EVALUATING ASPEN RESPONSES TO CHANGES IN ELK ABUNDANCE, DISTRIBUTION AND BEHAVIOR FOLLOWING WOLF REESTABLISHMENT IN WEST-CENTRAL YELLOWSTONE NATIONAL PARK

By

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ABSTRACT

The reintroduction of wolves to Yellowstone National Park (YNP) in the mid-1990's has created a unique natural experiment for the investigation of trophic cascades operating at large spatial scales and involving large terrestrial mammals. Wolves have been directly linked to changes in elk density/behavior and have been hypothesized to be the driving force behind observed changes in woody plant growth in the system. The primary objectives of this study were to investigate the occurrence of a trophic cascade among wolves, elk and aspen in an area of YNP where elk abundance and distribution changed dramatically as a direct result of wolf reestablishment in the system. In Chapter 2, I determined the distribution and demographic characteristics of aspen in the Madison headwaters study area (MHSA) and identified the environmental attributes associated with its distribution on the landscape. Additionally, I evaluated the morphology, productivity, and persistence of aspen in both clonal and seedling-established. In Chapter 3, I established a climate–growth relationship for aspen to investigate the occurrence of a shift in productivity related to climate coincident with the timing of wolf reestablishment. I used standard dendrochronology techniques to investigate growth trends and identified which climate variables are most important to aspen productivity in this region. Additionally, I established the timing of historic aspen recruitment in the MHSA using age of mature trees. In Chapter 4, I investigated a trophic cascade among wolves, elk and aspen. I reconstructed historical browse conditions for aspen to look for a shift in browse regimes that occurred concurrently with the changes in elk abundance/distribution by performing a dendrochronological analysis of aspen architectural morphology. I also evaluated plant height, productivity, and longevity of aspen where elk densities had declined dramatically in order to capture the expected growth response. I used ANOVA's and multiple comparison procedures to evaluate browse conditions and aspen growth among sites where elk densities have declined dramatically and those where elk densities have remained relatively constant.

CHAPTER 1

INTRODUCTION

Top predators can indirectly influence the distribution and composition of vegetation on the landscape through interactions with their herbivore prey in what is known as a trophic cascade (Lima 1998, Polis 1999). Trophic cascades are a well-studied ecological phenomenon (Schmitz et al. 2000, Werner and Peacor 2003, Peckarsky et al. 2008) and are believed to be among the most powerful of ecological interactions (Lima 1998). However, much of the evidence for this phenomenon comes from experimental studies of smaller taxa and few studies have been able to capture trophic cascades operating in complex large-scale terrestrial ecosystems (Schmitz et al. 2000, 2004). The reintroduction of wolves (*Canis lupus*) to Yellowstone National Park (YNP) in the mid-1990's has created a unique natural experiment for the investigation of trophic cascades operating at large spatial scales and involving large terrestrial mammals. The relatively recent re-establishment of the predator-prey relationship between elk (*Cervus elaphus*) and wolves in YNP has sparked significant interest in the study of plant responses to predicted changes in higher trophic levels. The reintroduction of wolves has been directly linked to changes in elk density (Eberhardt et al. 2007, Garrott et al. 2009a), habitat selection (Creel et al. 2005, Fortin et al. 2005), and behavior (Creel and Winnie 2005, Gower et al. 2009) and has been hypothesized to be the driving force behind observed changes in woody plant growth (Ripple et al. 2001, Larsen and Ripple 2003, Ripple and Beschta 2007, Beyer et al. 2007, and Halofsky et al. 2008).

The primary objectives of this study were to investigate the occurrence of a trophic cascade among wolves, elk and aspen in an area of YNP where elk abundance and distribution changed dramatically as a direct result of wolf reestablishment in the system (Becker et al. 2009, White et al. 2009). My study took advantage of data from a long-term elk demography study that was established prior to wolf reintroduction that resulted in a detailed account of how recolonizing wolves affected elk in a system where they were absent for more than 70 years prior (Garrott et al. 2009b). I had the unique opportunity to evaluate the occurrence of a trophic cascade in this system by linking potential changes in aspen growth directly to observed changes in elk abundance and distribution following wolf reintroduction.

The primary objectives in Chapter 2 were to determine the distribution and demographic characteristics of aspen in the Madison headwaters study area (MHSA) and to identify the environmental attributes associated with its distribution on the landscape. Additionally, I evaluated the morphology, productivity, and persistence of aspen in both clonal and seedling-established stands in the study area and related these findings to previous studies to assess the long-term trends in aspen regeneration and recruitment following the 1988 fires in YNP.

The objective of the third chapter was to determine if any plant-growth responses in aspen coincident with the timing of wolf establishment can be explained by shifts in climate. I use standard dendrochronology techniques to assess the climate–growth relationship for aspen in the MHSA to determine climatic influences related to aspen productivity. I identified which climate variables are most important to aspen

productivity in this region. I also evaluated the general trend in aspen growth related to climate for shifts in productivity that occurred concurrently with changes in elk abundance/distribution following wolf reintroduction. Additionally, I used tree age to establish an age structure of mature aspen in the MHSA to establish the timing of historic recruitment.

The primary objective of Chapter 4 was to test hypotheses relating browse conditions and aspen morphology to changes in elk abundance/distribution in the MHSA. This study was designed to address two questions relating to trophic cascades in the system: 1) was there a significant decline in browsing pressure on aspen following wolf reestablishment, and 2) was there a corresponding plant–growth response indicating that aspen were released from browsing pressure and are now growing vertically through the browse zone? I hypothesized that browsing pressure had declined dramatically in response to observed changes in elk abundance/distribution, and that aspen were now increasing in height and advancing through the browse zone. To address the first question, I reconstructed historical browse conditions for aspen to look for a shift in browse regimes that occurred concurrently with the changes in elk abundance/distribution by performing a dendrochronological analysis of aspen architectural morphology. To address the second question, I evaluated plant height, productivity, and longevity of aspen where elk densities had declined dramatically in order to capture the expected growth response. I used ANOVA's and multiple comparison procedures to evaluate browse conditions and aspen growth among sites where elk densities have declined dramatically and those where elk densities have remained relatively constant.

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CHAPTER 2

ASPEN POST-DISTURBANCE PRODUCTIVITY AND PERSISTENCE IN WEST-CENTRAL YELLOWSTONE NATIONAL PARK

Abstract

An episode of aspen seedling establishment was documented following the 1988 fires in Yellowstone National Park (YNP). The west-central portion of YNP was noted to be a hot-spot for seedling establishment. This area has also experienced significant changes in elk abundance and distribution following wolf reintroduction. Evidence that heavy browsing can hinder aspen regeneration suggests that a decline in ungulate densities would favor recruitment from the current cohort of post-burn suckers and seedlings. Although the most recent study of the post-burn aspen seedling establishment reports stunted growth, with stems exhibiting a high rate of previous browsing, recent shifts in elk abundance and distribution in the Madison headwaters study area may have alleviated browsing pressure sufficiently to offer post-burn suckers and seedlings some reprieve. The goal of this study was to determine the distribution and status of aspen in west-central YNP for both clonal and seedling-established stands and to build on previous investigations by adding another point in time in documenting the progress of the post-fire seedling establishment. In general, aspen stands in the MHSA occupied small areas and had low stem densities and poor productivity. The majority of stems were of a short shrubby stature with excessive branching. Clonal stands pre-dating the

1988 fires appear to be unsustainable. They were largely comprised of senescing mature trees with few to no recruitment stems. Aspen in seedling-established stands were found to be shorter and to occupy different types of sites than clonal stands. Evidence from this study indicates that seedlings are persisting in this area, but that the rates of seedling mortality have increased and stem densities are continuing to decline, despite recent declines in browsing pressure.

Introduction

Quaking aspen (*Populus tremuloides*) decline in the western United States has been a common topic in ecological research since ecologists and foresters first noticed the decline in the early 1900's. Many of the current aspen stands in the western U.S. are dominated by older age classes in varying stages of senescence, with little understory regeneration. Many are also experiencing succession to conifers due to lack of fire. These symptoms of aspen decline have been heavily documented in the scientific literature (Packard 1942, Krebill 1972, Olmstead 1979, Bartos 2001) and have been attributed to fire suppression, climatic variability, and high densities of ungulate browsers (Baker 1997, Kay and Bartos 2000, Kay 2001, Hessl 2002, Larsen and Ripple 2003, Gallant et al. 2003, Romme et al. 2005). It has been suggested that the paucity of aspen regeneration is the consequence of synergy among these variables (Romme et al. 1995), many of which reflect processes that have been altered by anthropogenic forces since Euro-American settlement (reviewed in NRC 2002).

However, there is substantial evidence to support the hypothesis that aspen has not declined across the West, but that there is variation in the seral stage of aspen across a patchy mosaic of aspen stands (Suzuki et al. 1999, Barnett and Stohlgren 2001, Hessl and Graumlich 2002, Kaye et al. 2003, Kashian et al. 2007), reflecting a population process that is operating over large spatial and temporal scales. Barnett and Stohlgren (2001) suggested that previous studies have focused on decadent and dying stands in areas of high ungulate densities and have failed to capture the range of variability in aspen regeneration across the landscape. There is ample evidence to show that aspen regeneration is episodic (Chapter 3 this volume, Romme 1995, Baker 1997, Ripple and Larsen 2000, Hessl and Graumlich 2002, Larsen and Ripple 2003), and it has been proposed that aspen clones can persist for thousands of years (Mitton and Grant 1996) in a shrub form until conditions are favorable for proliferation, creating a "window of opportunity" (Kemperman and Barnes 1976, Despain 1990, Jelinski and Cheliak 1992). Given the dynamic nature of the frequency and spatial extent of the biotic (e.g. herbivory, genetic variability, disease) and abiotic (e.g. fire, climate, geomorphology) processes affecting aspen regeneration in a heterogeneous landscape, it is not likely that all stands are affected equally, rather that aspen regeneration is dependent upon local conditions at a given time.

In contrast to the many studies that have demonstrated a major decline in the total acreage of aspen occupancy in the west since the early 1900's (Packard 1942, Krebill 1972, Olmstead 1979, Bartos and Campbell 1998), recent studies indicate that aspen decline has occurred to a lesser extent than previously reported (Brown et al. 2006), and

some have even documented aspen range expansion during the 20th century (Kulakowski et al. 2004). Further, an episode of seedling establishment following the 1988 fires in Yellowstone National Park (YNP) – a rare and sparsely documented event for aspen in the Rocky Mountain West – provides evidence that not only are aspen able to maintain their former range through episodic regeneration, they can colonize new areas by way of seed dispersal. Researchers studying the extent of the seedling establishment in YNP documented the colonization of aspen seedlings into areas where no known aspen had historically existed (Romme et al. 1997, 2005, Stevens et al. 1999, Turner et al. 2003). It is clear from the contrasts in the aspen literature that we have a well-developed understanding of aspen ecology at the individual stand level, but that our understanding of the long-term population processes of aspen that occur on large spatial and temporal scales is limited. In order to further develop this understanding we must continue to study the processes of aspen regeneration, including rare events of colonization into new areas through seed dispersal that occur at the scale of centuries (Eriksson and Fröborg 1996).

The goal of this study was to determine and document the distribution and status of aspen in the Madison Headwaters study area (MHSA) of west-central YNP for both clonal stands of pre-fire distribution and post-burn seedling-established stands. Prior to the 1988 fires in YNP there were very few known adult aspen stands; only ~1% of the land cover within YNP (Despain 1990) and only ~0.2% in the MHSA (Newman and Watson 2009) was classified as aspen. However, several researchers investigated the seedling-establishment event in YNP and discovered a surprising amount of aspen

seedling establishment across the landscape (Romme et al. 1997, 2005, Turner et al. 2003). Turner et al. (2003) identified the environmental attributes that best described where post-fire aspen seedlings were most likely to occur – including severely burned forest and proximity to known adult aspen stands – and developed a predictive model for the probability of aspen seedling occurrence. This model resulted in a map depicting the probability of occurrence for aspen seedlings throughout the YNP landscape that indicates the West-Central portion of YNP, (an area coincident with the MHSA), has a high probability of post-fire aspen seedling occurrence, relative to other areas of the park.

The MHSA has also experienced significant changes in elk (*Cervus elaphus*) abundance, distribution, and behavior in recent past as a result of wolf (*Canis lupus*) reintroduction (Becker et al. 2009, Garrott et al. 2009b, Gower et al. 2009a, Gower et al. 2009b, and White et al. 2009). In the absence of wolves, the resident elk herd remained stable for over 30 years, varying from 400-800 animals (Craighead et al. 1973, Aune 1981). Following wolf establishment in the study area, (winter 1998-1999), this non-migratory elk population declined dramatically, with spring estimates of ~74 elk in 2009. Within the MHSA elk distribution has changed from nearly equal proportions in each of the three river drainages (see Study Area description) to over 92% of the elk population residing in the Madison canyon by spring 2009 (Garrott et al. 2009b, White et al. 2009, R.A. Garrott, Montana State University – *unpublished data*).

Evidence that heavy browsing can hinder the transition of aspen suckers into the canopy (Romme et al. 1995, Kay and Bartos 2000, Kay 2001, Romme et al. 2005) suggests that a decline in ungulate densities would favor recruitment from the current

cohort of post-burn suckers and seedlings. Although the most recent study of the post-burn aspen seedling establishment reports stunted growth, with stems exhibiting a high rate of previous browsing (Romme et al. 2005), the recent shifts in elk abundance and distribution in the MHSA may have alleviated browsing pressure sufficiently to offer post-burn suckers and seedlings a reprieve from at least one mechanism of inhibition for aspen recruitment, potentially allowing for successful recruitment if conditions become favorable.

This study builds on previous research by extending the time series of analysis of recent aspen seedling establishment in west-central YNP while also providing a detailed description of the distribution and dynamics of this species (clonal and seedling-established) in a high elevation area that is outside the known pre-fire distribution of aspen in YNP and where elk densities have declined dramatically. Documenting aspen regeneration in MHSA and tracking their progress through this new era of low elk density will contribute to a better understanding of the roles of ungulate herbivore densities in aspen regeneration following a disturbance event. The primary objectives of this study were to:

1. Identify and map aspen stands and areas where aspen are present within the MHSA;
2. Determine their distribution and demographic characteristics;
3. Identify the environmental attributes controlling aspen distribution in the MHSA;
4. Evaluate productivity, growth form, and persistence of aspen in the MHSA;

5. Analyze differences in plant growth, site characteristics, demographics, and distribution between suckers and seedlings, and ;
6. Compare my findings to those of previous studies that investigated seedling establishment and the persistence of aspen in YNP following the 1988 fires.

Study Area

The study area for this research was selected to address woody plant responses to observed changes in elk abundance and distribution following wolf reintroduction in West-Central YNP (Chapter 4, this volume) and builds upon a long term study of elk demography spanning the period of wolf reintroduction (Garrott et al. 2009b). The study area and methods described here were specifically selected to facilitate analyses of aspen related to observed changes in the abundance and distribution of the resident elk herd.

The MHSA (Figure 2.1) spans ~36,190 ha encompassing portions of the Central Plateau and Madison Plateau in west-central YNP and the associated Firehole, Madison, and Gibbon river drainages (Garrott et al. 2003). The boundaries of the study area are defined by elk winter home ranges estimated by Gower et al. (2009). Elevation in the MHSA ranges from 2048-2560 m and the topography is comprised of relatively flat undulating terrain dissected by steep canyons. Climate in central YNP is characterized by long cold winters and short cool summers with snowpack persisting typically 6-7 months of the year (8-9 mo/yr. on the Madison Plateau) (Newman and Watson 2009). The mean annual temperature for the period 1997-2007 was 3° C (Newman and Watson 2009). Mean annual snowpack depth was ~1 m for the same period, but could reach

several meters at higher elevations. Mean annual precipitation varies greatly (Newman and Watson 2009).

The study area is composed of large tracts of forests with interspersed meadow complexes. The non-forested areas consist of wet meadows, dry meadows, talus slopes, and geothermal areas. Wet and dry meadow complexes comprise ~20% of the landscape and occur on the fertile soils of alluvial plains deposited between adjacent lava flows (Newman and Watson 2009). Forested land covers ~80% of the study area, of which approximately 53% burned in the fires of 1988 (Newman and Watson 2009), which created a mosaic of burned and unburned forest across the landscape (Romme and Despain 1989). Approximately 95% of forested land in the MHSA is dominated by lodgepole pine (*Pinus contorta*). These large expanses of lodgepole pine occur on poorly developed rhyolitic soils from lava flows and are differentiated by varying stages of stand succession (Newman and Watson 2009). Other tree species that occur, but are less common in the study area are: whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*) (Newman and Watson 2009). Aspen are rare in the study area and are typically found in talus and at low elevations in the ecotone between conifer forests and meadow complexes (Newman and Watson 2009).

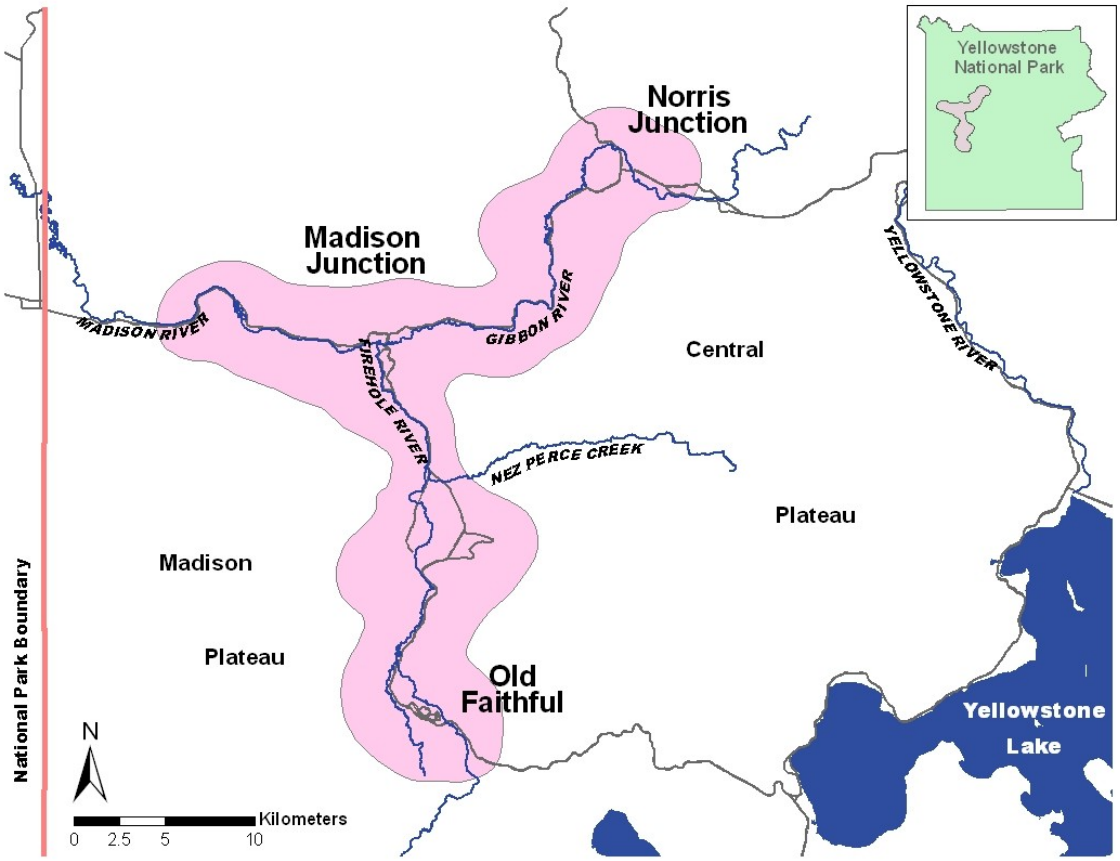


Figure 2.1: Map of the MHSA, west-central Yellowstone National Park, Wyoming, USA, including the Gibbon River, the Firehole River, and the Madison River drainages. The study area boundaries are defined by estimated winter home ranges for the resident elk herd (Gower et al. 2009).

