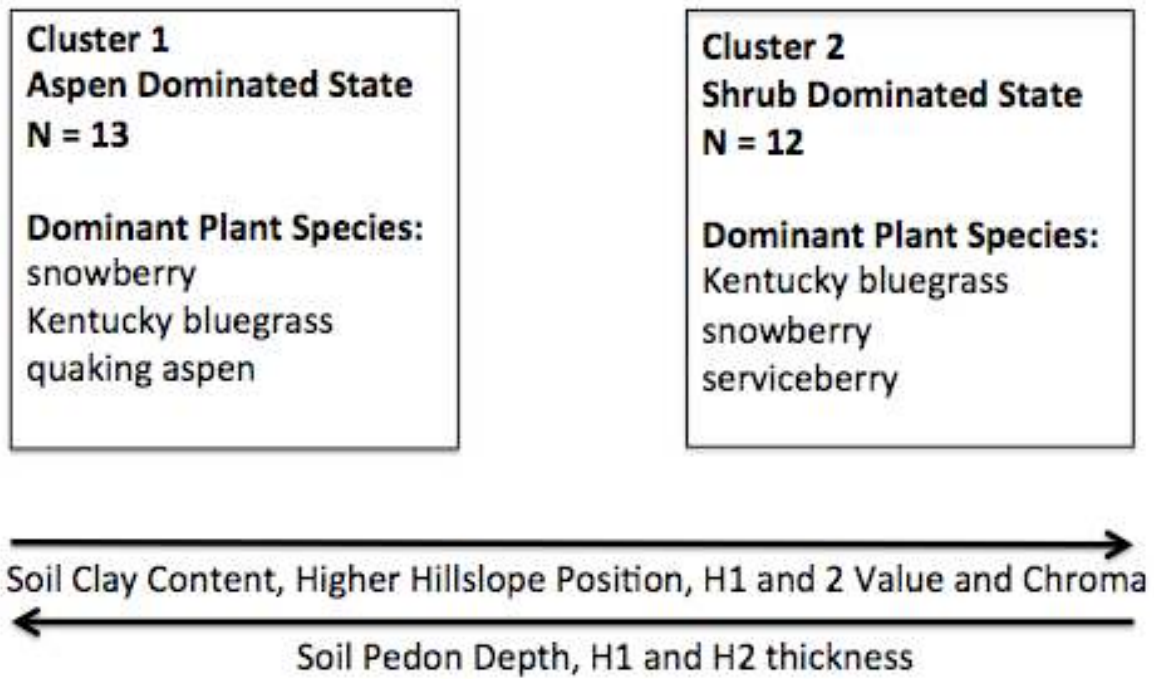Figure 3.3: Results of random forest analysis showing the importance of variable to plot classification for the DeBeque site.