Methods

Mapping Aspen Stands

Linear transects were surveyed for aspen stands in the MHSA during the summer of 2009. Survey routes were established using a geographic information system (GIS), where transect lines running East to West and North to South were overlaid as a grid on a map of the study area with 800 m spacing between lines (Figure 2.2). Transects were

surveyed by two field researchers spaced 100 m apart, off trail, through a variety of habitat types. This differs from previous studies that investigated the presence of aspen seedling establishment via trail corridors (Romme et al. 1997, Turner et al. 2003, Romme et al. 2005) and helps to expand our knowledge of the current distribution of aspen in west-central YNP. The survey efforts were stratified by drainage in an effort to maintain equal sample sizes among the three drainages, as the environmental and ecological characteristics vary among them. To increase the probability of encountering aspen, priority was given to transects passing through areas identified as having a high probability of aspen seedling establishment by Turner et al. (2003), and also where aspen have been historically documented (Despain 1990). This prioritization of aspen presence may have introduced some bias into our understanding of where aspen occurs on the landscape, but minimized the time spent in the field in non-aspen vegetation. In the Madison and Gibbon drainages, the majority of transects planned for the study were successfully surveyed. However, in the Firehole drainage aspen were found to be diffuse throughout the extent of the burned forest and it was not possible to survey all planned transect routes in this drainage due to time constraints of the sampling effort. Thus, selected transect routes were surveyed in an effort to obtain a representative sample across all environmental gradients where aspen were expected to be found in this drainage.

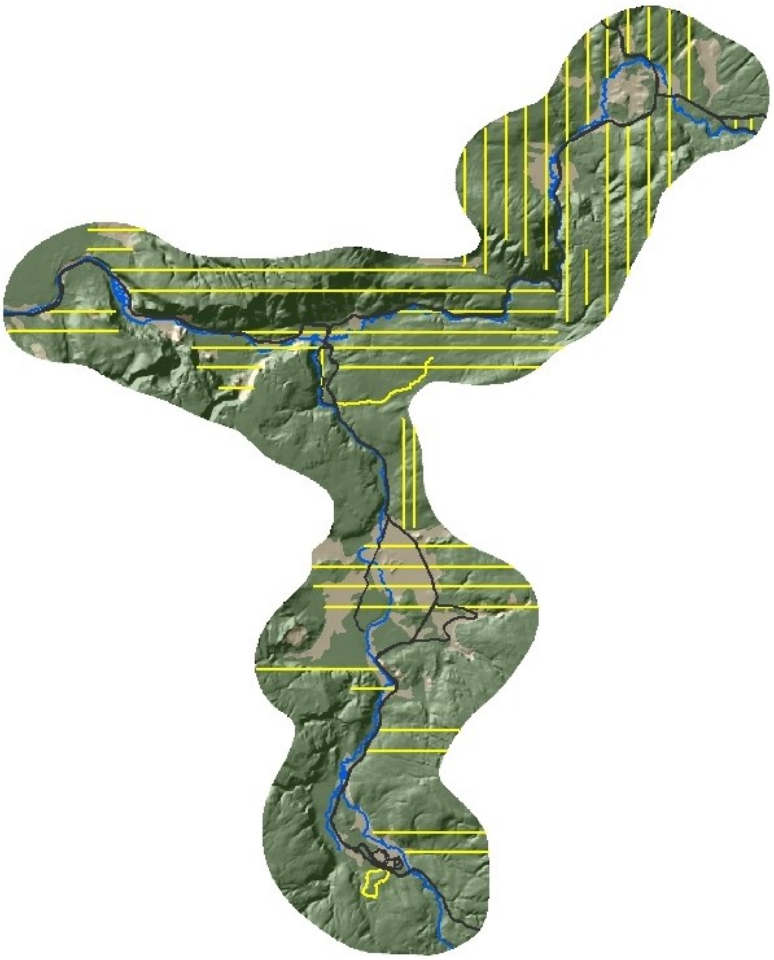


Figure 2.2: Map of the MHSA illustrating transects surveyed for aspen (yellow lines). The green area is forested habitat and the brown areas are meadow complexes.

When a group of aspen was encountered along a transect a handheld GPS (Global Positioning System) device was used to map the perimeter of the stand. A stand was defined as an area ≥ 100 m^2 with ≥ 20 aspen stems. In much of the Firehole drainage, aspen were diffuse and no clear stand perimeter could be defined. In cases like this, a point was plotted every 0.5 km along the transect being surveyed using a GIS. These points were selected arbitrarily as the "stand center", from which belt transects for

sampling would originate. If the arbitrary point did not meet the above criteria (area $\geq$100 m^2 with $\geq$ 20 aspen stems) then the stand center was moved to a nearby location that satisfied these criteria. If aspen were absent or few at a site, the point location was skipped and the next point on the transect where aspen were present was sampled.

Sample Plot Selection

Once an aspen stand was located and mapped, 1-3 sample plots (depending on stand area and stem density) were located within each stand. Sample plots were constrained to locations with sufficient individual stems within the browse zone (20-150 cm) to provide for 20 stems per plot. The lower bound of the browse zone (20 cm) was determined by the average height at which the lowest browsing was observed across stands (established via preliminary observations across multiple sites prior to sampling). The upper bound of the browse zone (150 cm) was determined as the maximum height at which we can be reasonably certain that the leader stems are accessible to elk for browsing (Keigley 1997). Elk are the primary ungulate browsers in the MHSA, with deer and moose occurring in low densities during the snow-free months (Garrott et al. 2005).

No more than three plots were established for any one aspen stand to minimize the total number of stems destructively sampled, as aspen are sparse in this region. Efforts were made to attain a representative sample of aspen stems that would capture any within-stand variability of site characteristics (e.g. slope, substrate, stand complexity, vegetative composition). Where stands were of a generally circular shape, the approximate center of the stand was located, and from this point random compass

bearings were used to determine vectors along which belt transects would be established (Figure 2.3). The 360° of a compass were divided by the number of sample plots (1-3) to be surveyed within a respective aspen stand. The belt transects were of variable width and length dependent upon stem density and landscape characteristics, as stem density was typically very low. A typical belt transect was 5 m wide. Length was determined by the distance required to encounter 20 stems within the browse zone along the belt transect. If a bearing was randomly selected for a belt transect that would not provide at least 20 stems to sample, the bearing was shifted to the nearest bearing that had enough stems to sample.

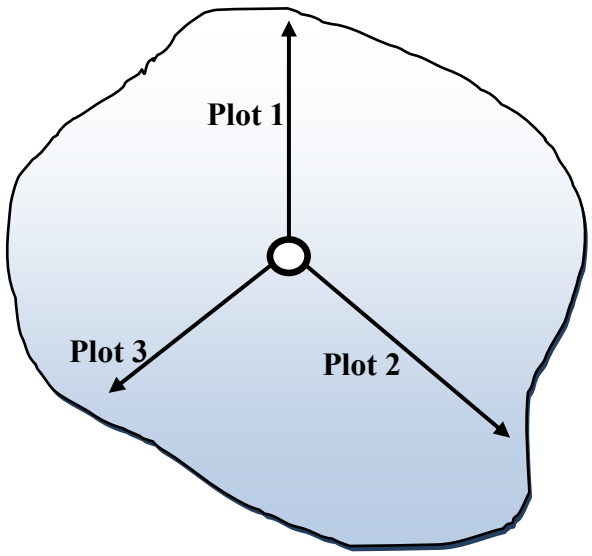


Figure 2.3: Schematic of sample plot selection for circular aspen stands. Belt transects radiate out from the approximate center point of the stand. Each vector represents a belt transect.

Where stands contoured the topography longitudinally, taking a long slender shape, belt transects were oriented so as to cross section the length of the stand (Figure

2.4). These types of stands were divided into 1-3 segments, depending on total stand area and density of aspen stems. As before, belt transects were of variable length and width and ran through the center of each stand segment, alternating between uphill and downhill starting points, if applicable. Belt widths were typically 5 m and transect length was determined by the distance required to encounter 20 stems. In cases where no clear stand perimeter could be defined (common in the Firehole drainage), the center point was located and the same methodology for establishing sample plots for circular stands was used.

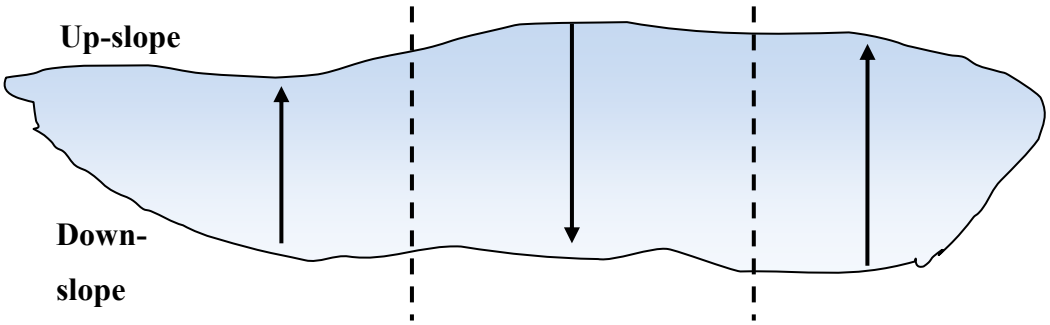


Figure 2.4: Schematic of sample plot selection for longitudinal aspen stands. Stands were divided into segments and belt transects were established to cross-section each segment, typically alternating uphill-downhill orientation.

The belt transect method could not be used for one stand, where stem density was relatively high, because little distance would have been gained along the transect before encountering 20 stems. Thus, the plots would be spatially concentrated near the center of the stand, possibly resulting in a sample that is not representative of the full range of within-stand variability. A variable-radius circle plot was used for this stand, the radius of which was determined by the area required to encompass 20 stems for sampling. The

location of these plots (n= 3) within the stand was selected to capture any within stand variability in plant growth, vegetation community composition, or environmental attributes.

Biotic and Abiotic Site Characteristics

Site characteristics and cover type were determined for each plot. The environmental attributes included were slope, aspect, elevation, soil type and geology, snow water equivalent (SWE), heat load, and burn class (whether or not the stand had burned in the 1988 fires). Slope, aspect, and elevation were all recorded in the field using a compass, clinometer, and handheld GPS device. Soil type and geology were derived using ARC-GIS (version 9.3.1, ESRI Inc.) from geospatial data provided by the YNP Spatial Analysis Center (1997). Geology data were derived from 7.5 minute USGS surficial geology maps for the Madison Junction and Old Faithful quadrangles that were digitized and published by the National Park Service as part of the Geologic Resources Evaluation Program.

SWE is a measure of the amount of water in a column of snow that accounts for both snow pack depth and density, and is a common metric of snow pack used in ecological studies. The spatially explicit Langur snow pack model was developed and validated for the Yellowstone area by Watson et al. (2009) and was used in these analyses to estimate the peak of an average snow year (01 March 1993) at a spatial resolution of 285 m. These data were obtained from the California State University-Monterey Bay Ecosystem Science and Visualization website (http://ynp.csumb.edu/data/data.htm).

Mean SWE was calculated from these geospatial data for the area encompassed within each mapped aspen stand using a GIS for the analysis of the effects of peak snow pack on aspen growth and persistence in the MHSA.

Heat load is a measure of potential direct incident solar radiation that incorporates latitude, slope, and aspect while accounting for the cumulative heat effect of elapsed daylight hours. Heat load is important to plants during the growing season as a driver of soil temperature, length of growing season, spring leaf-out date, and rate of photosynthesis and evapotranspiration. Heat load also influences snow pack dynamics, which in turn may serve as a proxy for growing season length for shorter plants, soil moisture, or incidence of browsing by ungulates (e.g. Visscher et al. 2006, Jenkins and Wright 1987). Heat load was calculated at the scale of individual aspen stands using the methods of McCune and Keon (2002). While the models developed by McCune and Keon (2002) are limited in that they do not account for cloud cover or topographic shading, the majority (78%) of the sampled stands are located on southerly slopes descending from the plateaus, which lack any significant topographic features that would result in shading.

Burn class was categorized as either **burned (BF)** or **unburned (UF)** as evidenced by regenerative lodgepole and charred logs or stumps. These observations were cross-validated with geospatial data delineating the perimeter of burned areas and qualifying burn severity from the 1988 fires in YNP. The burn area perimeter data were published by the YNP Spatial Analysis Center (1989).

Biotic components that could potentially influence aspen productivity and persistence were also assessed. They included stand area, stem density, dominant cover type, and whether the contemporary cohort of new shoots that established following the 1988 fires had originated as suckers or seedlings. Cover type was classified as follows:

Aspen (AS): Predominantly comprised of quaking aspen.

Lodgepole Pine (LP): Predominantly comprised of lodgepole pine.

Mixed Conifer Forest (MC): Comprised of varying proportions of lodgepole pine, whitebark pine, subalpine fir, Engelmann spruce, and Douglas-fir.

Thermal (TH): Geothermally influenced landscape and vegetation.

Wet Meadow (WM): Composed primarily of sedges.

Dry Meadow (DM): Composed primarily of grasses.

Talus (TS): Outcroppings of coarse rocky debris, or scree fields. Lacks any significant canopy closure.

Extant aspen stands were classified as having originated from seedling establishment or clonal shoot development based on a qualitative assessment of stand features, the historical distribution of known aspen stands (Despain 1990), and prior knowledge from previous studies that confirmed the origin via genotyping (Stevens et al. 1999) and distribution (Romme et al. 1997, 2005) of seedling-established stands that were spatially proximate to those examined in this study. The predicted distribution of post-fire aspen seedlings (Turner et al. 2003) was also considered. Stands having originated from seed (hereafter referred to as seedling-established) were identified by: 1) lack of any mature trees, 2) occurrence within a burned forest near locations where

seedling establishment has been previously confirmed, and 3) site characteristics (i.e. not being confined to steep talus slopes, a feature indicative of the pre-fire distribution of clonal aspen stands in the MHSA). Stands predating the 1988 fires and reproducing primarily by vegetative reproduction (hereafter referred to as clonal) were identified by: 1) the presence of mature trees, 2) pre-fire distribution, as indicated on historical vegetation maps (Despain 1990), and 3) occurrence as small sparse stands confined to steep southerly talus slopes. While this categorization lacks rigorous scientific confirmation of the origins of stems within stands, the spatial association of aspen stands identified in the current study with those identified in previous studies, and the categorization of stands using the aforementioned criteria likely provide reasonable support for such designation. Stands for which a confident classification could not be made were excluded from any analyses involving stand origin.

Observations and Sampling

The first 20 aspen stems encountered along a belt-transect, (or in a variable-radius circular plot), that were within the browse zone (20-150 cm in height) were selected for measurement, with 50% of those subsequently being selected for destructive sampling. Where there were multiple stems emerging from the soil at the same point, the stem that appeared to be the dominant of the group was selected for observation and sampling. In some instances, stem densities were too low to provide for 20 stems, in which case as many stems as were available were included in the observations.

Height to the base of the current year's growth (H_{BCYG}) was measured as an indication of net height gain prior to the current growing season for each of the 20 stems selected for observation to characterize the overall height of regenerative aspen.

Stem cross sections or increment cores were collected for dendrochronological analysis to characterize the age structure of regenerative aspen and to determine the age at which an individual stem either entered the browse zone or was initially browsed. Samples were collected from no more than 50% of the individuals observed within a plot, totaling no more than 10 individual stems sampled per plot. Stems that were > 5 cm diameter at the segment being sampled were cored using a 4 mm diameter increment borer. Cross sections were collected from stems that were ≤ 5cm diameter at the section of the stem being sampled. It was necessary in most cases to collect cross sections, rather than cores, as the stem diameters were typically ≤ 5cm. In most cases, multiple samples were collected from each of the stems selected for sampling. A section was collected from the base of each stem to determine total age of the plant. For plants exhibiting signs of exposure to intense browsing, a sample was taken from the live portion of the stem just below the lowest cluster of dead stems as a means of determining the age at which the plant was initially browsed. For plants that showed no obvious signs of exposure to intense browsing, a section was taken at 20 cm from the base as a means of determining the age at which the plant entered the browse zone and was accessible to ungulates. Cross sections were surfaced using a razor blade to elucidate the annual rings. Increment cores were mounted and prepared following standard dendrochronology techniques (Stokes and Smiley 1968). Ages were determined using a dissecting scope to count the

number of annual rings. Cross-dating methods were not employed, as the majority of trees within the browse zone were < 20 years of age and could not be reliably cross-dated due to the shortness of tree-ring series and the lack of sensitivity of tree-ring widths during the juvenile growth stage.

Cross sections were collected from up to three dead aspen stems (< 150 cm in height) per plot in order to evaluate the average age at which a stem that was unable to grow beyond the browse zone died in a given stand. These samples were prepared and examined in the same manners as live cross sections.

The size class distribution (SCD) of stems was characterized for each stand in order to assess the current rate of recruitment of young stems into the canopy, and to estimate average stem density. Each stem in a plot, including those growing outside the browse zone, was categorized based on a three class division of stem height; **SCD**1: <20 cm, **SCD2**: 20-150 cm, and **SCD3**: >150 cm.

Analysis Methods

Due to the nature of aspen and their position on the landscape in the MHSA it was not possible to design an orthogonal study having equal representation of aspen stands across the full range of environmental gradients; thus, the distributions for environmental data were skewed and often required the use of non-parametric significance tests. The Wilcoxon Rank Sum test was used for two-sample comparisons between suckers and seedlings. The Kruskal-Wallis Rank Sum test was used to assess drainage-wise differences in environmental attributes and H_{BCYG} followed by *post hoc* non-parametric

Tukey-type multiple comparison procedures (Zar 1984) where significant differences were revealed.

Stepwise forward regression was performed to determine which environmental variables best explained variation in H_{BCYG} across stands. The environmental variables incorporated for possible inclusion in the final model included: CLONE (a factor indicating whether a stand originated clonally, or from the post-fire seedling establishment), elevation, slope, SWE, and heat load. CLONE was included in all models to account for known differences in plant physiology and productivity between seedlings and suckers of clonal species (McDonough 1985, Schier et al. 1985, Raphael and Nobel 1986). Only stands that could be characterized as either clonal or seedling-established were included in the forward stepwise regression (n=25). H_{BCYG} was log transformed for linearity. Pearson's correlation coefficients (*r*) were calculated to assess multicolinearity among predictor variables considered in the forward stepwise regression analysis. All statistical analyses were performed using program R (R Development Core Team, 2011).

Results

During the summer of 2009 forty eight transects of variable length were surveyed in the MHSA for a total distance of 226 km. Thirty one aspen stands were located and mapped; 11 in the Firehole River drainage, 10 in the Madison Canyon, and 10 in the Gibbon River drainage. For each identified stand, 1-3 plots were sampled totaling to 69 plots for the entire study area. Observations were recorded for 1,327 individual live

aspen stems, and a total of 2,532 samples was collected from 636 individual live stems selected for sampling. Cross sections were collected from 56 dead stems within the browse zone. In total, for all sample types, 2583 samples were collected to assess the state of aspen regeneration in the MHSA.

Distribution and Environmental Attributes

The spatial arrangement of aspen stands on the landscape differed across drainages with respect to their associated environmental attributes. In the Gibbon and Madison drainages, aspen tended to be confined to small stands found on steep (~40°) southerly aspects in rocky outcroppings at the convex break in the slope near the plateau edge. Very few aspen exist in the Gibbon drainage, where the regenerative lodgepole forest is very dense with post-burn saplings and deadfall. No aspen were found north of the Gibbon Canyon, except for the rare discovery of small groups of stems (1-6) found interspersed with the lodgepole saplings. Aspen in the Firehole drainage were found to be diffuse throughout the burned forest, occurring primarily on southerly aspects, favoring no particular slope steepness (median= 18, range: 0 – 40).

Sixteen clonal stands and nine seedling-established stands were identified in this study. Six of the 31 stands could not be confidently classified as either clonal or seedling-established and were excluded from subsequent analyses investigating differences between suckers and seedlings. All but one seedling-established aspen stands occurred in the Firehole drainage, along with two clonal stands. All but two of the clonal stands were located in the Madison and Gibbon drainages. Of the two clonal stands

located in the Firehole, one occurred in an unburned forest. Suckers occurred in both burned and unburned forests and in a variety of habitat types (TS, MC, LP, AS). Seedlings occurred in burned stands (by definition) of primarily lodgepole pine with much downed woody debris from the 1988 fires.

Elevation: Elevation recorded at located aspen stands ranged from 2076 – 2418 m. Elevation differed among drainages (χ^2= 7.10, df= 2, p= 0.029 from a Kruskal-Wallis rank sum test) with stands located in the Madison having a lower average elevation of 2192 m (2076 – 2409), and stands in the Firehole and Gibbon drainages averaging 2290 m (2205 – 2411) and 2279 m (2145 – 2418), respectively (Figure 2.5, Tables 2.1 and 2.2). This difference among drainages in elevation recorded at sampling sites corresponds well with the topographic characteristics of the study area, where the Madison Canyon is at lower elevations downstream of the other two drainages (see Study Area description).