Figure 3.4: State-and-transition model for the DeBeque site showing an aspen and shrub dominated state.
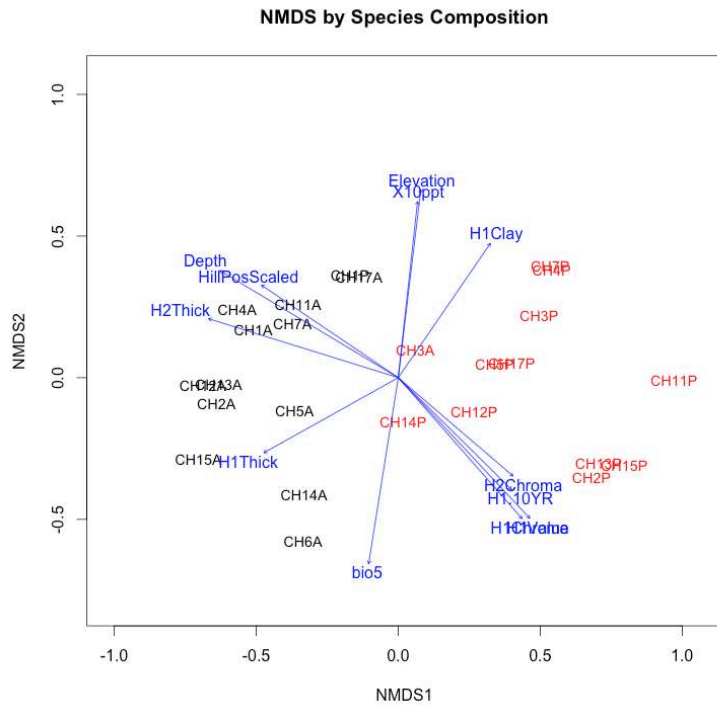
Figure 3.5: Species composition NMS plot for the DeBeque site based on species compositional differences. Plot colors represent hierarchical cluster membership. Plots in black are considered the aspen dominated state. Plots in red are the non-aspen dominated state. Blue vectors represent abiotic variables significantly correlated (p ≤ 0.05) with axes.
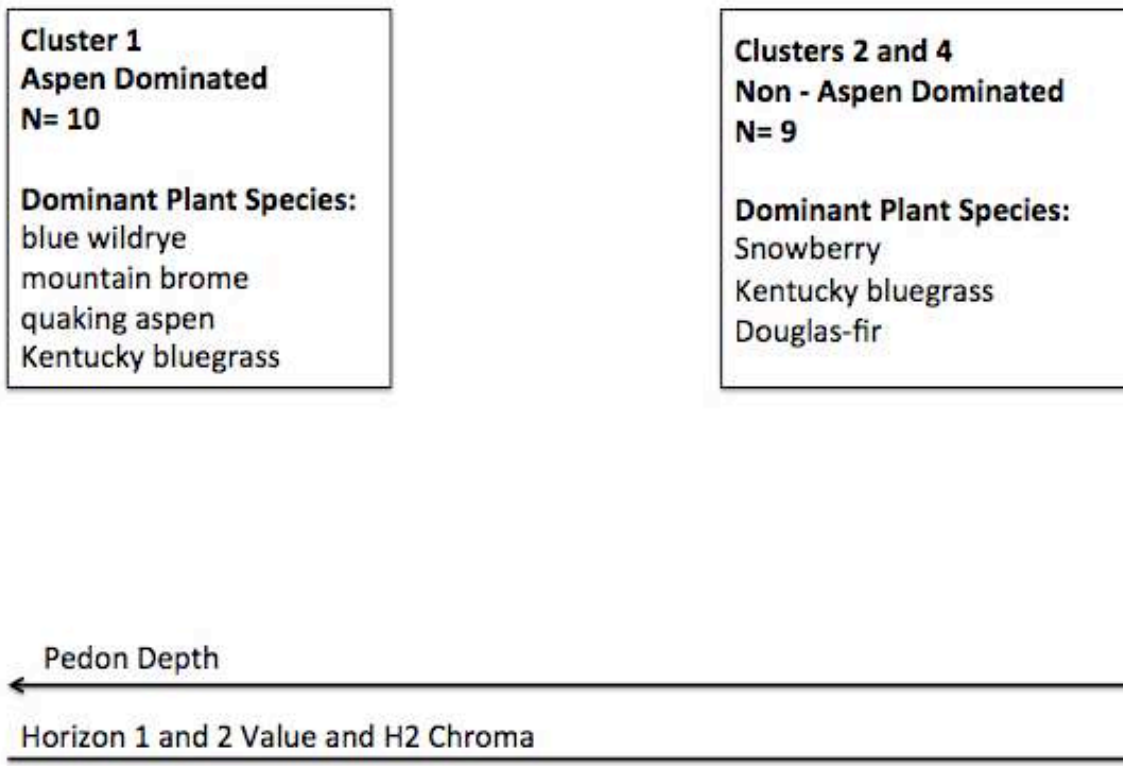
Cluster 1
Aspen Dominated
N= 10

Dominant Plant Species:
blue wildrye
mountain brome
quaking aspen
Kentucky bluegrass