Table 2.1: Results from a Tukey-type non-parametric *post hoc* multiple comparison procedure (Zar 1984) assessing the statistical significance of observed differences in elevation between drainages (95% family-wise confidence level).

Drainage (1-2)	**Rank Sum 1**	**Rank Sum 2**	**Diff**	**p**
Firehole - Gibbon	211.5	187.5	24.0	0.236
Firehole - Madison	211.5	97.0	114.5	0.015
Gibbon - Madison	187.5	97.0	90.5	0.027

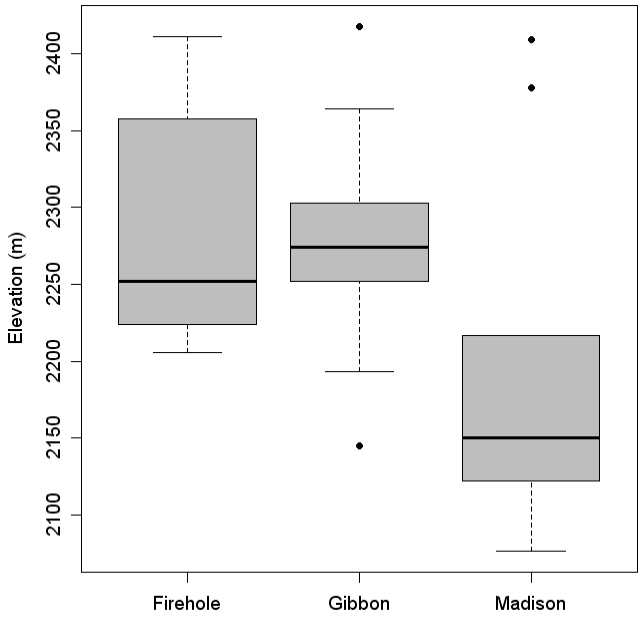


Figure 2.5: Drainage-wise difference in elevation for aspen stands located in the Madison headwaters study area.

Slope and Aspect: Slope ranged from 0° to 40° throughout the MHSA, although most aspen stands were confined to steep slopes with a southerly aspect. Of the 31 stands included in this study, 15 of them (48.4%) had a slope ≥ 35°, and 20 (64.5%) had a slope ≥ 30° (Table 2.2). Slope differed across drainages (χ^2= 10.05, df= 2, p= 0.007 from a Kruskal-Wallis rank sum test), where the average slope in the Firehole (16.6°) drainage was significantly less than the other two drainages (Gibbon= 36.8°, Madison= 30.7°). The difference in slope between stands found in the Madison and Gibbon drainages was not significant (Figure 2.6, Table 2.3). Fifteen of the 31 stands (48%) occurred on warmer, drier aspects between 135°– 225°, all of which had a slope > 30° (Figure 2.7). Clonal stands were generally found on steeper slopes than seedling-established stands (mean slope: clonal= 33°, seedling= 13°) (Figure 2.6).

Table 2.2: Site attributes for aspen stands in MHSA, grouped by river drainage. Averages for each drainage shown in shaded rows. Stand origin describes whether aspen regeneration within a stand was from clonal reproduction or post-fire seedling establishment. Cover type: aspen (AS), mixed conifer (MC), lodgepole pine (LP), and talus (TS). Burn class: unburned forest (UF), and burned forest (BF).

Stand	Stand Origin	Stand Area (ha)	Elevation (m)	Slope (deg)	Aspect	Cover Type	Burn Class	SCD 1	SCD 2	SCD 3	Total Stems	Density (stems/ m^2)
Firehole		1.95	2279	17				10.3	72.3	2.5	85.1	1.70
01	clonal	0.81	2198	33	SW	TS	UF	14	39	1	54	-----
02	seedling	3.49	2381	20	SW	LP	BF	30	77	0	107	0.05
10	seedling	3.57	2219	12	W	LP	BF	6	50	3	59	-----
11	seedling	6.01	2212	0	FLAT	LP	BF	19	80	0	99	0.32
13	clonal	0.49	2268	39	W	LP	BF	0	59	14	73	1.14
20	seedling	1.62	2213	0	FLAT	LP	BF	0	219	0	219	7.85 *
32	-----	2.27	2211	31	SE	LP	BF	9	41	10	60	0.53
12	seedling	❖	2279	16	E	LP	BF	21	107	0	128	0.70
17	seedling	❖	2383	15	NE	LP	BF	4	44	0	48	0.05
18	seedling	❖	2397	20	NE	LP	BF	8	22	0	30	-----
19	seedling	❖	2308	0	FLAT	LP	BF	2	57	0	59	2.95
Gibbon		2.05	2273	37				13.7	38.8	22.7	75.2	0.66
03	clonal	0.73	2274	38	W	TS	BF	25	15	36	76	0.20
04	clonal	1.14	2265	26	S	LP	BF	20	68	18	106	0.93
05	clonal	1.06	2308	38	SW	TS	BF	29	38	8	75	0.64
07	clonal	0.57	2389	36	S	LP	UF	3	47	16	66	0.46
08	clonal	0.32	2358	37	SW	LP	UF	25	49	13	87	-----
09	-----	10.88	2203	40	S	LP	BF	20	48	0	68	0.32
14	clonal	0.16	2147	38	N	TS	UF	1	31	23	55	1.96
15	clonal	0.32	2260	39	NW	TS	UF	0	24	98	122	-----
16	clonal	0.97	2299	37	W	TS	BF	14	39	9	62	0.05
21	clonal	0.16	2229	40	S	LP	BF	0	29	6	35	0.70
Madison		3.07	2192	31				0.5	35	11.9	47.4	0.77
22	seedling ♦	3.90	2162	37	S	TS	BF	0	26	23	49	0.53
23	-----	0.05	2409	30	SW	MC	BF	0	20	0	20	0.40
24	-----	0.89	2214	40	SW	LP	BF	0	57	0	57	0.42
25	clonal	2.84	2131	40	SE	AS	BF	3	38	24	65	0.64
26	-----	0.22	2149	37	W	MC	BF	0	18	13	31	0.62
† 27	clonal	11.21	2141	10	NW	MC	BF	1	52	0	53	1.13
28	clonal	5.44	2088	12	N	LP	BF	0	41	10	51	0.68
29	clonal	0.08	2385	30	W	MC	BF	0	20	6	26	2.07
30	-----	2.03	2152	40	SW	MC	BF	1	50	0	51	0.69
31	clonal	0.24	2090	30	S	MC	BF	0	28	43	71	0.56

♦ Determined to be seedling established via genotyping by Stevens et al. (1999)

* Extremely high stem density relative to other stands in the study area

† Stand previously mapped as aspen by Despain (1990)

❖ No distinct stand perimeter could be defined; stand area could not be calculated.

Table 2.3: Results from a Tukey-type non-parametric *post hoc* multiple comparison procedure (Zar 1984) assessing the statistical significance of observed differences in slope between drainages (95% family-wise confidence level).

Drainage (1-2)	Rank Sum 1	Rank Sum 2	Diff	p
Firehole - Gibbon	103.0	215.0	112.0	0.016
Firehole - Madison	103.0	178.0	75.0	0.041
Gibbon - Madison	215.0	178.0	37.0	0.148

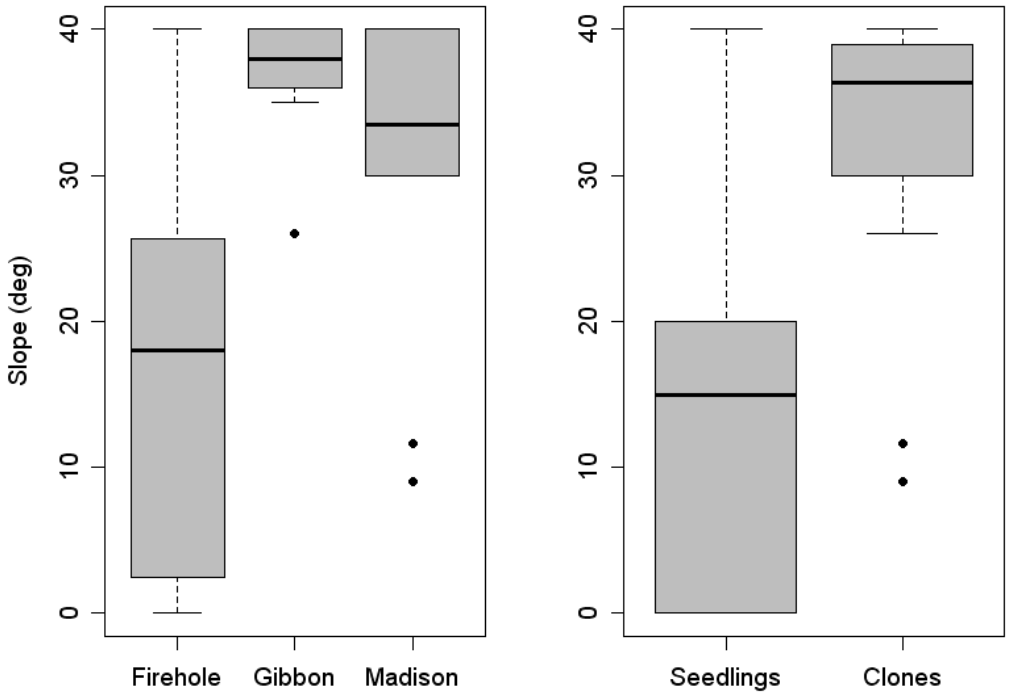


Figure 2.6: Difference in slope by drainage and stand origin (clonal and seedling-established) for aspen stands located in the Madison headwaters study area.

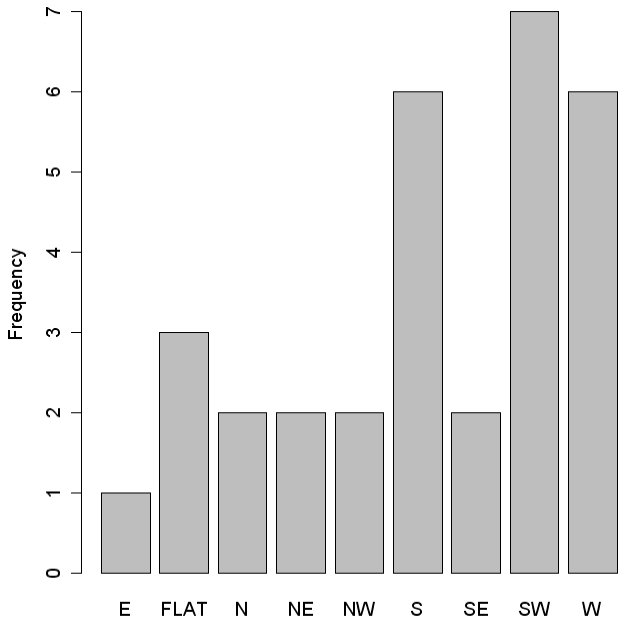


Figure 2.7: Frequency distribution of the number of aspen stands in the Madison headwaters study area observed within each aspect class.

Cover Type: All stands except one (Stand 27) occurred in forested habitat dominated by lodgepole pine, and 26 of the 31 stands (84%) occurred in forested habitat that had burned in the 1988 fires (Table 2.2). In burned areas, aspen were encompassed by or interspersed with lodgepole pine regeneration. In much of the Gibbon and Madison drainages, stands occurred in scree fields and talus patches surrounded by conifer forests. Stand 27 is unique relative to other aspen stands in this study area. It is located in Cougar Meadows, a dry meadow complex at the edge of a small patch of unburned mixed conifer forest. This stand was previously mapped as a mature clonal stand predating the 1988 fires (Despain 1990) and resembles aspen stands in the Northern Range of YNP with regards to its position in the landscape (Mueggler 1985, Despain et al. 1986, Marston and

Anderson 1991, Gallant et al. 2003). This stand was also a likely source of propagules for the post-fire seedling establishment.

Soils and Parent Material: All but two of the 31 stands were located on the plateaus or on the slopes descending from them to the canyon bottoms. Soils at these sites were characterized as nutrient poor glacial till, derived from rhyolitic ash and lava flow that covers much of the study area. Two stands were located in the canyon bottoms on alluvial plains, both of which occurred in burned forest that had likely encroached on the adjacent meadows since the previous disturbance event. One of these two stands (Stand 20, Table 2.2) occurred on a bed of alluvium at the base of Fairy Falls. The soils in Stand 20 are characterized as inceptisols, mollisols, and thermal soils that maintain an average soil temperature of > 8° C in some areas. Stand 20 had a significantly greater density of young aspen stems than the rest of the stands (discussed in next section).

Stand Size and Stem Density

The median area of the discrete aspen stands in the MHSA was 0.97 ha (0.05 – 11.21). The mean stand area (2.12 ha) is biased high as a result of two relatively large stands (Stand 9 and Stand 27) (Figure 2.8). The larger of the two outlier stands (Stand 27) was mapped as a previously known aspen stand prior to the 1988 fires (Despain 1990) and is located at the forested edge of an adjacent meadow complex, typical of larger contiguous aspen stands occurring in other areas of the GYE (Mueggler 1985, Despain et al. 1986, Marston and Anderson 1991, Gallant et al. 2003). Mean stand area

did not differ significantly among drainages (means: Firehole= 1.95 ha, Gibbon= 2.05 ha, Madison= 3.07 ha, χ^2= 1.67, df = 2, p= 0.433, Kruskal-Wallis rank sum test) (Figure 2.9).

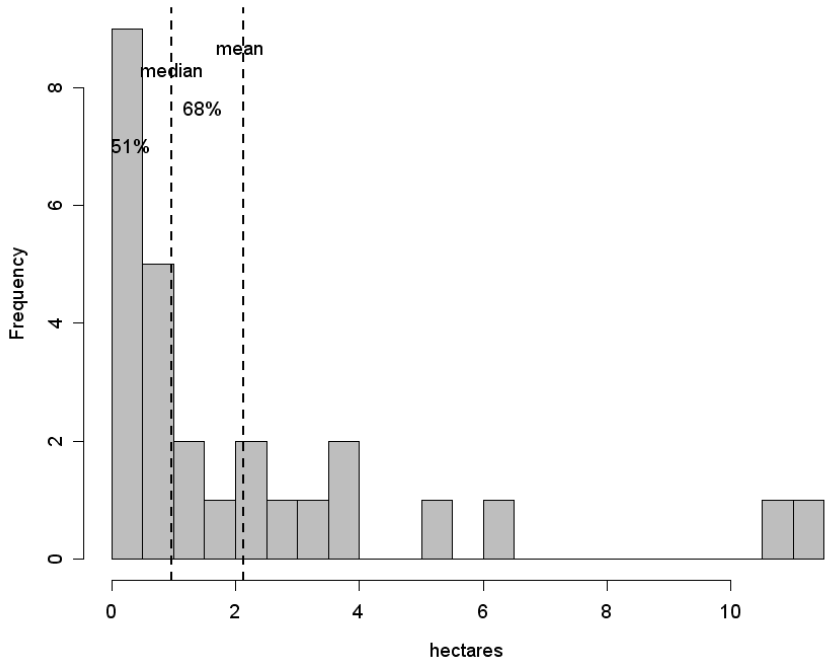


Figure 2.8: Frequency distribution of stand area for aspen stands in the Madison headwaters study area. Fifty one percent of stands have an area ≤ the median value (0.97 ha) and 68% of stands have an area ≤ the mean value (2.12 ha).

Mean stem density was 0.91 stems/m^2 (0.05 – 7.85), with a median of 0.59 stems/m^2. The mean was biased high due to the influence of Stand 20 (Figure 2.10), a very dense stand relative to the study area, for which a stem density of 7.85 stems/m^2 was recorded. Stand 20 was determined to be atypical of aspen stands in the MHSA and was excluded from further analyses.

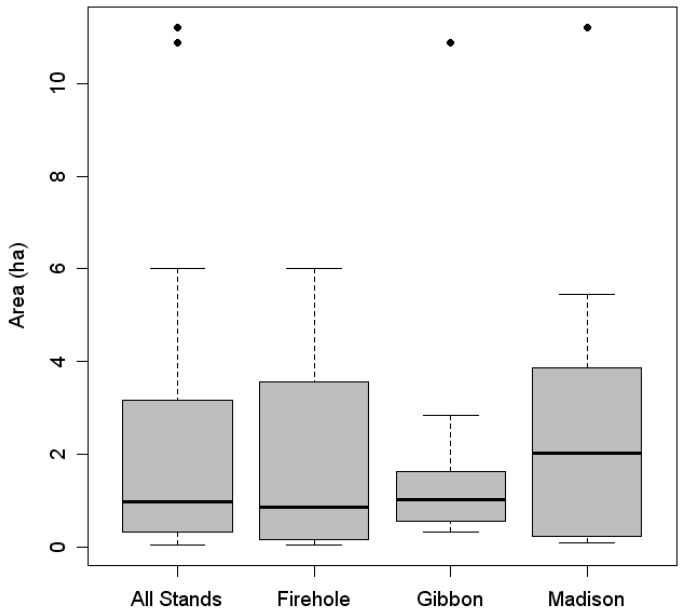


Figure 2.9: Boxplot illustrating similarity of stand area across drainages. Notice the two outliers with relatively very large stand area occur in the Madison and Gibbon drainages.

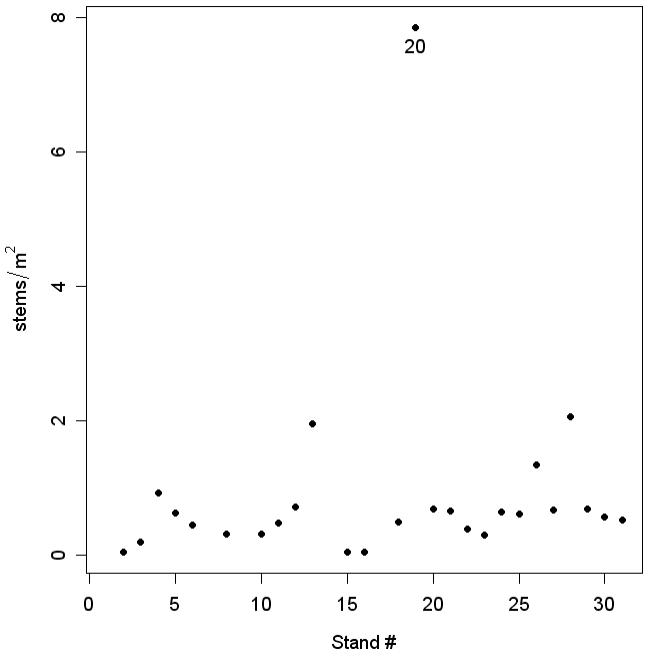


Figure 2.10: Scatterplot illustrating the extreme disparity in stems/m^2 between Stand 20 and all other stands in the MHSA.

Mean stem density excluding Stand 20 was 0.64 stems/m^2 (0.05 – 2.07). Stem density (excluding Stand 20) was significantly different between seedling-established stands and clonal stands (W= 64, p= 0.03, Wilcoxon Rank Sum Test), where mean stem density for seedlings and suckers was 0.34 and 0.84 stems/m^2, respectively (Figure 2.11). Mean stem density did not differ significantly among drainages (means: Firehole= 1.31, Gibbon= 0.67, Madison= 0.80, χ^2= 3.52, df = 2, p= 0.173, Kruskal-Wallis Rank Sum Test).

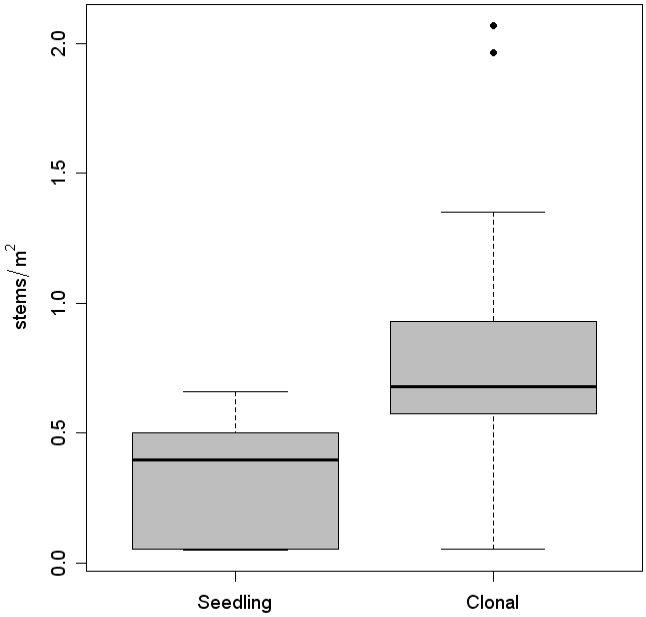


Figure 2.11: Difference in stem density between clonal stands and seedling-established stands for aspen stands in the Madison headwaters study area.

Size Class Distribution and Plant Height

Aspen stands with an effective canopy of mature aspen trees were largely lacking throughout the study area. Mature trees existed in only 11 of the 31 stands and occurred only in low numbers in clonal stands that predated the 1988 fires. There were very few

trees (14%) that grew beyond the browse zone, extending into the canopy. The majority of stems observed (median= 72.5% across all stands) occurred within the browse zone, most of which exhibited signs of an historical period of intense browsing, as evidenced by multiple clusters of dead browsed stems. Very few stems were shorter than 20 cm (median= 4.5% across all stands), indicating that saplings were quickly entering the browse zone uninhibited by browsing or other obstructions to vertical growth. (The mean age at which stems were initially browsed is 1.6 years.) However, it is recognized that the lower bound of the browse zone in this study area was defined as 20 cm in height, which is relatively low for a species known to achieve over a meter in vertical growth in the first growing season following a disturbance (Despain 1990).

Mean H_{BCYG} for all stands in the study area was 89.0 cm (11.0 – 700.0), but varied among the three drainages (χ^2= 11.69, df = 2, p= 0.003, Kruskal-Wallis rank sum test) (Table 2.4). H_{BCYG} in the Firehole was significantly different from the other two drainages, which did not differ from each other (Figure 2.12). Mean H_{BCYG} was 101.5 cm (SD= 24.6) for the Madison canyon, 92.7 cm (SD= 26.7) in the Gibbon drainage, and 56.7 cm (SD= 21.9) for the Firehole drainage. H_{BCYG} was also significantly different between seedlings and suckers (W= 15, $p < 0.001$, Wilcoxon rank sum test). Mean H_{BCYG} for suckers and seedlings was 108.0 cm (SD= 27.1) and 63.7 cm (SD= 29.4) respectively (Figure 2.12).

Table 2.4: Results from a Tukey-type non-parametric *post hoc* multiple comparison procedure (Zar 1984) assessing the statistical significance of observed differences in H_{BCYG} between drainages (95% family-wise confidence level).

Drainage (1,2)	Rank Sum 1	Rank Sum 2	Diff. in Medians	p
Firehole – Gibbon	95.0	186.0	91.0	0.026
Firehole – Madison	95.0	215.0	120.0	0.013
Gibbon – Madison	186.0	215.0	29.0	0.197

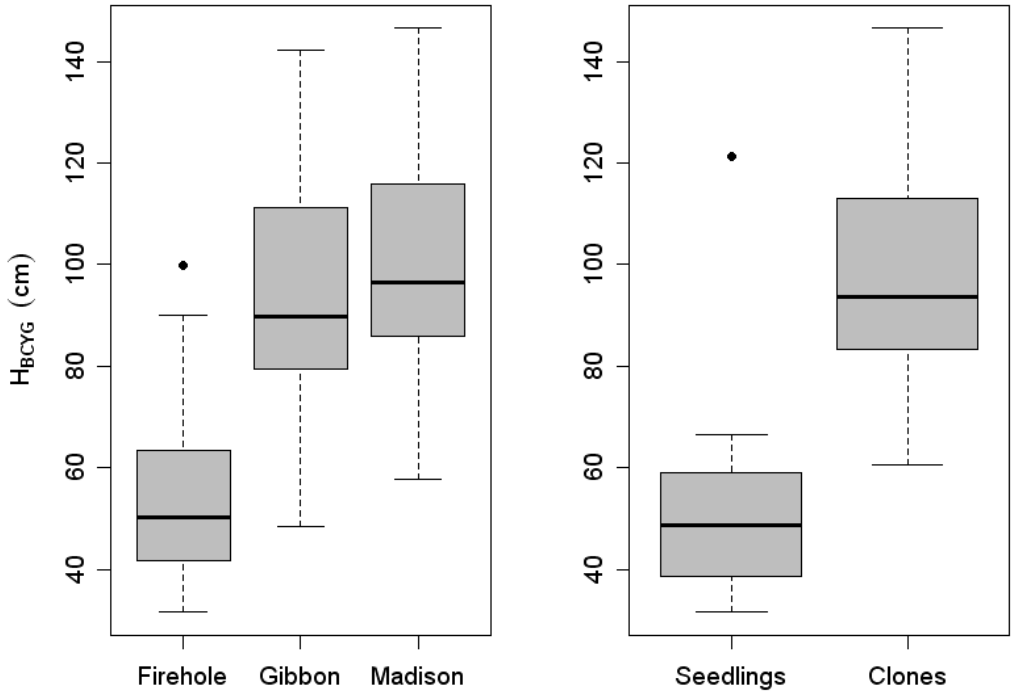


Figure 2.12: Difference in H_{BCYG} (cm) by drainage and stand origin (clonal or seedling-established) for aspen stands located in the Madison headwaters study area.

Moderately strong correlations were observed between plant height and environmental variables, as well as among pairs of environmental variables (Figure 2.13). H_{BCYG} was found to be correlated with three out of the four environmental variables considered in this analysis. H_{BCYG} is negatively correlated with elevation (r= -0.43),

indicating that aspen were taller at lower elevations. Elevation may serve as a proxy for differences in local temperature, accumulated snowpack, or other environmental phenomenon affecting the physiology of plants in a heterogeneous landscape (Fritts 1976). Naturally, elevation was found to be strongly positively correlated with SWE (r= 0.67), where the accumulated maximum snowpack in an average winter was higher at higher elevations. Slope was found to be positively correlated with H_{BCYG} (r= 0.56) indicating that aspen were taller on steeper slopes. While this may be generally less intuitive with respect to plant growth, approximately 75% of aspen stands identified in this study were situated on steep south to southwest facing slopes, most of which are clonal stands. Given the nature of aspen distribution in the MHSA, this relationship may be a function of stand origin rather than slope steepness. Additionally, these stands were likely exposed to a greater intensity of solar inputs (Fritts 1976), resulting in increased rates of snow ablation and increased soil temperatures, thus influencing growing season length and rates of photosynthesis and respiration (Fritts 1976). This theory is supported by the negative correlation of slope with SWE (r= -0.48), where snow accumulation was greater on less severe slope angles. H_{BCYG} also has a strong negative correlation with SWE (r= -0.57), indicating that aspen were taller where snow accumulation was less significant, further supporting the aforementioned relationships. Clearly, the noted correlation among the environmental variables suggests that they are not acting independently in explaining the observed differences in plant growth across the study area, making it difficult to identify the strength of influence of any one variable. Topographic features of a landscape are strongly linked to climate patterns and other

environmental phenomenon influencing plant growth at a local scale. Thus, the diagnostic physical attributes of a landscape related to plant growth operate synergistically with climatic phenomenon in dictating gradients of differential plant growth on a heterogeneous landscape.

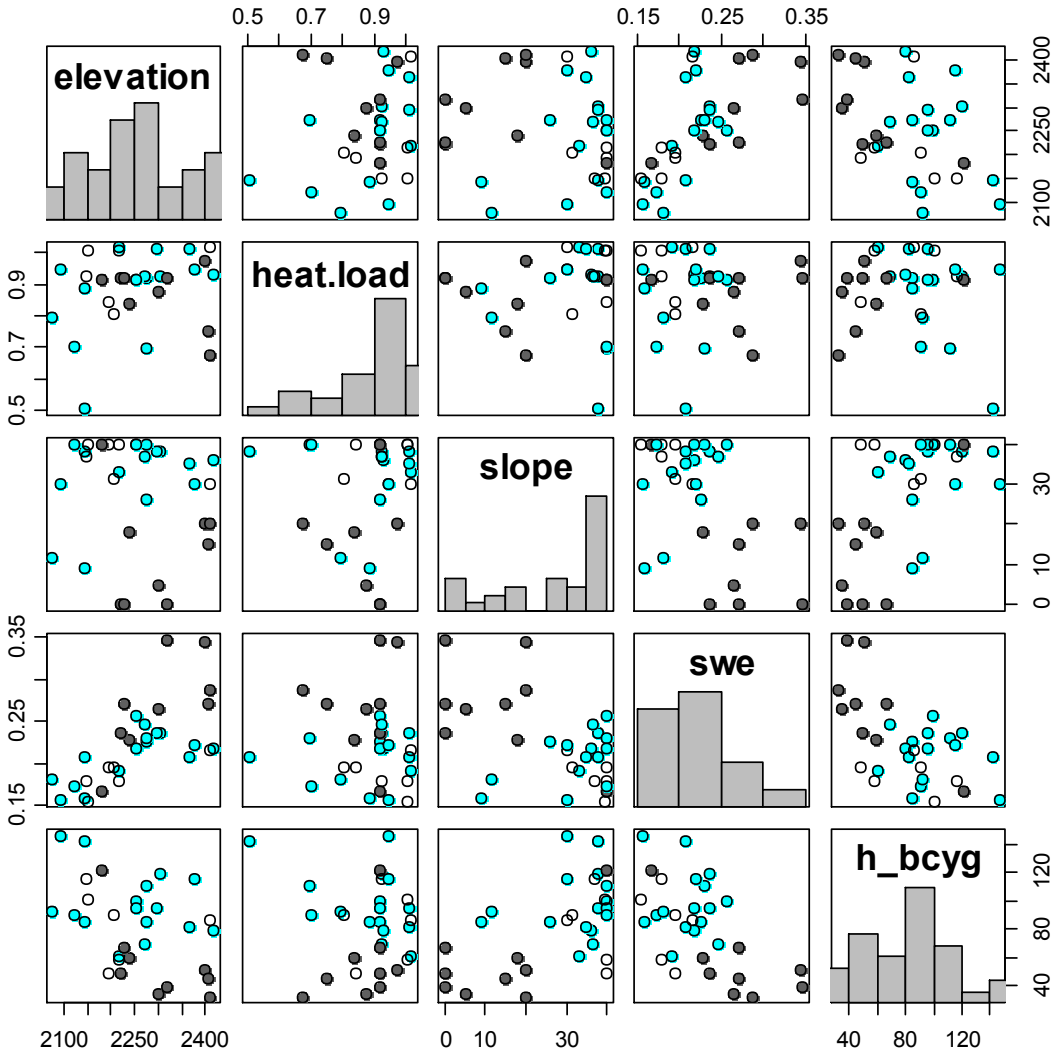
Results from the forward stepwise regression analysis indicate that elevation and slope were the most significant environmental variables, after accounting for stand origin, explaining 67% of the variation in mean H_{BCYG} across stands (Table 2.5). Coefficient estimates from the linear model reveal a negative relationship between H_{BCYG} and elevation and a positive relationship between H_{BCYG} and slope.

Table 2.5: Results from multiple linear regression analysis on H_{BCYG} for aspen stems in clonal and seedling-established stands (n=25).

Model: H_{BCYG} ~ CLONE + elevation + slope

Variable	**Estimate**	**Std. Error**	**t**	**p**
(Intercept)	7.631	1.245	6.129	<0.001
CLONE:suckers	0.266	0.148	1.796	0.087
elevation	-0.002	0.001	-3.096	0.006
slope	0.014	0.005	2.884	0.009

Multiple R-squared= 0.7121, Adjusted R-squared= 0.671
F-statistic= 17.31 on 3 and 21 DF, p-value= 6.28E-06



	elev	h_bcyg	heat load	slope	SWE
elev	1	**-0.43**	0.18	-0.09	**0.67**
h_bcyg	**-0.43**	1	-0.09	**0.56**	**-0.57**
heat load	0.18	-0.09	1	0.03	-0.04
slope	-0.09	**0.56**	0.03	1	**-0.48**
swe	**0.67**	**-0.57**	-0.04	**-0.48**	1

Figure 2.13: Correlations (α= 0.05) among environmental variables related to H_{BCYG}. Scatter plots are coded by stand origin; cyan= clonal, grey= seedling-established, white= unclassified. Significantly strong relationships are bolded in the table of Correlation Coefficients (r-values).

Age Structure

The year of origination was determined for 635 individual regenerative aspen stems originating as either clonal suckers or seedling colonizers. The median age of stems observed in this study is 11 yrs and ranged from 2 to 47 years. Figure 2.14 indicates that there was a pulse of stem origination in the years immediately following the 1988 fires, peaking between 1990-1991, and a subsequent pulse peaking between 1998-2001. The majority (78%) of stems originated sometime after 1995, with most stems (32%) originating during the second pulse. Clonal stands and seedling-established stands differ in the proportions of stems originating during each of the pulses. In clonal stands, 26% and 63% of stems originated during the first and second pulse, respectively, making up 89% of all suckers sampled. In seedling established-stands, 41% of stems originated during the second pulse, with only 11% originating during the first pulse of stem initiation, making up 52% of all stems sampled in seedling-established stands. The majority (51%) of stems in seedling-established stands originated sometime between 2000-2005. This suggests that either seedling establishment is ongoing, or that relatively few individuals from the orignial cohort of seedling colonizers have survived and are now reproducing vegetatively in response to environmental cues in a similar manner as pre-burn clonal stands. Stems greater than 20 years of age, predating the 1988 fires, made up only 2.4% of all live stems sampled, suggesting that recent aspen regeneration was stimulated by fire and aspen suckers originating prior to the fires were either non-existent or were burned in the fire.

The median age at death for dead stems sampled in this study is 10 years and ranged from 5 to 21 years. If these stems belonged to the cohort of stems that originated immediately following the 1988 fires, as did 57% of live stems sampled, they would have died on average between 1998 and 2000; just prior to the beginning of the second pulse of stem initiation (Figure 2.15).

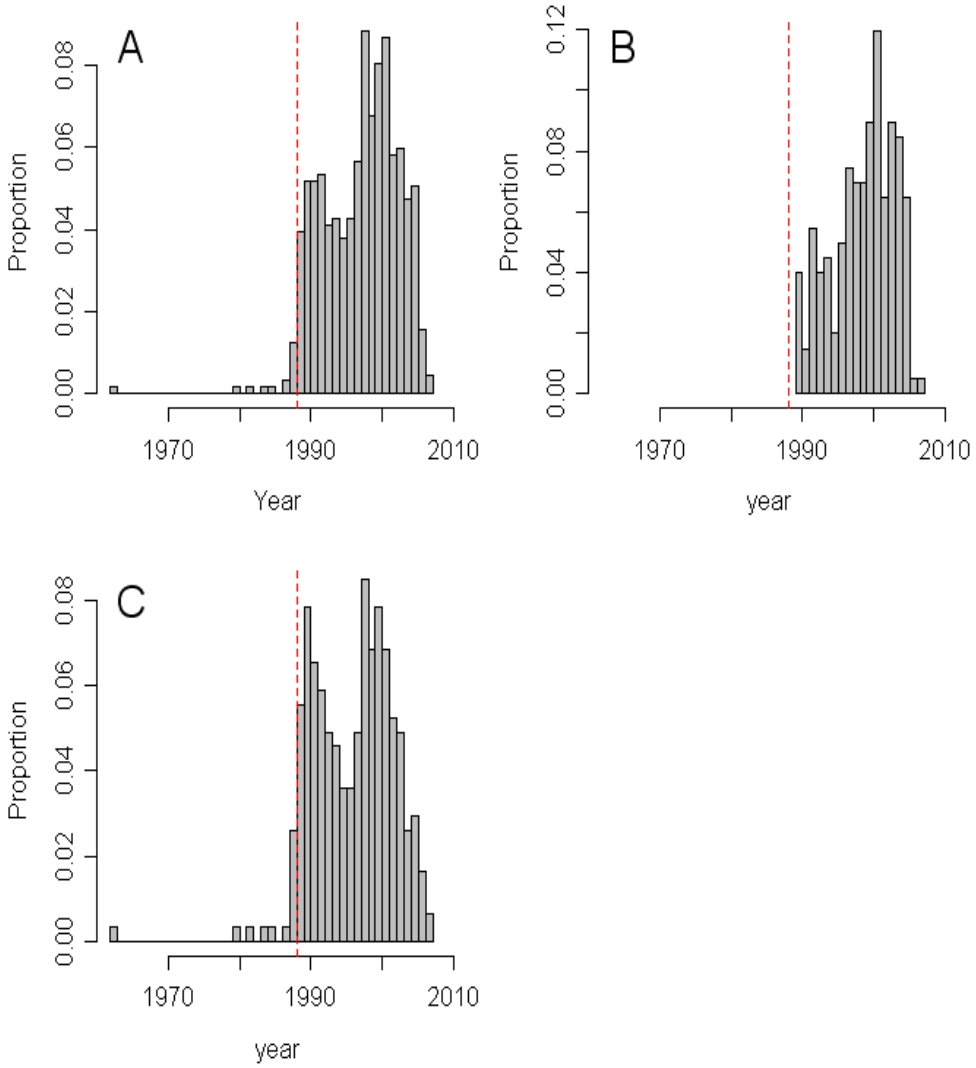


Figure 2.14: Age structure for post-burn regeneration in the MHSA. Proportion of stems originating each year for all stems (A), stems in seedling-established stands (B), and stems in clonal stands (C). The dashed vertical red line demarcates the 1988 fires in YNP.

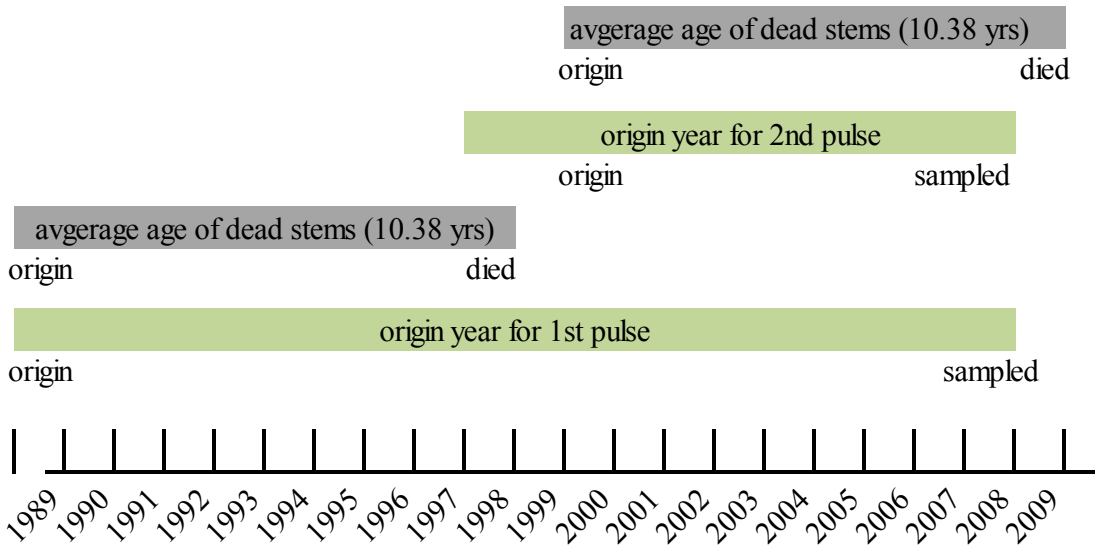


Figure 2.15: Timeline of longevity of regenerative aspen stems relative to their average year of origin. Stems originating in the post-fire pulse (1989) were approximately 20 years old. Stems originating in the 2000 pulse were approximately 9 years old. The grey bars represent the average life span of dead aspen stems sampled in the MHSA.

Discussion

Distribution and Stand Characteristics

Aspen are relatively rare in MHSA and were found to be patchily distributed throughout the MHSA in very small stands, and generally took one of three forms. The rarest form of aspen stands found in the MHSA is more characteristic of larger contiguous aspen stands found elsewhere in YNP where aspen are more common (Mueggler 1985, Despain et al. 1986, Marston and Anderson 1991, Gallant et al. 2003). Only one stand of this type was found and was the largest stand mapped in this study. This stand type is typically found at the forest's edge forming an ecotone between an extensive conifer forest and a large meadow complex. This stand was previously mapped

as part of the known pre-fire distribution of aspen in YNP (Despain 1990). The age structure and size class distribution of this stand typifies what has been described in other studies as "decadent and dying" (Bartos 2001), characterized by senescent mature trees with very little regeneration and no apparent cohort of recruitment stems to succeed the relicts of a prior episode of recruitment (Romme et al. 1995, Ripple and Larsen 2000, Hessl 2002, Larsen and Ripple 2003, Kimble et al. 2011).