Clusters 2 and 4
Non - Aspen Dominated
N= 9

Dominant Plant Species:
Snowberry
Kentucky bluegrass
Douglas-fir

Pedon Depth

Horizon 1 and 2 Value and H2 Chroma

Figure 3.6: State-and-transition model for Gunnison site depicting an aspen and shrub dominated state.
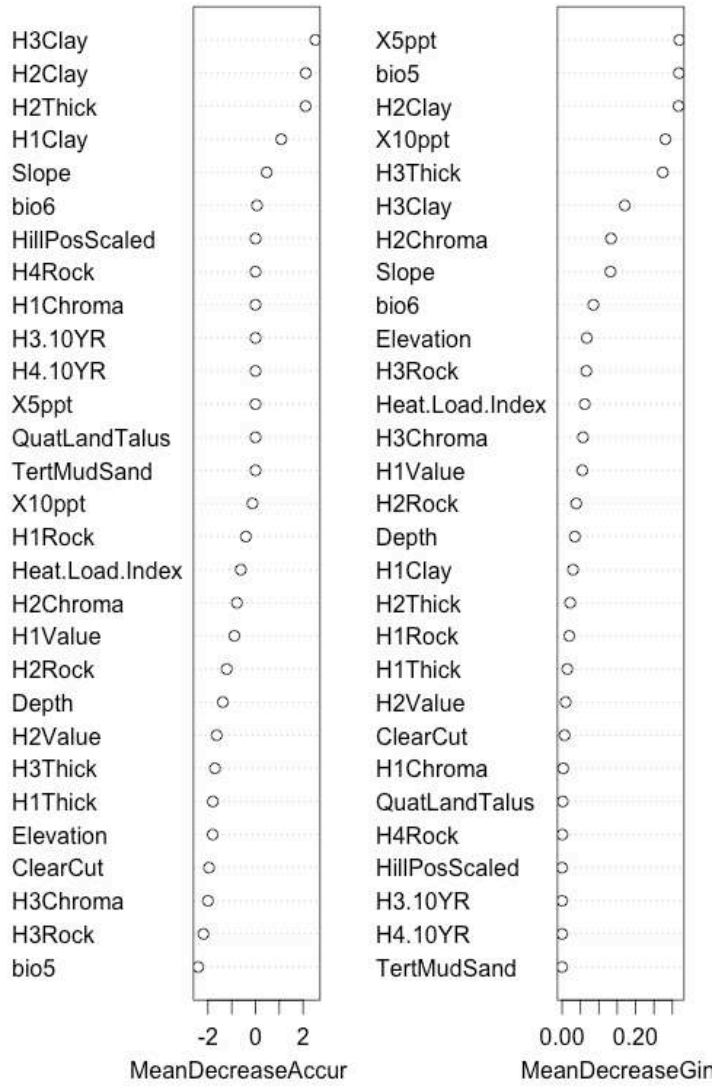
Figure 3.7: Results of random forest analysis showing the importance of variable to hierarchical clustering plot classification for the Gunnison site.
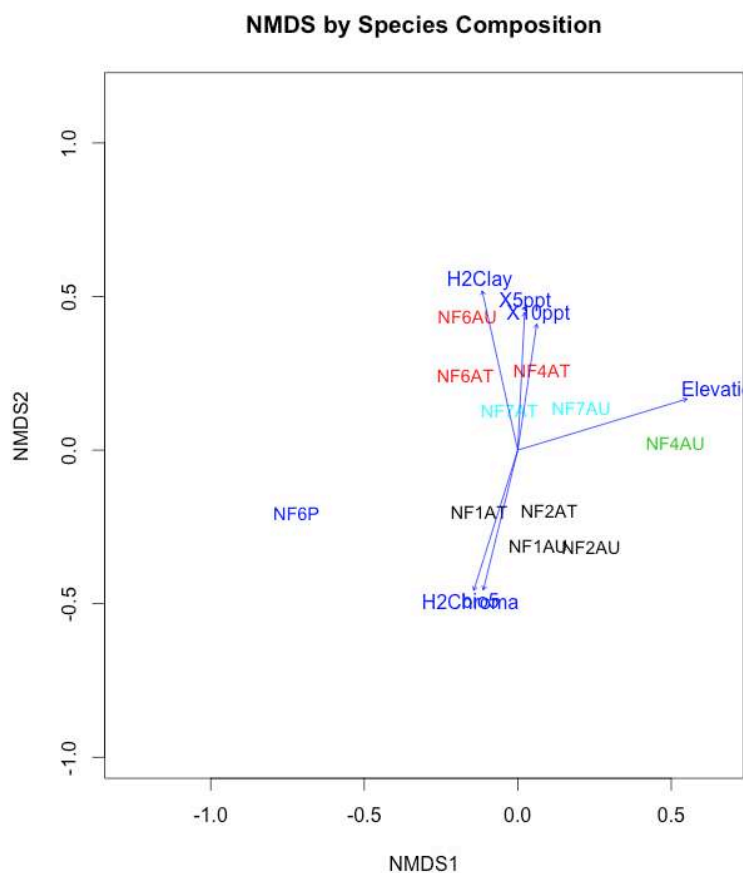
FIGURE 3.8: Species composition NMS plot for the Gunnison site based on species compositional differences. Plot colors represent hierarchical cluster membership. Plots in dark blue comprise the non-aspen dominated state. Plots in all other colors are considered members of the aspen dominated state. Blue vectors represent abiotic variables significantly correlated ($p \leq$ 0.05) with NMS axes.