The most common form of aspen in the MHSA appeared to match what Larsen and Ripple (2003) had previously described as "scree stands," typically growing on steep southerly slopes in scree fields or talus patches near the plateau's edge. This stand type was largely comprised of clonal stands and makes up the majority of the sparse pre-fire distribution of aspen in the MHSA. Scree stands are the typical stand type at higher elevations for this region, where aspen prefer south-facing slopes due to colder temperatures and shorter growing seasons (Packard 1942, Langenheim 1962, Reed 1971).

The third form of aspen found in the MHSA did not appear as a typical "stand" where a definite stand boundary could be defined. The seedling-established aspen were found to be dispersed diffusely throughout the burned forest, interspersed with lodgepole saplings, and were found primarily in the Firehole drainage. This form of aspen was typically found on shallower slopes and was not confined to talus patches, as were clonal stands found in the Madison and Gibbon drainages (Figure 2.8). Only one of the nine seedling-established stands had a slope > 20°. This particular stand (Harlequin Lake stand – Stand 22) was confirmed to have originated during the post-burn seedling establishment (Stevens et al. 1999) and took the form of a typical "scree stand." It is

likely that a number of the stands for which reproductive origins could not be classified were similar to the Harlequin Lake stand, having established from seed on steep, south-facing scree slopes. The spatial distribution of seedling-established aspen stands across the study area corresponds well with the location of stands previously identified (via genotyping) as having originated from the post-burn episode of seedling establishment (Romme et al. 1997, 2005, Stevens et al. 1999). The location of seedling-established stands and their associated slope angle also corresponds well with areas modeled by Turner et al. (2003) as having a high probability of aspen seedling occurrence. Turner et al. (2003) found that the density of newly established aspen seedlings was greater on less severe slope angles, suggesting that lower angle slopes had a greater propensity for acting as a catchment for both moisture and dispersing aspen seeds, resulting in higher rates of germination and higher stem densities.

Most aspen in the MHSA appeared as post-burn regeneration with very few mature trees and occurred in or adjacent to conifer forests that had burned in the 1988 fires in YNP. Only 2.4% of stems sampled originated prior to the fire event (Figure 2.15). It is to be expected that a pulse of stem origination should occur following a disturbance event such as the 1988 fires, as aspen is a disturbance responsive species (Bartos and Mueggler 1981, Bartos and Debyle 1989). Romme et al. (2005) documented that 36% of the 173 seedlings they examined in seedling-established stands originated in 1989, the growing season immediately following the fires, noting that the percent of stems originating in each subsequent year gradually declined. This suggests that the seedling establishment following the 1988 fires was a pulse event, facilitated by

temporarily favorable conditions for regeneration. Romme et al. (2005) also examined stems that appeared to be suckers from seedling-established individuals, noting the earliest suckers to have originated in 1992. This may have marked the initiation of clonal reproduction among seedlings that successfully established following the 1988 fires. Clonal reproduction likely increased dramatically in subsequent years, contributing to the second pulse of stem origination observed in my study. The second pulse of stem origination (1998-2001) occurred across the entire study area, in both clonal and seedling-established stands and may be best explained by a favorable climate during the prior growing season, as episodes of extensive clonal reproduction are associated with favorable growing conditions (Romme et al. 1995). A chronosequence developed from cores of mature aspen in the MHSA exhibits above average radial growth in 2000, and was preceded by a significantly cool and moist summer during the previous growing season (Chapter 3, this volume), supporting this theory.

The lack of a robust cohort of 'recruitment' stems was used by St. John (1995) and Kimble et al. (2011) as an indicator of unsustainable aspen stands, whereby young aspen stems were not sufficiently replacing senescing trees, ultimately trending towards decadent and dying stands of mature aspen. The observed size class distribution among clonal stands predating the 1988 fires in the MHSA is indicative of the suppressed recruitment exhibited by unsustainable aspen stands (St. John 1995, Kimble et al. 2011). The lack of a cohort of 'recruitment' stems may be a function of poor site productivity, intense ungulate browsing, and interspecific competition.

Stand Size and Stem Density

Aspen stands in the MHSA were relatively small (51% of stands were less than 1 ha in area) and had low stem densities (0.64 stems/m^2). This is similar to aspen in the Southern Rocky Mountains surrounding Rocky Mountain National Park where 58% of stands had an area < 0.5 ha and 90% were less than 2 ha and were found to be patchily distributed (Kashian et al. 2007). The mean stem density for seedling-established stands in the MHSA (0.34 stems/m^2) was significantly lower ($p= 0.03$) than the stem density observed in 2000 by Romme et al. (2005) (mean= 1.07 stems/m^2). This indicates a significant rate of seedling mortality ongoing in seedling-established stands in this region. Romme et al. (2005) observed an annual rate of seedling mortality of 6.18% from 1996 to 2000 for plots sampled in the Old Faithful region, an area near the majority of stands classified as being seedling-established in the present study. A comparison of the stem density observed in 2009 in my study to the 2000 estimate by Romme et al. (2005) reveals a 20.35% annual mortality rate of seedlings in the MHSA for the period 2000 to 2009. If the seedling-established stands found in the MHSA during my study are representative of those found in the Old Faithful region by Romme et al. (2005), then these observations indicate a substantial increase in the mortality rate of aspen seedlings that established following the 1988 fires in YNP.

Romme et al. (2005) posited that the post-burn seedlings have been undergoing a "long-term population process" whereby the initial high density stands of newly established seedlings are being quickly thinned to lower densities with lower overall genetic diversity. This follows an established model of population dynamics of clonal

species (reviewed in Eriksson 1993, Tuskan et al. 1996, discussed in Romme et al. 2005) where individual genotypes of a high density seedling establishment that are poorly suited for local environmental conditions quickly die off, leaving relatively few, well adapted individuals. The majority of extant regenerative aspen stems in seedling-established stands originated during the second pulse of stem origination. This suggests that few individuals from the initial cohort of post-burn seedlings are still living, and those that have persisted are now reproducing clonally. It is not likely that the second pulse of stem origination is the result of a subsequent episode of seedling establishment given that the specific conditions required for successful sexual reproduction in aspen (McDonough 1979) have not occurred in the MHSA since 1988. Further, Romme et al. (2005) reported that no new seedling establishment has been observed in the 1988 burn area where seedlings were not previously documented.

Plant Height

Although H_{BCYG} varied across drainages, the drainage factor essentially served as a mask for CLONE. Eight out of nine seedling-established stands were located in the Firehole drainage, while 14 of the 16 clonal stands occupied the Madison and Gibbon Drainages. Furthermore, the observed difference in H_{BCYG} between clonal (Gibbon, Madison) and seedling-established (Firehole) stands is confounded by the geographic arrangement of these stand types in the MHSA. Elevation, slope, and SWE all varied with stand origin. Due to the nature of the distribution of aspen across the MHSA it was not possible to determine which of these factors was most significant in explaining

differences in H_{BCYG} between clonal and seedling-established stands. However, much of the difference in H_{BCYG} is likely explained by the lack of a parent root structure to subsidize seedlings during the growing season. Such subsidies would likely promote greater radial growth and shoot elongation and increase resilience to the effects of drought (Gifford 1966, Jones et al. 1985, Raphael and Nobel 1986), browsing, insect defoliation, or other stressors. The lack of such subsidies and the lack of an extensive root network for acquisition of resources has likely inhibited seedlings from flourishing in a site that is dry, nutrient poor, and replete with lodgepole saplings, a dominant early seral competitor (Peet 1978). While they do not require well-developed soils for establishment and growth (Despain 1990), aspen seedlings were observed to be poor early seral competitors when exposed concurrently to browsing and interspecific competition in an experimental setting (Romme et al. 2005), suggesting that the ability to produce enough food to compensate for the energy costs of both growth and maintenance is sufficiently inhibited when there is a significant level of browsing pressure and low resource availability. Additionally, access to more abundant resources through the parent root structure likely offsets the costs associated with the production of chemical defense compounds for suckers under conditions of heavy browsing (Hwang and Lindroth 1997, Osier and Lindroth 2006, Stevens et al. 2007), allowing them to allocate more resources to plant growth and maintenance, as compared to seedlings. Donaldson et al. (2006) experimentally demonstrated a marked difference in relative growth rate and phenotypic responses of aspen under varying treatments of competition and nutrient availability, where the production of secondary compounds was related to diminished relative growth

rate for plants experiencing both competition and limited nutrient resources. This relationship suggests that, for aspen growing in poorly developed soils, suckers are relatively more robust to the indirect negative effects of browsing (i.e. production of secondary compounds) on plant growth, as compared to seedlings, and experience greater productivity and a lower mortality rate during historical periods of intense ungulate browsing. Seedlings are thus hindered in their ability to make any significant gains in vertical growth and compensate for any height loss due to browsing.

Results from the forward stepwise regression revealed that, after accounting for stand origin (CLONE), elevation and slope were significant in explaining variation in H_{BCYG} across stands. Elevation had a negative relationship with H_{BCYG}, where plants were taller at lower elevations. This finding is consistent with other aspen studies in the Rocky Mountains (Jelinski and Cheliak 1992, Jelinski 1993, Mitton and Grant 1980, Romme et al. 2005) and may be attributed to lower average temperatures at higher elevations, which translates to fewer growing-degree-days, lower rates of photosynthesis, reduced hydraulic conductance (Wan et al. 2001, Fraser et al. 2002), and colder minimum temperatures that may result in frost damage. However, the observed relationship between plant height and elevation may be partially a function of increased SWE at higher elevations (Figure 2.14) contributing to differences in soil moisture, timing of snow ablation, and the length of the growing season for shrubby short statured aspen. Elevation and SWE were significantly correlated ($r= 0.67$) and a linear model incorporating CLONE, slope, and SWE explained nearly as much variation in H_{BCYG}

across stands (r^2= 0.63) as did the top model (H_{BCYG} ~ CLONE + slope + elevation, r^2= 0.67).

H_{BCYG} was positively correlated with slope, where plant height increased as slope increased (Figure 2.14). There are several possible explanations for this relationship. First, all stands with a slope < 20° were located in the Firehole drainage, as were seedling-established stands. Thus, the observed relationship between plant height and slope is confounded by, and likely best explained by the relationship between plant height and stand origin. Second, stands with steeper slope angles were mostly confined to patches of scree and talus amidst a lodgepole pine forest. These rocky slopes typically occurred at the convexity in slope at the plateau's edge. It is likely that there are differences in hydrological dynamics, competitive interactions, and other local site differences that may drive the relationship between plant height and slope. Lastly, snow accumulation, ablation, and heat load (although heat load was not a significant covariate in regression analysis) are likely different on low angle slopes than high angle slopes, given that aspects were southerly where aspen were found to be growing on steep slopes. Snow ablation rates are likely higher on steeper slopes with southerly aspects in the northern hemisphere, resulting in a relatively longer growing season as compared to aspen growing on shallower slopes. Slope was significantly negatively correlated with SWE (r= -0.48). Unfortunately, the relationship between H_{BCYG} and environmental variables cannot be teased apart with the current data, due to the effects of multicollinearity among the environmental variables.

Romme et al. (2005) observed a mean plant height of 27 cm (16.5 – 43.2) for seedling-established stands located in the Firehole drainage in 2000 and observed only negligible height gain from 1996 – 2000. The difference between mean plant height observed in 2000 by Romme et al. (2005) and that observed in 2009 for seedling-established stands in the present study (63.7cm) indicates that stems in the seedling-established stands are continuing to grow vertically through the browse zone, albeit very slowly (4.1 cm/yr). If this growth rate persists, it would take another 21 years for these plants to grow beyond the browse zone (150cm) and have the potential for successful recruitment into the canopy. The upper limit of the browse zone was set conservatively for this study and it is likely that many of these plants would be subject to browsing at heights greater than 200 cm, making them vulnerable to extreme dieback due to intense browsing conditions for approximately an additional 12 years at the current growth rate. The observed height growth and browsing conditions for the current cohort of aspen regeneration in the MHSA does not bode well for successful recruitment under current conditions. However, a recent decline in the abundance and distribution of elk in the MHSA may alleviate a significant impediment to aspen height growth and accelerate their advance through the browse zone (see Chapter 4, this volume).

Conclusions

The clonal stands pre-dating the 1988 fires in YNP found in the MHSA appear to be "unsustainable." They were largely comprised of senescing mature trees with few to no recruitment stems. There was no evidence of a previous cohort of recruitment stems

that had died in the fires that would indicate that aspen were successfully producing a new cohort of mature trees. The majority of stems were of a short shrubby stature with excessive branching. While some of the mature trees in the MHSA originated c. 1960, it is estimated that many originated in the early 1900's (Chapter 3 this volume) and are approaching the upper age limit of this short lived tree species.

In general, aspen stands in the MHSA occupied small areas and had low stem densities and poor productivity. Although some height growth since 2000 has occurred in seedling stands, it is modest and most of the aspen regeneration remains within the browse zone. Both suckers and seedlings exhibit poor productivity and height growth, suggesting that the mechanism of inhibition is affecting all aspen in this region, although not equally (suckers were taller than seedlings on average). The explanation for the slow growth rate (and the high mortality rate documented for seedlings) is likely an interaction among biotic and abiotic factors, resulting in poor growing conditions for aspen. Lodgepole pine is an aggressive early seral competitor (Peet et al. 1978) that likely has a competitive advantage over the shrubby stunted aspen in the expanse of nutrient poor rhyolitic soils in which they are growing. However, Romme et al. (2005) observed the negative effects of interspecific competition on aspen plant height in their experimental plots only when both interspecific competition with lodgepole pine and simulated browsing were present. Aspen are a preferred browse species for elk (Olmstead 1979, Houston 1982) and the majority of aspen stems within the browse zone in the MHSA showed evidence of intense ungulate browsing since their origination. The interaction

between browsing and interspecific competition has likely been a significant factor in limiting aspen growth in the MHSA.

The concept of a "window of opportunity" has been proposed for aspen (Jelinski and Cheliak 1992, Erikkson and Fröbor 1996), where aspen may reproduce sexually when environmental conditions are suitable and densities of ungulate browsers are low enough so as not to completely stymie successful recruitment by inhibiting vertical growth through the browse zone. It is believed that the environmental conditions following the 1988 fires in YNP created such a window of opportunity. Although it has been heavily debated in the scientific literature, no overwhelming consensus has emerged on evidence for a new cohort of recruitment stems to replace senescing aspen from this post-disturbance pulse of regeneration. One study concluded that elk densities are still too high to permit successful aspen recruitment (Romme et al. 2005). I contend that, while elk densities may have declined significantly in some areas, the window of opportunity was brief and the changes in elk abundance and distribution occurred too late to allow successful recruitment for this cohort of new aspen stems. Initial browsing during early stages of growth can induce phenotypic responses through changes in apical dominance that drastically diminish the chances of that stem ever achieving canopy height (Andrén and Angelstam 1993, Baker 1997). It has been suggested that while aspen may not be able to effectively deter browsing (via secondary compounds) at high ungulate densities (Wooley et al. 2008), they can be very *tolerant* to the effects of browsing and have the propensity to persist (Lindroth 2001, Myking 2011) in a phenotypic manifestation that has been described as "shrub aspen" (Despain 1990).

Shrub aspen are characterized as having short stature, excessive lateral branching, and poor productivity with no inclination toward substantial height growth. It is my contention that the current cohort of post-disturbance aspen regeneration in the MHSA has been relinquished to persistence in the form of shrub aspen, although they may proliferate in the advent of a future disturbance event if elk densities remain low. While high elk densities immediately following the recent episode of aspen seedling establishment in YNP may not have been favorable for successful recruitment of this newest cohort of aspen, a long term elk study in the MHSA has documented a recent dramatic decline in elk abundance following wolf recolonization (Garrott et al. 2009a), likely resulting in a significant reduction in browse pressure. Reduced browsing pressure may facilitate an environment where aspen can successfully regenerate into mature canopies in lieu of a future disturbance event (see Chapter 4 this volume).

The findings from this study have expanded our knowledge of the current distribution of aspen in the Madison headwaters region of YNP. The distribution of aspen previously described for this region (Despain 1990) is limited to those stands occupying the ecotone between expansive conifer forests and meadow complexes, and likely ignores less conspicuous aspen stand types. Scree stands are the dominant pre-fire stand type in the MHSA, occupying steep south-facing scree slopes and talus fields. This appears to be the landscape position that aspen has carved out for itself at high elevations in the Central Rocky Mountains (Langenheim 1962, Reed 1971). Although less abundant and less extensive than other stand types, the ecological role of scree stands at high elevation sites may be important and recognition of unique stand types should be

considered in management decisions and incorporated into future study designs. It is likely that responses to changes in ecological, environmental, and climatic factors may vary among stand types. Further study is required to better understand the ecological role and stand dynamics of high elevation aspen stands.

Additionally, the known distribution of seedlings in a region predicted as being a hot spot for seedling establishment following the 1988 fires has also been expanded, (although not confirmed through genetic analysis), from that defined in earlier studies (Romme et al. 1997, 2005; Turner et al. 2003). Previous studies were limited in the resolution at which they could map and characterize the post-fire seedling establishment, as they were necessarily restricted to trail corridors in order to document the range of seedling establishment across the massive spatial extent of YNP. They paint a broader picture of the seedling establishment across a large area, but offer only a glimpse into the extent of the seedling establishment and the associated site characteristics at a more local scale. This study has contributed a higher resolution description of where on the landscape post-disturbance aspen seedlings established and are currently persisting for this region of YNP. Additionally, this study has added another point in time in documenting the post-fire seedling establishment and supplements previous work by Romme et al. (2005).

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CHAPTER 3

CONTEMPORARY CLIMATE RESPONSE OF ASPEN IN WEST-CENTRAL YELLOWSTONE NATIONAL PARK

Abstract

The decline of quaking aspen in the western United States throughout the 1900's has been attributed to the collective influence of climate, fire suppression, and ungulate herbivory, although there is evidence that browsing is the dominant force inhibiting aspen recruitment when ungulate densities are high. Despite the well-documented decline of aspen during the 20th century, scientists have reported increases in aspen growth in the Greater Yellowstone Ecosystem (GYE) since the mid-1990's. Recent studies have attributed these increases in aspen growth to a trophic cascade among wolves, elk and aspen following wolf reintroduction, yet few have adequately accounted for the potential influence of climate on plant growth. The purpose of this study was to assess the climate-growth relationship for aspen in the west-central region of YNP to determine if the increases in aspen growth observed in the GYE following wolf reintroduction can be attributed, in part, to recent climate trends. Standard dendrochronology techniques were used to assess aspen productivity for mature aspen in the Madison headwaters study area for the period 1940 – 2008 to look for shifts in productivity occurring concurrently with wolf reintroduction. Interannual radial growth patterns were found to be significantly correlated with mean summer temperatures for both the current and prior growing

seasons. An increase in tree-ring widths associated with climate was observed for the decade following the 1988 fires in Yellowstone, peaking around the same time that wolves were becoming established in the system. However, this increase in productivity was modest and does not likely explain the increases in aspen growth observed in the GYE following wolf reintroduction.

Introduction

Ecologists and foresters have documented the decline of quaking aspen (*Populus tremuloides)* in the western United States throughout the 1900's, noting that many of the current aspen stands in the western United States are dominated by older age classes in varying stages of senescence, with little understory regeneration (Bartos 2001). Many are also experiencing succession to conifers due to lack of fire. The symptoms of aspen decline have been heavily documented in the scientific literature (Packard 1942, Krebill 1972, Olmstead 1979, Bartos 2001) and have been attributed to fire suppression, climatic variability, and high densities of ungulate browsers (Kay and Bartos 2000, Kay 2001, Hessl 2002, Larsen and Ripple 2003, Gallant et al. 2003, Romme et al. 2005, Baker 1997). Scientists have suggested that the lack of aspen regeneration and recruitment is a consequence of the collective influence of these variables (Romme 1995), some of which are processes that have been altered by anthropogenic forces since Euro-American settlement (reviewed in NRC 2002). Frey (2004) proposed that long-term processes (e.g. climate, succession, senescence) predispose aspen to states of infirmity. Predisposed stands are further stressed by short-term or "inciting" factors (e.g. drought, browsing,

insect outbreaks), which may then be further exacerbated by disease, fungal pathogens, or wood boring insects ("contributing" factors) often leading to stem mortality. Aspen is a disturbance responsive species that is known for producing high densities of vigorously growing suckers following fire events (Bartos and Mueggler 1981, Bartos and Debyle 1989). However, it has been demonstrated that heavy browsing can undo the beneficial effects of fire by limiting the advancement of aspen suckers into the canopy (reviewed in Hessl 2002 and Frey et al. 2004). There is evidence, that browsing is the dominant force inhibiting aspen recruitment when ungulate densities are high (Romme et al. 1995, Kay and Bartos 2000, Kay 2001, Romme et al. 2005).