Cluster 1
Aspen Dominated
N= 10

Dominant Plant Species:
blue wildrye
mountain brome
quaking aspen
Kentucky bluegrass

Clusters 2 and 4
Non - Aspen Dominated
N= 9

Dominant Plant Species:
Snowberry
Kentucky bluegrass
Douglas-fir

Pedon Depth
←——————————————————————————

Horizon 1 and 2 Value and H2 Chroma
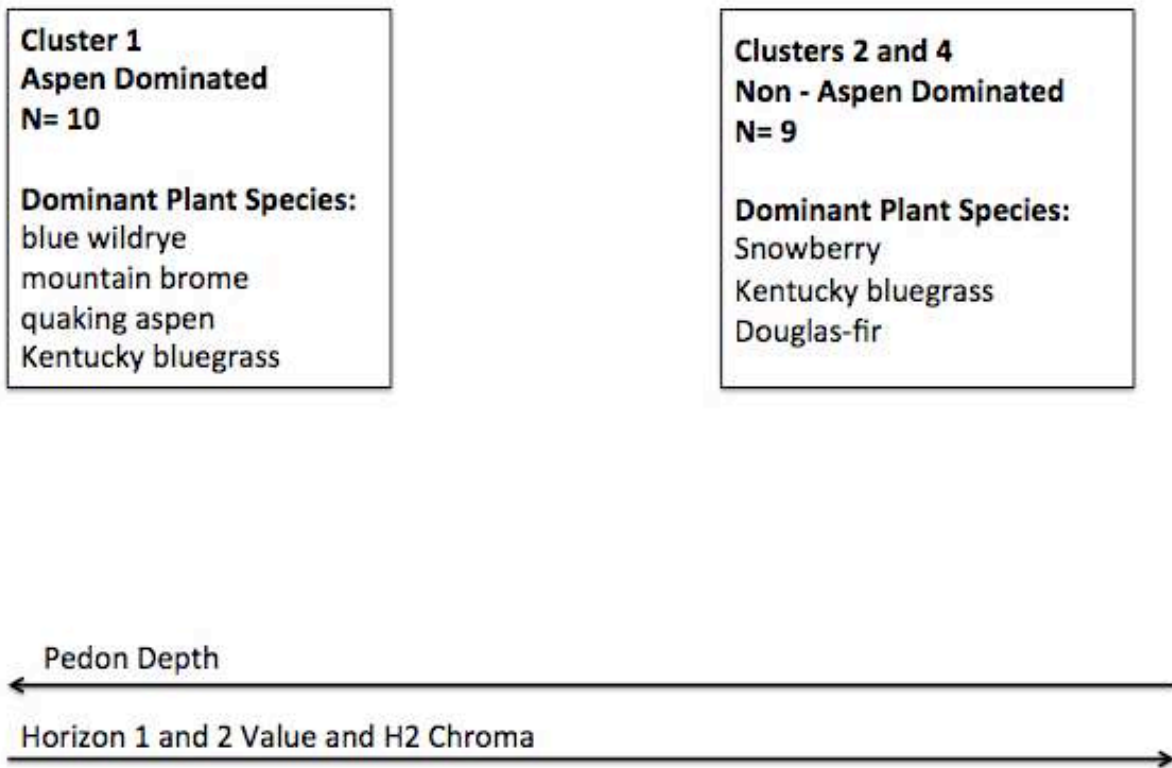——————————————————————————→

Figure 3.9: State and transition model for Douglas Pass site depicting an aspen and non-aspen dominated state.
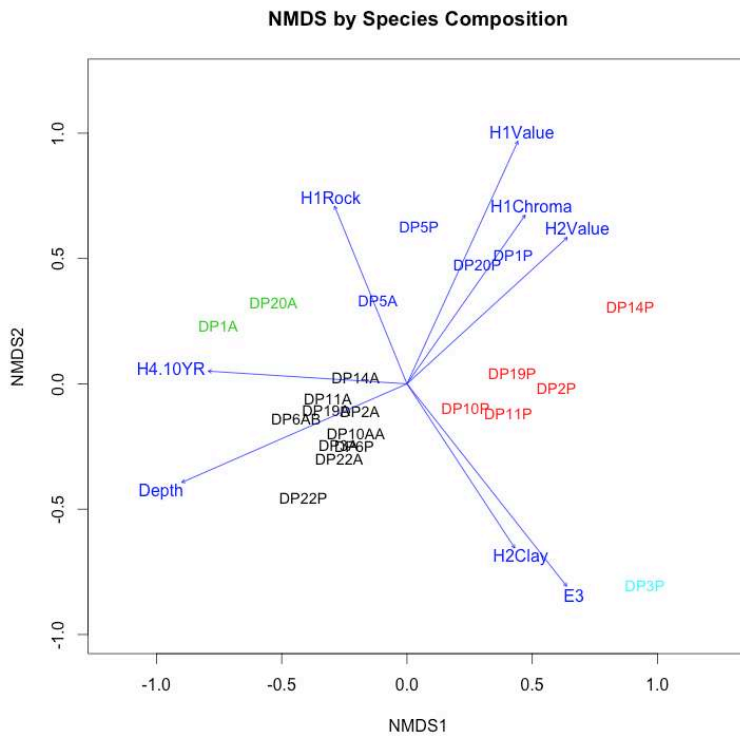
FIGURE 3.10: Species composition NMS plot for the Douglas Pass site based on species compositional differences. Plot colors represent hierarchical cluster membership. Plots in dark blue and red comprise the non-aspen dominated state. Plots in all other black are considered members of the aspen dominated state. Blue vectors represent abiotic variables significantly correlated ($p \leq 0.05$) with NMS axes.
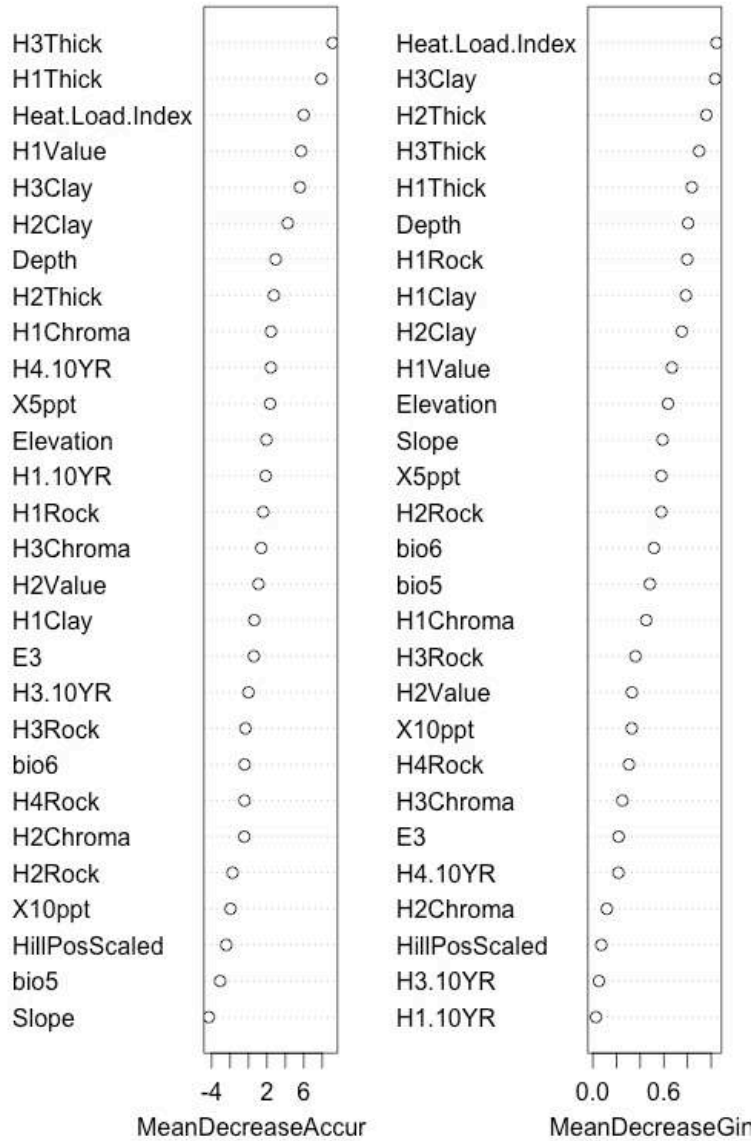
FIGURE 3.11: Results of random forest analysis showing the importance of variable to hierarchical clustering plot classification for the Douglas Pass site.