The theory that ungulate browsing is the dominant force in the suppression of aspen recruitment is supported by a number of studies in Yellowstone National Park (YNP) and the Greater Yellowstone Ecosystem (GYE) where historical paradigms of resource management have provided for a natural experiment. YNP has experienced dramatic shifts in resource management policies since its inception in 1872, including predator extirpation during the early 1900's, which alleviated top-down controls on elk (*Cervus elaphus*) populations. The elimination of predators was soon followed by significant increases in elk numbers that later prompted the implementation of population control measures by the National Park Service (NPS), where elk were culled into the late 1960's to reduce habitat degradation attributable to high elk densities (Houston 1982). Population control measures were terminated by 1970 and elk populations have since been allowed to increase dramatically under the "natural regulation" paradigm, whereby elk populations are supposed to be "naturally" limited by density-dependent factors

(NRC 2002). High elk densities during the 1900's are cited as the primary driver behind the deterioration of aspen stands in YNP (Houston 1982, NRC 2002). Many studies have demonstrated a correlation between periods of high elk densities and a lack of historic aspen recruitment in the GYE (St. John 1995, Romme et al. 1995, Ripple and Larsen 2000, Hessl and Graumlich 2002, Larsen and Ripple 2003, Kimble et al. 2011). Some suggest that there has not been any significant aspen recruitment on the Northern Range of YNP since the 1920's (Ripple and Larsen 2000). Similar observations have been reported for willow (*Salix* sp.) (Ripple and Beschta 2006, Beyer et al. 2007) and cottonwood (*Populus* spp.) (Ripple and Beschta 2004, Beschta 2005, Beschta and Ripple 2010) in YNP.

Despite the well-documented decline of aspen in the West during the 20th century, recent studies have reported increases in aspen growth on the Northern Range of YNP, attributing the growth to the reinstitution of an effective top predator (Ripple et al. 2001, Ripple and Beschta 2006, Ripple and Beschta 2007, Halofsky 2008). Since the reintroduction of wolves (*Canis lupus*) in 1995, elk densities have declined dramatically in areas of the GYE (Creel and Winnie 2005, Eberhardt et al. 2007, Garrott et al. 2009a) and there is some evidence that elk have adopted behavioral anti-predation strategies that have altered resource selection habits (Ripple et al. 2001, Larsen and Ripple 2003, Ripple and Beschta 2004, Fortin et al. 2005).

Although recent studies have provided evidence for increases in aspen productivity in YNP attributed to a trophic cascade following wolf reintroduction, few have effectively accounted for the potential influence of climate on plant growth. Of

those that have accounted for climate, some used coniferous species (e.g. *Pseudotsuga menziesii*) as a proxy for aspen climate-growth responses, rather than the species of interest (Hessl and Graumlich 2002), while others incorporated climate variables that are likely uninformative about aspen growth (Kauffman et al. 2010). For example, Kauffman et al. (2010) evaluated the relationship between basal area increment of aspen and Palmer Drought Severity Index (PDSI). PDSI was averaged across months for November through March for each year of the study as an index of winter precipitation. However, one of the notable shortcomings of the PDSI is that all precipitation is assumed to be input as rain and the model does not account for moisture locked up in the form of snow or ice (Alley 1984). PDSI is thus a poor index for winter precipitation and provides little information on aspen growth responses to climate. Other studies sought to establish correlations between episodes of aspen regeneration and recruitment with climate (Larsen and Ripple 2003), rather than assessing the climate-growth relationship directly through dendrochronological analyses.

The purpose of this study was to assess the climate-growth relationship for aspen in the west-central region of YNP, covering the period of wolf reintroduction, to determine if the increases in aspen growth observed in the GYE following wolf reintroduction can be attributed in part to recent climate trends.

The annual rings found in the xylem of trees growing in temperate climates provide a reliable record of historical radial growth patterns that has been shown to be highly correlated with interannual variation in climate variables (e.g. temperature,

precipitation) (Fritts 1976, Cook and Kariukstis 1990). The primary objectives of this study were to:

1. Determine what climate variables are most important to aspen productivity in this region (the climate-growth relationship),
2. Assess the general growth trend in aspen and look for any change in radial growth coincident with the timing of wolf reintroduction,
3. Relate trends in interannual tree-ring width variation to historic climate data, and
4. Establish the age structure for mature aspen growing in the study area.

Study Area

The study area for this research was selected to address aspen responses to observed changes in elk abundance and distribution following wolf reintroduction in West-Central YNP (Chapter 4, this volume) and is affiliated with a long term elk population ecology study spanning the period of wolf reintroduction (Garrott et al. 2009b). The study area and methods described here were specifically selected to facilitate analyses of aspen related to observed changes in the abundance and distribution of the resident elk herd.

The MHSA (Figure 3.1) spans ~36,190 ha encompassing portions of the Central Plateau and Madison Plateau in west-central YNP and the associated Firehole, Madison, and Gibbon river drainages (Garrott et al. 2003). The boundaries of the study area are defined by elk winter home ranges estimated by Gower et al. (2009). Elevation in the MHSA ranges from 2048-2560 m and the topography is comprised of relatively flat

undulating terrain dissected by steep canyons. Climate in central YNP is characterized by long cold winters and short cool summers with snowpack persisting typically 6-7 months of the year (8-9 mo/yr. on the Madison Plateau) (Newman and Watson 2009). The mean annual temperature for the period 1997-2007 was 3° C (Newman and Watson 2009). Mean annual snowpack depth was ~1 m for the same period, but could reach several meters at higher elevations. Mean annual precipitation varies greatly (Newman and Watson 2009).

The study area is composed of large tracts of forests with interspersed meadow complexes. The non-forested areas consist of wet meadows, dry meadows, talus slopes, and geothermal areas. Wet and dry meadow complexes comprise ~20% of the landscape and occur on the fertile soils of alluvial plains deposited between adjacent lava flows (Newman and Watson 2009). Forested land covers ~80% of the study area, of which approximately 53% was burned in the fires of 1988 (Newman and Watson 2009), which has created a mosaic of burned and unburned forest across the landscape (Romme and Despain 1989). Approximately 95% of forested land in the MHSA is dominated by lodgepole pine (*Pinus contorta*). These large expanses of lodgepole pine occur on poorly developed rhyolitic soils from lava flows and are differentiated by varying stages of stand succession (Newman and Watson 2009). Other tree species that occur, but are less common in the study area are: whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*) (Newman and Watson 2009). Aspen are rare in the study area and are

typically found in talus and at low elevations in the ecotone between conifer forests and meadow complexes (Newman and Watson 2009, Chapter 2, this volume).

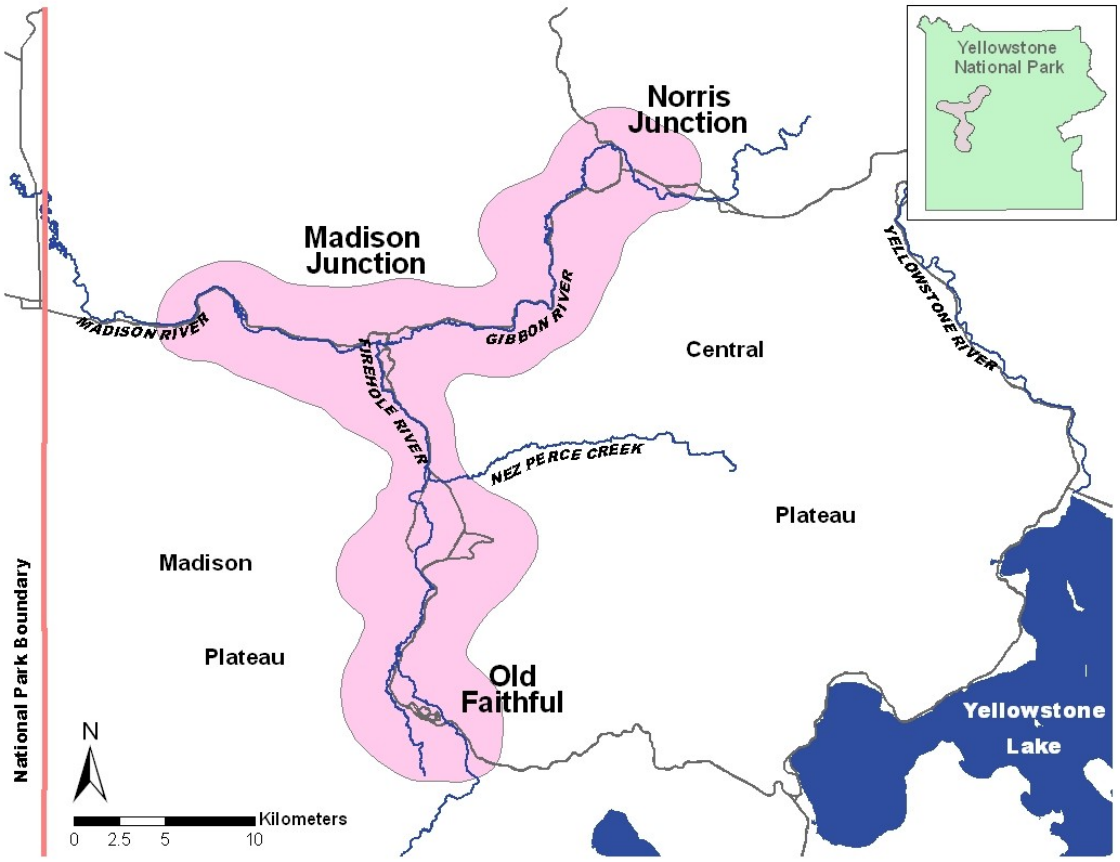

Figure 3.1: Map of the MHSA, west-central Yellowstone National Park, Wyoming, USA, including the Gibbon River, the Firehole River, and the Madison River drainages. The study area boundaries are defined by estimated winter home ranges for the resident elk herd (Gower et al. 2009).

Methods

During the summer of 2009 linear transects were surveyed in the MHSA to locate aspen stands throughout the study area. Survey routes were established using a

geographic information system (GIS) and were surveyed by two field researchers spaced 100 m apart, off trail, through a variety of habitat types. The methods for locating aspen are described in detail in Chapter 2, this volume.

Dendrochronological analysis was performed to assess long-term growth trends and examine the influence of climate on aspen growth in the MHSA. Increment cores were collected from up to three mature aspen trees per stand (depending on availability within a given stand) using a 4 mm diameter increment borer. The largest trees at a site were cored in an effort to obtain the longest chronology possible for assessing the climate-growth relationship. Aspen are notably susceptible to disease and fungal infestation that lead to heart decay (Hinds 1985), often making it difficult to extract increment cores from them. Coring height varied (mean= 60.5 cm, range= 10 to 103 cm) dependent upon the height at which an increment core could be extracted from an individual tree where the condition and quality of the sample would provide a reliable and discernable tree-ring series. In most cases, due to heart decay, multiple attempts were necessary to extract an increment core of a quality that would prove useful in dendrochronological analyses. Injury to the bole of aspen trees (e.g. coring) can expose them to increased vulnerability to disease and fungal infestation (Grissino-Mayer 2003), and so to minimize the impacts of coring on individual trees, no more than three attempts were made per tree to extract an increment core. Thus, given that multiple attempts were necessary for the majority of trees, I was unable to extract multiple cores per tree, which is a standard practice in the field of dendrochronology to increase dating accuracy.

Increment cores were dried and prepared for analysis in accordance with standard dendrochronology techniques (Stokes and Smiley1968). Each tree-ring series was examined under a dissecting scope and ring-widths were measured to 0.001 mm accuracy using a Velmex measuring system (TA 4030H1-S6 Unislide, Broomfield, New York). Series were visually crossdated using standard skeleton plotting techniques (Douglass 1941). Visual dating of tree-ring series was cross-validated using the quality control program COFECHA (Holmes 1983), a computer program that uses time-series correlations of measured ring-widths compared against a master chronology to assess and improve dating accuracy of individual tree-ring series. Series were omitted if they could not be reliably crossdated. In the case that some small portion of a series near the pith was unreadable (due to heart decay or breakage), that series was truncated to include only the outer most portion of the series that could be reliably dated. Given that the pith date of the series was not of primary interest in this study, these samples were truncated rather than discarded in an effort to maintain sample size for an already small collection of increment cores.

Crossdated series were detrended to remove effects of age-related growth trend and endogenous stand disturbance, so as to emphasize the climate–growth signal. Program ARSTAN (Cook 1985, Cook and Kariukstis 1990) was used to detrend individual tree ring series and build a standardized master chronology. Negative exponential curves and linear regressions were fit to individual series and interactive detrending methods were used to ensure the best fit for age-related growth trend.

The period following the 1988 fires in YNP was of particular interest for this study, with regards to the climate-growth response and plant productivity, in determining the differences in plant growth between burned (BF) and unburned (UF) stands. Separate composite chronologies were built from cores taken from BF (n=12) and UF (n=8) stands following the same procedures previously described for the period 1987-2008, starting the year prior to the 1988 fires. The two chronologies were then compared to evaluate the differences in post-fire growth response between BF and UF stands. A paired t-test was used to test the hypothesis that the difference in tree-ring widths between UF and BF chronologies was not significantly different from zero. Chronologies were paired on year. Pearson's correlation coefficients were calculated to assess the correlation of interannual ring width variation between the chronologies.

The influence of climate on aspen growth was assessed by comparing interannual variation in tree-ring widths to monthly climate data for the period January 1939 through August 2008. The climate variables considered in this analysis were mean monthly temperature (Tmean), monthly precipitation (Precip), and monthly Palmer Drought Severity Index (PDSI). PDSI is a modeled measure of soil moisture influenced by temperature and precipitation. Monthly PRISM (Precipitation-elevation Regressions on Independent Slopes Model - http://www.prism.oregonstate.edu/) data were used for temperature and precipitation variables for a polygon encompassing the MHSA, and PDSI data for Wyoming Climate Division 01 were obtained from the Northern Oceanic and Atmospheric Administration National Climatic Data Center. Pearson's correlation coefficients (r) were calculated for each month of a 20-month climate window – starting

January of the prior year (*t*-1) and extending to August of the current year (*t*) – with interannual ring width variation. Climate data from the prior growing season were used to account for the known influence of the prior growing season on the current season's growth (Fritts 1976). Correlations were also calculated for seasonal climate trends. Monthly climate data were pooled to obtain mean values for Winter (December – February), Spring (March – May), Summer (June – August), and Autumn (September – November). Correlations were not calculated for PDSI during winter months, as PDSI is limited in its ability to account for precipitation accumulated as snow (Alley 1984). The statistical significance of the relationship between climate variables and the chronosequence was determined using critical values of the Pearson's correlation coefficients (r) relative to sample size (n= 69 years) (critical values: $r = \pm 0.237$, $\alpha = 0.05$ and $r = \pm 0.308$, $\alpha = 0.01$). All statistical analyses were performed using program R (R Development Core Team, 2011).

Results

Aspen were found to be patchily distributed throughout the MHSA in very small stands. The most common form of aspen in the MHSA appeared to match what Larsen and Ripple (2003) had previously described as "scree stands," typically growing on steep southerly slopes in scree fields or talus patches near the plateau's edge. They were found growing at elevations between 2076 and 2275 m. Most aspen in the MHSA appeared as post-burn regeneration with very few mature trees and occurred in or adjacent to conifer forests that had burned in the 1988 fires in YNP. The observed size class distribution

among clonal stands predating the 1988 fires in the MHSA is indicative of the suppressed recruitment exhibited by unsustainable aspen stands (St. John 1995, Kimble et al. 2011). All stands were located on the plateaus or on the slopes descending from them to the canyon bottoms. They were found to be growing on the nutrient poor glacial till derived from rhyolitic ash and lava flows that cover much of the study area (see Chapter 2, this volume, for more detailed description of aspen distribution in the MHSA).

All increment cores were collected in the Gibbon and Madison drainages, as the Firehole drainage was largely comprised of seedling-established stands with very few mature aspen trees pre-dating the 1988 fires (Chapter 2, this volume). A total of 25 increment cores was collected during the summer of 2009. Seven of the 25 cores were excluded from the analysis due to poor sample condition, shortness of the series, or low correlation with the master chronology ($r < 0.40$). A sample was deemed too short if it did not pre-date the 1988 fires. A 68 year standardized chronosequence was developed for the period 1940 to 2008 (Figure 3.2) and is comprised of 18 increment cores from a total of 18 individual trees from nine different aspen stands. While the oldest tree sampled dates back to 1869, the chronosequence was truncated at year 1940 due to insufficient sample depth through the oldest portion of the chronology. The series was truncated at the point where bootstrapped confidence intervals for the standardized chronology became significantly inflated due to low sample size (Figure 3.2). (Bootstrapped confidence intervals and corresponding time-series graphs are standard output from program ARSTAN – Cook 1985). The average mean sensitivity (0.328) reveals that the individual tree ring series were fairly insensitive to environmental

variability, a characteristic commonly associated with difficulty in accurate crossdating. However, all series included in the final chronology were successfully crossdated, yielding a series intercorrelation of 0.54. Output from program ARSTAN reported a running r-bar (an index of signal strength) of 0.293 and an expressed population signal (EPS, a measure of common variability among individual tree-ring series) of 0.880 for the standardized chronology (Table 3.1). These chronology statistics may be considered to have weak to moderate signal strength in the context of more rigorous dendrochronological analyses, where pre-selected sites among a known distribution of the species of interest may be sampled to achieve a predefined sample size that would provide satisfactory statistical power. It was not possible to perform a power analysis for this study, given that the current distribution of mature aspen trees in this region was poorly defined and largely unknown. Aspen occurred only in small pockets in the study area prior to the 1988 fires, and were not considered a dominant cover type where found in their patchy distribution. (Aspen make up only 0.2% of the dominant cover type in the MHSA according to the known pre-fire distribution; see Chapter 2, this volume). Irrespective of the small sample size, given that mature aspen are so few in the MHSA, it is likely that a fair portion of the available population of mature aspen in the MHSA was sampled and the resulting chronosequence provides a relatively good common signal of the climate-growth response for aspen in the MHSA. The “residual chronology” from ARSTAN was used for all climate analyses, where autocorrelation from the previous year’s growth is modeled using an autoregressive process and removed, resulting in a chronology with an enhanced common signal without persistence (Cook 1985).

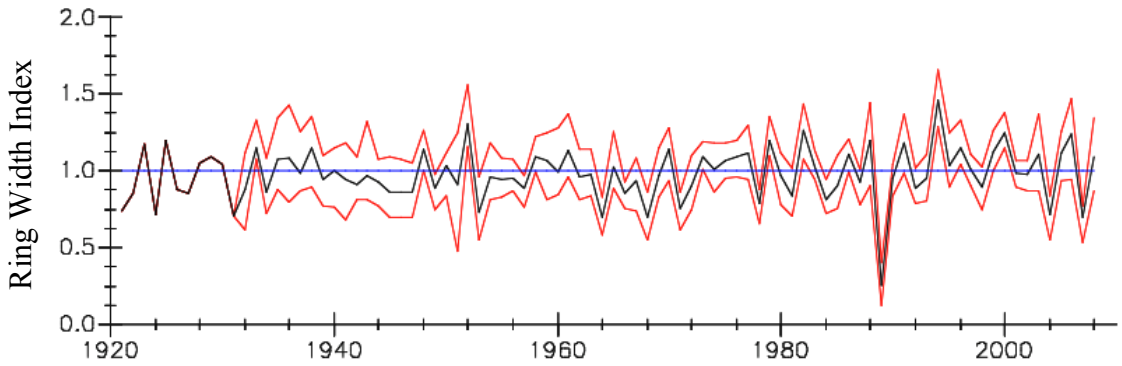

Figure 3.2: Residual chronology of tree-ring widths with bootstrapped confidence intervals for aspen in the MHSA. An index value of 1.0 represents mean ring width for the entire series and values above or below the mean represent periods of enhanced (above) or diminished (below) radial growth. Due to low sample size, the bootstrapped confidence intervals are inflated prior to 1940 and could not be computed by ARSTAN prior to 1932.

There was no evidence of a difference in the post-fire growth response between BF and UF stands; mean tree-ring width was not significantly different ($t = -1.05$, $p = 0.313$, Student's paired t-test) and the two chronologies were significantly correlated ($r = 0.70$, $p < 0.001$). Dramatically diminished radial growth was observed for both burned and unburned stands the year following the 1988 fires (Figure 3.3), suggesting that trees were responding primarily to climatic effects rather than ecological effects (e.g. fire) in a severe drought year. The lack of significant disparity between BF and UF post-fire growth response suggests that climate and fire are indistinguishable in ring widths and a composite chronology incorporating both BF and UF series is justified.

Table 3.1: Descriptive statistics for mature aspen sampled in the MHSA. Stand numbers correspond to the 31 stands identified in Chapter 2, this volume. Mean sensitivity (Means Sens.) and first order autocorrelation (ac(1)) from residual chronology statistics.

ID	Stand No.	Drainage	Elev. (m)	Slope (deg)	Aspect	Burn Class	Time Interval		No. Years	Pith	Coring Height (cm)	DBH	Corr. with Master	Mean Ring Width	Std dev	Mean Sens.	ac(1)
CGM02A	27	MADISON	2141	10	NW	BF	1931	2009	78	N	93	40.5	0.46	1.62	1.06	0.39	0.01
CGM03A	27	MADISON	2141	10	NW	BF	1929	2009	80	N	81	48.5	0.55	1.63	0.99	0.41	-0.08
EPM01A	08	GIBBON	2358	37	SW	UF	1926	2009	83	Y	----	----	0.44	0.41	0.15	0.43	-0.07
GFA01A	14	GIBBON	2147	38	NW	UF	1962	2009	47	Y	61	20.5	0.66	1.71	0.71	0.40	-0.03
GFA03A	14	GIBBON	2147	38	NW	UF	1964	2009	45	Y	65	12.5	0.47	1.22	0.39	0.30	-0.01
NTC01A	16	GIBBON	2299	37	W	BF	1935	2009	74	N	35	20.5	0.73	0.99	0.56	0.49	-0.15
PMD01A	25	MADISON	2131	40	SE	BF	1961	2009	48	Y	34	13	0.65	0.96	0.50	0.30	-0.06
PMD02A	25	MADISON	2131	40	SE	BF	1920	2009	89	N	80	21	0.57	1.05	0.45	0.34	0.04
PMT01A	07	GIBBON	2389	36	S	UF	1957	2009	52	Y	50	15	0.55	1.16	0.79	0.51	0.02
PMT02A	07	GIBBON	2389	36	S	UF	1953	2009	56	Y	36	17.5	0.63	1.09	0.81	0.49	-0.02
PMT03A	07	GIBBON	2389	36	S	UF	1955	2009	54	Y	42	15.5	0.61	1.24	0.68	0.49	0.10
SSP01A	28	MADISON	2088	12	N	BF	1939	2009	70	N	100	27.5	0.45	1.33	0.41	0.28	-0.17
SSP02A	28	MADISON	2088	12	N	BF	1922	2009	87	N	103	19	0.52	0.84	0.47	0.40	0.01
SSP03A	28	MADISON	2088	12	N	BF	1929	2009	80	N	78	23	0.53	1.25	0.45	0.24	0.00
STC02A	15	GIBBON	2260	39	NW	UF	1950	2009	59	N	20	24.5	0.70	1.05	0.60	0.46	0.00
STC03A	15	GIBBON	2260	39	NW	UF	1931	2009	78	N	63	19	0.48	1.15	0.46	0.32	0.04
TAC01A	03	GIBBON	2274	38	W	BF	1956	2009	53	N	----	17.5	0.42	1.25	0.71	0.41	0.09
TAC02A	03	GIBBON	2274	38	W	BF	1869	2009	140	Y	----	28.5	0.45	0.67	0.31	0.38	-0.08

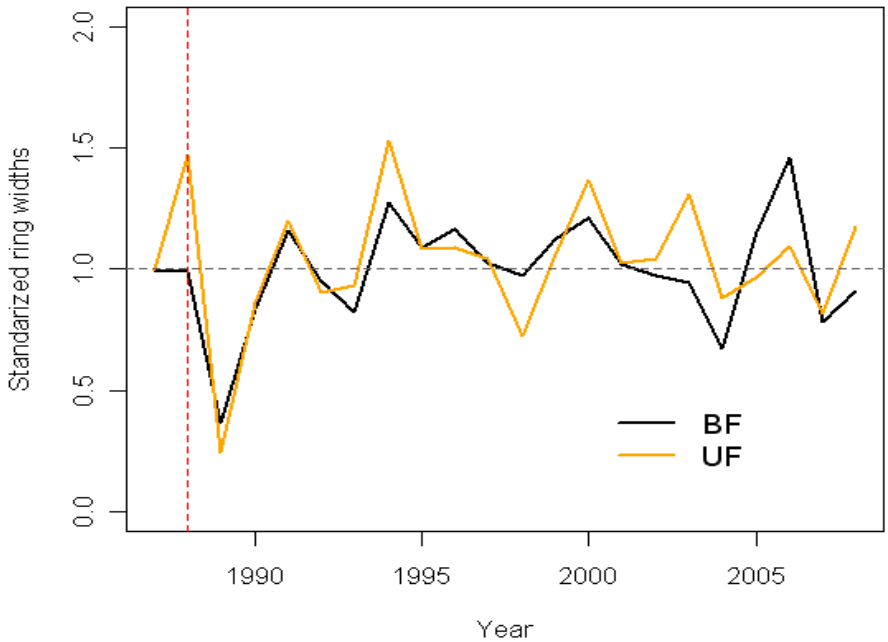

Figure 3.3: Residual chronologies for aspen occurring in burned forests (BF) and unburned forests (UF) showing similar growth response to ecological (fire) and climatic drivers. The dashed vertical red line demarcates the 1988 fire event in YNP.

Due to the high incidence of heart rot among trees sampled, the pith date was undeterminable and the year of origination could not be established for a number of trees. Tree age was successfully determined for 10 of the 25 trees. There appears to have been an episode of aspen recruitment in the MHSA from 1950-1960 (Figure 3.4). It is recognized, however, that a sample size of n= 6 is relatively small to declare this as an episodic recruitment event. It is also recognized that the trees from which the pith was successfully extracted were likely of a younger cohort not currently sustaining heart rot. Many of the trees for which the true age could not be determined were successfully dated back to the early 1900's from the truncated increment cores and likely originated around the turn of the 20th century, considering the average life span of aspen trees (~120 years).

Figure 3.4: Decade of origination for mature aspen trees in the MHSA (n=10).

Results from the correlation analysis for the climate-growth response of aspen in the MHSA reveal that radial tree growth was positively correlated with Tmean during the current growing season (*t*) and negatively correlated with Tmean of the prior growing season (*t*-1) for the period 1940-2008 (Figure 3.5). Ring width variation was significantly positively correlated with mean monthly temperature for June (*t*) (r= 0.302, p= 0.012) and August (*t*) (r= 0.257, p = 0.012) of the current growing season, and in the negative direction for prior June (*t*-1) (r= -0.293, p = 0.015). Mean July (*t*-1) temperature of the prior growing season was nearly significantly correlated (r= -0.227, p = 0.061).

Summer Tmean (*t*) was the only seasonal temperature variable significantly correlated with ring width variation (r= 0.256, p = 0.034), supporting the trend of a positive relationship between temperature and ring widths during the current growing

season (Figure 3.6). Oddly, summer mean temperature during the prior growing season (*t*-1) was not significantly correlated with ring widths, even though June (*t*-1) Tmean was significant. Although not significant, this was the only season to have a negative relationship with radial growth, which provides mild support for the negative correlation between monthly mean temperatures and ring width variation observed for the prior growing season.

Precipitation was not significantly correlated with ring width variation for any month or season, although July (*t*-1) of the prior year was nearly significant ($r = 0.230$, $p = 0.057$, Figure 3.5). Although correlations between precipitation and ring width variation were not significant, a general pattern can be seen for monthly means, where radial growth is negatively related to precipitation during the current growth period and positively related to precipitation of the previous growing season. This suggests an inverse relationship to that observed between temperature and radial growth.

Interestingly, Spring and Summer PDSI of the current growing season were significantly negatively correlated with ring width variation ($r = -0.300$, $p = 0.012$, and $r = -0.49$, $p < 0.001$, respectively), suggesting that aspen were putting on more radial growth during drought conditions (Figure 3.6). This is counterintuitive given that negative values of PDSI indicate drought conditions, typically associated with poor plant productivity. PDSI was not significantly correlated with ring widths for any month, individually.

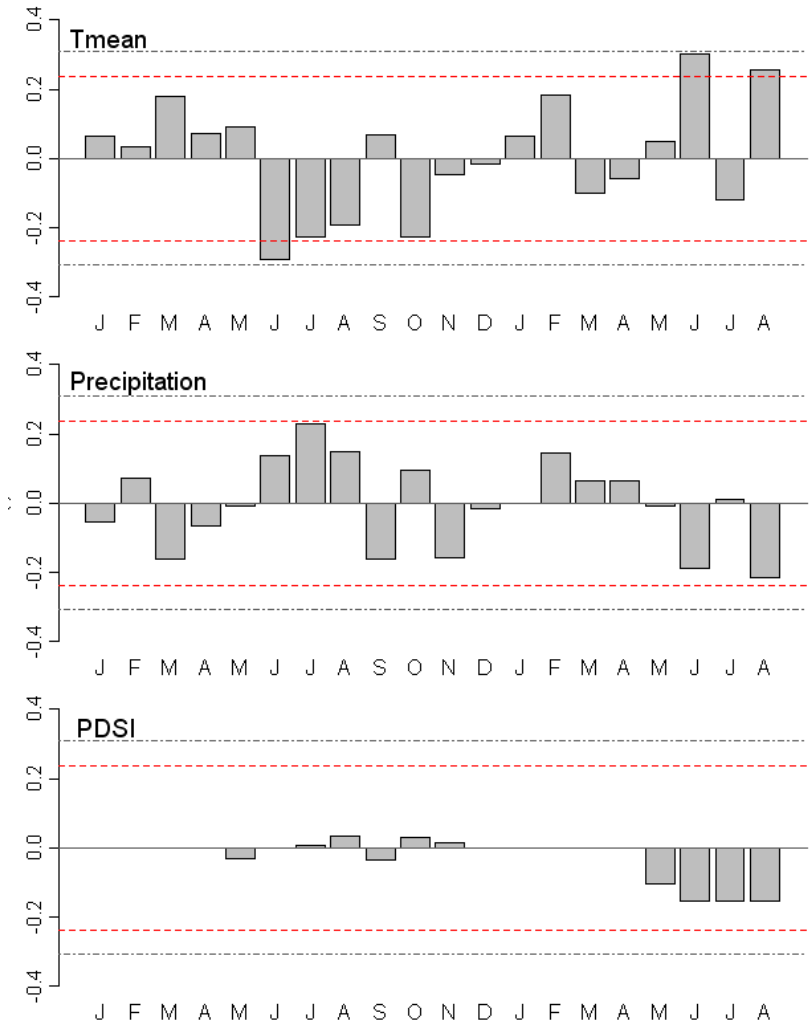

Figure 3.5: Pearson's correlation coefficients between the residual chronology for aspen in the MHSA and monthly climate variables (mean temperature, precipitation, and PDSI) for the period 1940 – 2008. Months start with January of the prior growing season (*t*-1) and end August of the current growing season (*t*). Alpha levels demarcated by dashed horizontal lines; (r= ±0.237, α= 0.05), red line; (r= ±0.308, α= 0.01), gray line. (r) not calculated for PDSI for winter months.

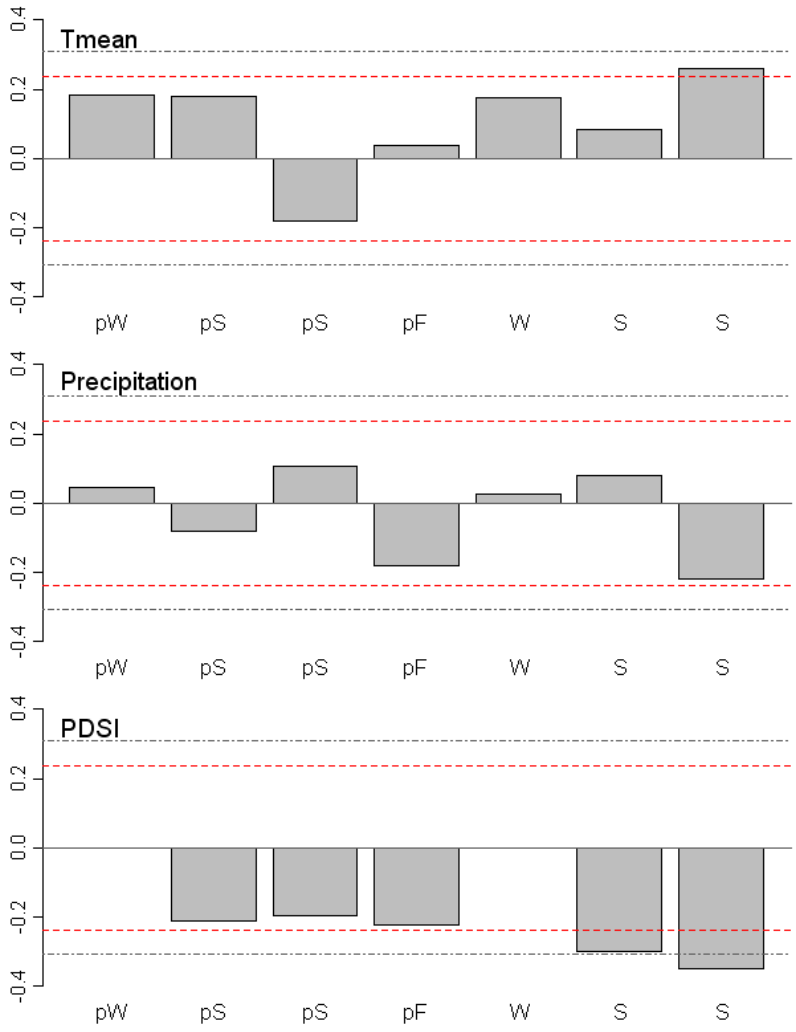

Figure 3.6: Pearson's correlation coefficients between the residual chronology for aspen in the MHSA and seasonal climate variables (mean temperature, precipitation, and PDSI) for the period 1940 – 2008. Seasons are as follows: Winter (December, January, February), Spring (March, April, May), Summer (June, July, August), and Fall (September, October, November). Alpha levels are demarcated by dashed horizontal lines; (r= ±0.237, α= 0.05), red line; (r= ±0.308, α= 0.01), gray line. A lowercase "*p*" indicates prior growing season (*t*-1). (r) not calculated for PDSI for winter months.

Radial tree growth appears to have increased modestly over the period 1940-2008, (although not substantially), indicating that conditions may have improved in the MHSA with respect to aspen productivity (Figure 3.7). There was a dramatic anomalous decline in ring widths the growing season following the 1988 fires, followed by a period of above average radial growth. This post disturbance productivity was accompanied by significant sucker production, beginning in 1989 (Chapter 2, this volume). Ring widths peaked during the 1994 growing season. This increase in radial growth was preceded by a significantly cool and moist summer during the previous growing season (Figure 3.8), indicating that radial growth is largely determined by stored carbohydrates from the prior growing season, (low June temperatures and high July precipitation during the prior growing season were related to increased radial growth). Above average growth was also observed for the 2000 growing season, the timing of which is coincident with the second pulse of new stem initiation in the MHSA during the period following the 1988 fires (Chapter 2, this volume). The growth trend appears to have declined over the past decade (Figure 3.7).

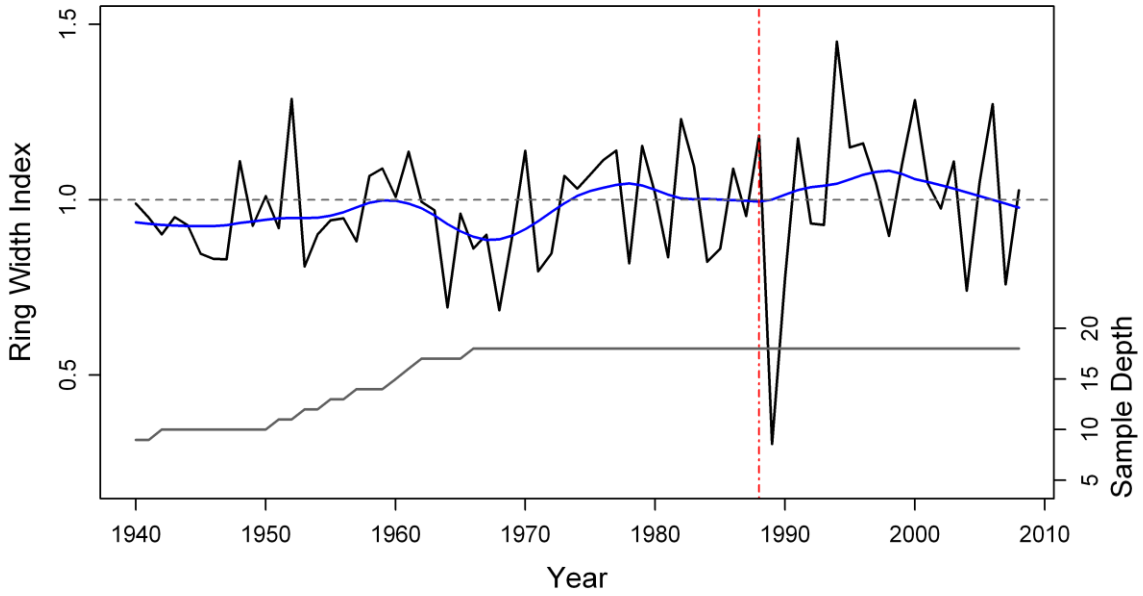

Figure 3.7: Residual chronology for aspen in the MHSA. The mean standardized ring width is 1.0 (dashed horizontal gray line). Values above or below the mean represent periods of enhanced (above) or diminished (below) radial growth. The solid blue line is a Lowess smoother with a 15 yr. window illustrating the general growth trend. The dashed vertical red line demarcates the 1988 fire event in YNP. Sample depth is displayed (solid gray line) to indicate change in sample depth throughout the chronology.

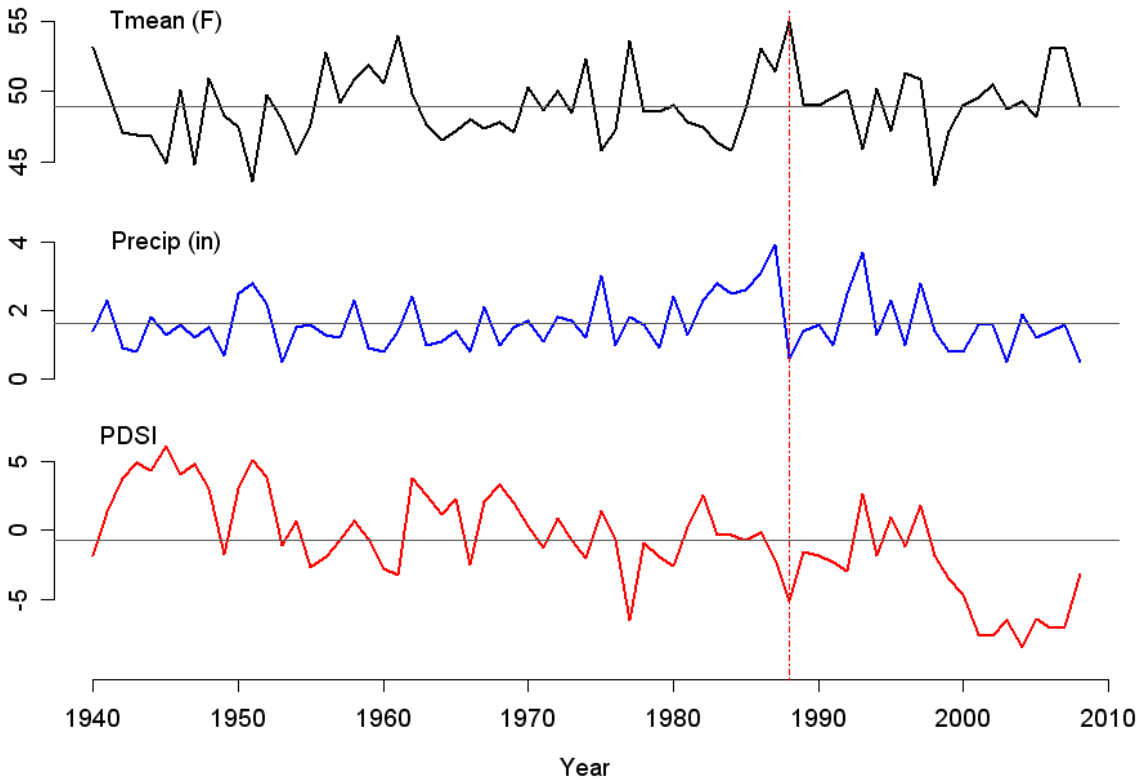

Figure 3.8: Time series for June Tmean, July Precip, and Summer PDSI. The red vertical dashed line demarcates the 1988 fire event in YNP and the grey horizontal lines are means for the time period.