All Clusters
Aspen Dominated State
N= 9

Dominant Plant Species:
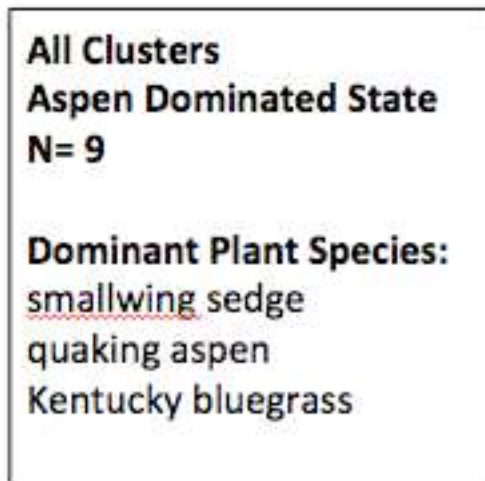smallwing sedge
quaking aspen
Kentucky bluegrass

Figure 3.12: State-and-transition model for the Moffat site consisting of one aspen dominated state.
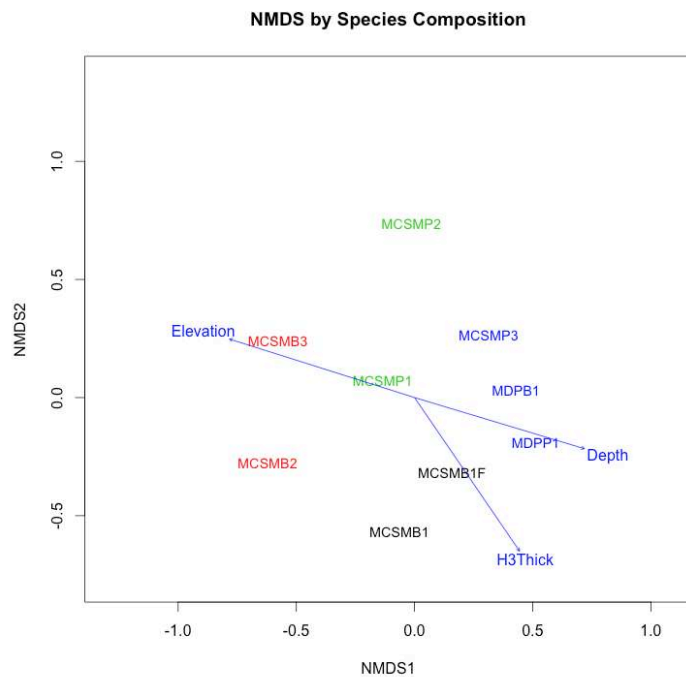
FIGURE 3.13: Species composition NMS plot for the Moffat site based on species compositional differences. Plot colors represent hierarchical cluster membership. Blue vectors represent abiotic variables significantly correlated ($p \leq 0.05$) with NMS axes.
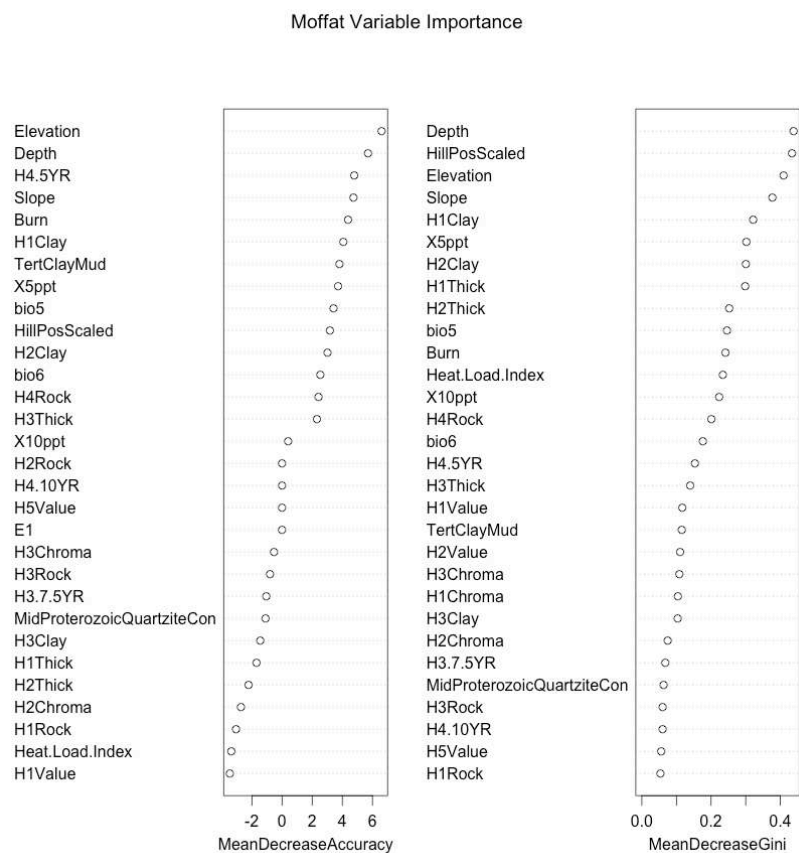
Figure 3.14: Results of random forest analysis showing the importance of variable to hierarchical clustering plot classification for the Moffat site.

CHAPTER 4

CONCLUSION

INTRODUCTION

The goals of this project were to further understanding of aspen ecosystem dynamics and provide locally-relevant aspen woodland STMs for landowners and land managers in western Colorado. This work yielded some useful information. However, it gave rise to more questions related to aspen management and ecology. Below I first synthesize the main findings from each data chapter, then reflect on the issues I encountered over the course of this project and provide suggestions for future research related to aspen and STMs.

SYNTHESIS

The findings in Chapter 2 indicate that, while a number of variables may be affecting aspen health in western Colorado, in the stands I sampled and among the factors I accounted for, the presence and intensity of herbivore is having the most significant effect on stand regeneration. The type of stand or sub-type can also influence the role herbivory plays. Large stable stands may be experiencing less targeted browsing by large herbivores when compared to smaller isolated stable and seral stands. The presence of other types of damage known to impact stand health was observed in my study sites, however these other types of damage were not as prevalent in stands with low juveniles stem densities.

In Chapter 3, I concluded that I needed to treat each research site as a distinct ecological site. My classification of species associations and correlated abiotic variables showed that similar vegetation associations were observed to occur on these different ecological sites. The STMs I developed do shed some light on abiotic drivers of differences in species compositions, but

ultimately, they are incomplete. To capture variation in management treatments within my sample, I was forced to sample in areas with different abiotic characteristics, precluding an analysis of management treatment effects under the same abiotic conditions. To sample all vegetation types and a variety of aspen treatments within a single ecological site would require a planned experimental approach in which a number of treatments were administered to a single area.

THE FUTURE OF ASPEN IN THE WESTERN COLORADO

We lack a complete understanding of the interactions of all of the factors that contribute to aspen stand loss and the impacts they will have on aspen in the future. Multiple climate models predict increased temperatures, less precipitation in the form of snow, lower total annual precipitation, and increases in extreme weather events such as droughts in the western United States (Morelli and Carr 2011, Cayan et al. 2008, Dettinger 2005, Knowles and Cayan 2004). It is suggested that these changes will reduce suitable aspen habitat in coming decades (Worrall et al. 2013). However, this situation may not be that simple. Increased fire frequencies may increase aspen extent in certain areas (Morelli and Carr 20011, Shepperd et al 2006). Yang et al. (2015) modeled changes in aspen and associated conifer and shrub species distributions. Their model suggested that under current climate conditions, many aspen stands are capable of persisting for centuries in the absence of fire, however aspen coverage would see a slight increase at upper elevations and significant decrease at lower elevations with a 2-5 °C increase in annual temperatures. Morelli and Carr (2011) suggest decentralized approaches to research, monitoring, and management in the future because it is likely that shifts in suitable aspen habitat will differ by location (Hogg 2001). This supports the need for further work to develop site-specific aspen woodland STMs reflecting these local dynamics.

The ecological site concept put forth by the NRCS classifies land according to its abiotic characteristics (soils, climate, relief, etc.) and uses STMs to describe the potential vegetation states that may occur on that site. Two of the problems inherent in this concept are: 1) abiotic gradients can occur within an ecological site, and 2) similar vegetation states can occur across multiple ecological sites. This can become problematic when attempting to develop an STM for a particular ecological site. It is possible the abiotic variability described by a single STM may not align with the abiotic limits I have placed on a particular ecological site and I am left with a partially completed STM.

Attempting to develop state-and-transition models for forested or woodland systems presents a unique set of challenges. I used a combination of rangeland and forestry inventory techniques in order to accurately measure overstory and understory characteristics, however I was forced to adapt my methods to the environment in which I worked. Due to the thickness of understory vegetation and time constraints, I did not include several typical rangeland inventory measurements. I did not measure gaps between plant bases, count ungulate dung, or measure shrub height while taking line point intercept measurements. In order to include tree foliar cover in my foliar cover measurements I took readings using a GRS densiometer. I used absolute foliar cover, while the forestry community more commonly uses canopy cover. This can create compatibility issues for those of us interested in comparing across vegetation types.

Another challenge encountered throughout this project was the issue of locating suitable study sites. Determining the locations of aspen stands that had been subjected to different management treatments or disturbances required sending inquiries to a number of federal and

state agencies. I was unable to find sites within the same general area and was forced to travel to multiple counties in western Colorado. One obvious shortcoming of this work was the lack of the inclusion of long term climate data as a means to explain ecosystem dynamics. Climate directly and indirectly influences abiotic and biotic factors within an ecosystem in major ways. While I do acknowledge that, obtaining accurate long-term climate data for western Colorado proved difficult. Models such as PRISM do exist and can give estimates, however, climate stations are few and far between and continuous monitoring for any time period beyond the last two decades is almost non-existent.

MANAGEMENT IMPLICATIONS

With respect to the roles of management in aspen dynamics and regeneration, I found that clear felling treatments at the Gunnison site stimulated new aspen growth. However, prescribed burns at the Moffat site were not associated with regeneration, contrary to expectation. It may be that the isolated stands at the Moffat site receive more browsing pressure because they are islands of relatively rich browse material, while an the area surrounding my Gunnison plots contained much more high quality browse, so browsing pressure was more dispersed. The density of class 3 stems per hectare was negatively correlated with the proportion of stems browsed, indicating that browsing is likely limiting young stem survival and therefore stand regeneration. This finding highlights the role of large ungulate herbivory in limiting aspen regeneration, and suggests that more research is needed to investigate the interactions of different disturbance regimes (such as browsing and fire) on aspen regeneration. I did not study the effects of herbivore exclusion on aspen regeneration, but my results suggest that this is a measure that could improve regeneration, as others have found (Rolf 2001). As this study reinforces, some stands are seral, and may be expected to transition to a conifer forest. Other stands are self-

replacing. Future climate trends may also affect the ability of some ecological sites to support aspen in the future, which may affect managers' cost benefit calculations. It is up to land managers to weigh the costs and benefits of allocating resources to preserve aspen stands on their land, and in cases where stands are not self-replacing, they may not be able to preserve these stands. As STMs for aspen woodlands are further refined, they should assist managers in identifying how factors within their control, such as the judicious manipulation of disturbance regimes, interact with factors beyond their control, such as climate and variability in other abiotic factors, to affect the outcomes of any planned management or natural disturbance.

Finally, my results point to the challenges of describing woodland ESDs and developing data-driven STMs for these sites. The issues summarized in this chapter are ones that the NRCS and other agencies seeking to develop STMs for woodland will need to address if they aspire to develop empirically-derived, data-driven models for aspen woodlands. The results reported in this thesis highlight the heterogeneity of abiotic conditions that support aspen stands across western Colorado, and the apparently strong role of abiotic gradients within ecological sites in conditioning plant community responses to disturbance.

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