Discussion

Radial growth in aspen found in the MHSA was related to temperature and precipitation during the prior growing season. This relationship is commonly observed in dendrochronology, as trees utilize stored photosynthate from the prior growing season for shoot elongation and radial growth during the early portions of the current growing season when soil temperatures are low and trees have not yet reached their potential for carbohydrate production (Fritts 1976, Landhäusser and Lieffers 2003, Steele et al. 1997). Cool, moist summers translate to increased soil moisture and reduced rates of

evapotranspiration that result in a surplus of photosynthate reserves for early season growth the following year. Similar relationships have been observed for aspen on the Northern Range of YNP (Jules et al. *unpublished*) and for other areas of North America (Hogg et al. 2005, Leonelli et al. 2008). The positive correlation with June (*t*) Tmean of the current year may indicate that a combination of ample photosynthate reserves from the prior year's growth and warmer average June temperatures of the current growing season facilitate enhanced radial growth. Warmer June temperatures may influence the timing and rate of early season photosynthetic activity. It is apparent from Figures 3.7 and 3.8 that major peaks in radial growth are concurrent with above average temperatures and preceded by below average temperatures.

It is not surprising that PDSI was not significantly correlated with interannual ring width variation at the scale of a single month but was at the time scale of "seasons," given that the a drought period defined by Palmer (1965) spanned a period of several months or years. That a negative correlation was observed, where ring width increased with decreasing PDSI (tending towards more severe drought) is counterintuitive. This relationship can be seen in the modern period of Figures 3.8 and 3.9, where the recent increase in radial growth is accompanied by a significant decline in PDSI to the lowest values for the length of the series. This suggests a weak relationship between PDSI and ring width variation in aspen for the study area. This may be due to that fact that PDSI data were from Wyoming Climate Division 01. While the study area lies within the boundaries of this climate division, it is also near the border of Wyoming Climate

Division 02 and the continental divide. PDSI values for the climate division may not accurately represent local conditions in the study area.

Correlations between climate variables and ring width variation were generally weak. This is likely due, in part, to small sample size. The signal strength for growth responses to climate is vulnerable to sample size, where variance increases significantly at low sample sizes (Shiyatov et al. 1990). The weak correlations may additionally be attributed to site index. It has been found that aspen sensitivity to climate varies across a gradient of site productivity (Leonelli et al. 2009, Jules et al. *unpublished*). Leonelli et al. (2009) found that aspen ring widths on low-productivity sites had weak correlations with climate variables and showed higher interannual variability. They suggested that aspen's weak response to climate at marginal sites may be due to low nutrient availability limiting their ability to take advantage of favorable climatic conditions. This theory applies to aspen growing in the MHSA, as all mature aspen sampled in this study were growing on nutrient poor glacial till derived from rhyolitic lava flows (see Chapter 2, this volume). Though the correlations presented here are weak, the relationships they depict between radial tree growth and climate are supported by the findings of other studies with larger sample sizes that observed similar relationships (Leonelli et al. 2009, Salzer et al. 2009, Jules *unpublished*) and fall in line with commonly observed trends in dendrochronology (Fritts 1976, Landhäusser and Lieffers 2003, Steele et al. 1997).

A modest increase in radial growth was observed from 1940-2008 with the period of greatest productivity occurring over the decade following the 1988 fires. While a post-fire growth recovery period has been documented for a number of tree species, marked

by an ephemeral increase in ring widths (e.g. Py et al. 2006), it is not likely that the observed increase in radial growth for aspen in the MHSA following the 1988 fires is a result of this phenomenon. Py et al. (2006) reported a lag effect of three years for the post-fire growth recovery for singleleaf pine (*Pinus monophylla*) in central Nevada, USA. The peak in radial growth for aspen in the MHSA in this study occurred in 1994, six years after the 1988 fires, twice the lag time for the post-fire growth response observed by Py et al. (2006). Additionally, the 1994 growing season was preceded by a cool, moist summer (Figure 3.8), indicating that radial growth increased in response to favorable climatic conditions. Furthermore, eight of the 18 trees included in the final chronology were from unburned stands. Given that interannual ring width variation for aspen growing in UF and BF stands was not significantly different (p-value= 0.313, Figure 3.3), it is evident that aspen were responding to climatic influences, rather than an exogenous stand disturbance. Jules et al. (*unpublished*) also reported above average ring widths for mature aspen in unburned stands on the Northern Range of YNP during the same period. They revealed strong correlations between ring widths and climate variables related to soil moisture condition, providing further affirmation that the increased ring widths occurring six years after the 1988 fires were in response to climate rather than fire. However, due to the weak correlations between climate and aspen productivity and the temporal association between the 1988 fires and the subsequent growth response, the primary driver of this ephemeral increase in aspen productivity cannot be confidently distinguished.

The increasing trend in ring widths for aspen in the MHSA following the 1988 fires offers mild evidence that any observed increases in aspen productivity in this region coincident with the timing of wolf reintroduction (winter 1995-1996) may be partially explained by an ephemeral shift toward favorable growing conditions, albeit a modest shift. Climatic conditions during this period may have facilitated a level of productivity that allowed aspen to be robust to the negative effects of ungulate herbivory and advance through the browse zone, increasing the potential for recruitment. Given the described synergy among factors contributing to aspen decline (Romme et al. 1995, Frey et al. 2004), it is likely that any observed increases in woody plant growth during this period are related to both favorable climatic conditions and changes in elk abundance and distribution. In addition to partially explaining observed height increases in aspen, favorable climatic conditions have also likely facilitated ongoing regeneration for more than a decade after the 1988 fires (see Chapter 2 this volume, Romme et al. 1995, Halofsky et al. 2008).

Although the pith date could not be established for the majority of stems in this study, further eroding an already small sample size, the age structure of mature aspen presented here (Figure 3.4) provides evidence that there has been successful aspen recruitment in YNP since the 1920's (Ripple and Larsen 2000). Successfully dated trees provide evidence for an episode of aspen recruitment in the MHSA during the 1950's and 1960's that corresponds with a period of above average radial growth (Figure 3.7). Most of the mature aspen in the MHSA occur in dense coarse talus that likely precluded elk from browsing these individuals, which agrees with the findings of other studies (Ripple

and Larsen 2000, Larsen and Ripple 2003). Larsen and Ripple (2003) documented an episode of aspen recruitment during the 1960's and 1970's in YNP for stands occurring in scree fields, but concluded that the rocky substrate precluded elk from browsing suckers in these stands, allowing aspen to successfully grow through the browse zone and reach canopy height. The results from the present study corroborate the conclusions from previous studies that have demonstrated continuous aspen recruitment at the landscape level in the Rocky Mountain West that seems to vary spatially depending on ecological context (Suzuki et al. 1999, Hessl and Graumlich 2002, Kashian et al. 2007).

It is interesting to note the period of low productivity (narrow ring widths) occurring during the late 1960's to early 1970's (Figure 3.7). Some studies have noted that no successful aspen recruitment occurred in stands accessible to ungulates on the NWR during the this same period (Ripple and Larsen 2000, Larsen and Ripple 2003) when elk numbers declined substantially due to population control measures implemented by the National Park Service (Eberhardt et al. 2007). It was suggested that, although elk numbers had declined dramatically, the lack of predation risk in the absence of wolves allowed elk to continue to utilize aspen across the region (Ripple and Larsen 2000, Larsen and Ripple 2003). It was also suggested that climate was generally favorable during this time and could not explain the lack of recruitment (Romme et al. 1995, Ripple and Larsen 2000, Larsen and Ripple 2003). However, growth trends of mature aspen in the MHSA indicate that climate may not have been favorable during this period.

Conclusion

Results from this study indicate that aspen productivity increased modestly over the past 68 years and was greatest during the decade following the 1988. This increase in productivity may have provided enough energy reserves to allow for notable increases in plant growth in regenerative aspen stems, despite ungulate herbivory. This trend persisted through the period of wolf reintroduction and was possibly amplified by declining elk numbers (Eberhardt et al. 2007, Garrott et al. 2009a). It appears, however, that the growth trend has been declining since around 2000. Growth trends may continue to decline as climate trends toward warmer and drier conditions, as indicated in the climate literature. Salzer et al. (2009) reported an unprecedented increase in ring widths in bristlecone pine (*Pinus longaeva*) at tree-line in the West that is strongly associated with a warming trend in a heat limited environment. This increase occurred over the second half of the 20th century and was greater than for any other period in the 3,700 year chronology developed in this study. There is also evidence for a major decline in snowpack in the Rocky Mountain west over the past 30 years that is strongly related to increasing temperatures (McCabe and Wolock 2009, Pederson et al. 2011). Balling et al. (1992a, 1992b) reported a trend toward warmer drier climate in YNP for the period 1895-1990. Warming trends have also been linked to the timing of spring onset. Aulte et al. (2011) found that the onset of spring in Western North America has occurred 1.5 days earlier, on average, each decade since the middle of the 20th century. A warming climate may initially increase plant productivity at high elevation sites by increasing the length of

the growing season, but long term trends toward increased aridity will likely result in major shifts in vegetation communities on the landscape. If the observed warming trend continues, aspen will likely suffer increased moisture stress and the potential for successful recruitment will be further diminished.

This study established a climate–growth relationship for aspen in the west-central portion of YNP from empirical data that can be used to directly assess the influence of climate on contemporary aspen growth, as it relates to current ecological issues. The results from this study contribute to a growing body of literature investigating the causes of the observed increases in aspen growth in YNP and the surrounding areas by providing an account of climatic influences on aspen growth. This study provides mild evidence that recent increases in aspen growth in YNP are likely the result of a synergy among factors influencing plant growth, including climatic variability. Continued investigation of the potential factors (biotc and abiotic) contibuting to aspen growth are needed to adequately account for the relative influence of each in assessing the relationship between wolves, elk , and aspen.

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CHAPTER 4

TROPHIC CASCADES AMONG WOLVES, ELK, AND ASPEN IN THE MADISON HEADWATERS STUDY AREA

Abstract

Trophic cascades are a widely studied phenomenon in community ecology, yet our knowledge of these interactions is limited. Few studies have been able to adequately capture trophic cascades operating in complex large-scale terrestrial ecosystems due to the lack of ability to use experimental manipulation. The reintroduction of wolves *(Canis lupus)* to Yellowstone National Park (YNP) in 1995-1996 created a unique "natural experiment" to study trophic interactions in a terrestrial system among wolves, elk, and aspen. This study took advantage of data from a long-term elk demography study that was established prior to wolf reintroduction and resulted in a detailed account of how recolonizing wolves affected elk in a system where they were absent for more than 70 years prior. Significant changes in the abundance and distribution of the Madison headwaters elk herd were observed following wolf establishment. The spatial arrangement of these changes made it possible to directly test for the occurrence of a density-mediated trophic cascade. The objectives of this study were to answer the following questions: 1) was there a marked decrease in browsing pressure on aspen where elk densities declined, and 2) was there a corresponding plant-growth response indicating that aspen were released from browsing pressure and are now growing

vertically through the browse zone? Historical browsing conditions and aspen height were observed for aspen stands in the Madison headwaters study area to assess the occurrence of a density-mediated trophic cascade following wolf reintroduction. Browse conditions and aspen morphology in stands where elk densities declined dramatically following wolf reintroduction were compared to stands that experienced persistent heavy browsing throughout this period. A major decline in browsing pressure along with a modest increase in aspen height and leader longevity was detected, supporting the hypothesis of a density-mediated trophic cascade. However, the magnitude of the growth response was weak, suggesting that browsing was not the dominant limiting factor to aspen growth in the study area and that aspen may be more strongly limited by bottom-up regulation.

Introduction

Predators indirectly play a significant role in shaping the structure and function of ecosystems through the top-down forces exerted on a food web via predator-prey interactions in what is known as a trophic cascade (Lima 1998). Trophic cascades are a well-studied ecological phenomenon (Lima 1998, Schmitz et al. 2000, Werner and Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005, Peckarsky et al. 2008), particularly in aquatic systems (Shurin et al. 2002), and are among the most powerful of ecological interactions (Lima 1998). The classical view of trophic cascades is of predators reducing the density of an herbivore population (density-mediated trophic cascade, or DMTC), thereby releasing the associated plant community from growth-limiting herbivory

pressure (Beckerman et al. 1997, Schmitz et al. 1997). Historically, trophic cascade studies have primarily focused on the DMTC's (Schmitz et al. 2000, Preisser et al. 2005). However, the mere presence of a predator can induce behavioral adaptive anti-predatory defense strategies in prey species that can alter patterns of herbivore resource utilization and elicit changes in vegetation community dynamics, resulting in a behaviorally-mediated trophic cascade (BMTC – Beckerman et al. 1997, Schmitz et al. 1997). A number of experimental studies have demonstrated the ecological importance of the non-consumptive effects of predation (reviewed in Lima 1998, Peckarsky et al. 2008). Preisser et al. (2005) have shown through their meta-analysis of published trophic cascade studies that behavioral effects equal or exceed the strength of density effects in their impact on ecosystems and are more powerful and rapid. However, there is greater evidence of this in aquatic systems and for systems operating at small spatial scales (Lima 1998). Although study of the relative importance of DMTC's and BMTC's in structuring ecosystems is becoming an increasingly important topic in community ecology and ecosystem management (Berger et al. 2001, Soulé et al. 2003), few studies have been able to unveil the underlying mechanisms driving trophic cascades in complex large-scale terrestrial ecosystems due to the lack of ability to use experimental manipulation as a means to study cause-and-effect relationships (Schmitz et al. 2000, 2004). Effectively capturing trophic cascades in large-scale terrestrial ecosystems requires well designed long-term studies in tractable systems with established controls, conditions typically not found in natural systems.

Understanding the role of trophic interactions among large mammals in shaping terrestrial ecosystems is imperative to the development of comprehensive conservation and resource management strategies aimed at restoring populations of large carnivores previously lost from the landscape. The scientific community has been presented with a unique "natural experiment" for the study of trophic cascades in a large-scale terrestrial system in Yellowstone National Park (YNP). The reintroduction of wolves *(Canis lupus)* to YNP in 1995-1996 was lauded as a great conservation achievement whereby a previously extirpated apex carnivore was reestablished and expected to restore top-down processes and lost trophic relationships to the ecosystem (NRC 2002). Prior to releasing wolves into the Park, scientists attempted to forecast the ecological impacts of restoring wolves to a system where they have been absent for more than 70 years. Predictions were made about the direct effects that wolves might have on their prey (e.g. elk - *Cervus elaphus*, bison - *Bison bison*, beaver - *Castor canadensis*, moose - *Alces alces shirasii*), as well as their competitors (e.g. coyote - *Canis latrans*) (Varley and Brewster 1992, Boyce 1993, Cook 1993). Most notably, scientists and the general public alike were concerned about the potential impacts of wolf predation on YNP's elk herds and the indirect effects on vegetation communities, an often contentious subject in the media and the scientific literature. Although much debate has ensued over the primary drivers, there is substantial evidence to show that the decline of aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), and riparian willow (*Salix* spp.) throughout the Greater Yellowstone Ecosystem (GYE) over the past century is largely attributable to high densities of ungulate browsers, suggesting that intense herbivory is the dominant limiting

factor for height growth among these species in the GYE (Houston et al. 1982, Romme et al. 1997, Keigley 1997, Ripple and Larsen 2000, Kay 2001, NRC 2002, Kauffman et al. 2010).

Since wolves were reintroduced, significant changes in elk densities (Eberhardt et al. 2007, Garrott et al. 2009a), habitat selection (Creel et al. 2005, Fortin et al. 2005), group size (Creel and Winnie 2005, Gower et al. 2009b), and vigilance (Laundré et al. 2001, Creel et al. 2008, Gower et al. 2009a) have been documented for elk herds in the GYE. Investigations of trophic cascades under this newly restored trophic structure have related these changes in elk abundance and behavior to increased height growth and decreased utilization in aspen (Ripple et al. 2001, Larsen and Ripple 2003, Ripple and Beschta 2007, Halofsky et al. 2008), cottonwood (Beschta 2005), and willow (Ripple and Beschta 2006, Beyer et al. 2007). However, many of these studies have been limited in their explanatory power, providing only correlative evidence for a trophic cascade in a wolf-elk-browse system. One of the limitations of recent studies investigating trophic cascades on the Northern Winter Range (NWR) of YNP has been the inability to isolate the relative influence of wolf predation on the observed elk population decline (Eberhardt et al. 2007) from other sources of elk mortality. Although wolf predation certainly has contributed to declining elk densities in YNP, ascribing predator offtake as the sole driver of a DMTC in this system ignores the complexity of influences on elk demographics in YNP. In the years immediately surrounding the reintroduction of wolves the elk population was concurrently being affected by extensive late-season hunts at the Park's northern border, predation on calves by a burgeoning population of grizzly bears,

drought-induced deterioration of forage quality, and a severe winter that resulted in significant mortality (NRC 2002, Vucetich et al. 2005).

Another challenge in the investigation of trophic cascades in YNP has been teasing apart the relative influence of changes in elk density versus elk behavioral responses to predation risk. Although a significant decline in elk density on the NWR since wolf reintroduction has been well documented (Eberhardt et al. 2007), a number of studies investigating trophic cascades in YNP have given little attention to the density effects and have attributed observed increases in plant growth primarily to behavioral responses of elk to predation risk (Ripple et al. 2001, Ripple and Beschta 2004, Ripple and Beschta 2006, Ripple and Beschta 2007, Beyer et al. 2007, Halofsky et al. 2008). However, these studies lack any rigorously collected empirical wildlife data to support their conclusions that wolves have reinstituted a "landscape of fear" (Laundré et al. 2001, Ripple and Beschta 2004) and initiated a BMTC. For example, Ripple and Beschta (2006) relate disparities in observed browse pressure and plant height in willow among different sites on the NWR to "risky places" for elk on the landscape (e.g. presence of escape impediments or obstructions of viewsheds). However, empirical evidence of elk behavior demonstrating the association between these landscape attributes and "risk" is lacking. In contrast, other investigations in the GYE that incorporated empirical wildlife data found no evidence for a BMTC involving aspen (Kauffman et al. 2010) or willow (Creel and Christianson 2009). Continued investigation on the effects of elk abundance and behavior on woody plant growth are needed to better describe the relationship between elk behavior and resource utilization in the face of predation risk.

Long-term datasets detailing the abundance, distribution, and behavior of large mammalian herbivores in both the absence and presence of their primary predators are needed to adequately capture a trophic cascade and reveal the underlying mechanisms driving them in large-vertebrate terrestrial systems. Such studies are rare and usually serendipitous, as most studies are initiated in response to, rather than in anticipation of changes in trophic structure. However, a long-term winter study of elk demography in the Madison headwaters study area (MSHA) in the west-central portion of YNP, initiated in 1991 prior to wolf reintroduction and continuing through 2009, provided such an opportunity. The MHSA is home to a resident non-migratory non-hunted elk population that remained relatively stable prior to wolf reintroduction (Garrott et al. 2003). Following wolf establishment in the study system (winter 1998-1999), the Madison headwaters elk herd experienced significant changes in abundance and distribution as a direct result of wolf predation (Becker et al. 2009, Garrott et al. 2009a, White et al. 2009). The changes in elk abundance and distribution in the MHSA due to wolf predation differed by drainage, where each of the three river drainages in the study experienced an isolated population response, resulting in a gradient of browse pressure across drainages directly linked to predator offtake. Herbivores, and thus herbivory pressure, were uniformly distributed throughout the study area prior to wolf reintroduction and were subsequently reduced dramatically in two of the three river drainages comprising the study area (see Study Area description).

In addition to having spatially isolated demographic responses to wolf predation, detailed studies of elk behavior (Gower et al. 2009b, Gower et al. 2009a) and spatial

patterns (Gower et al. 2009c, White et al. 2009) in both the presence and absence of wolves allowed for the density effects of wolf predation to be isolated from the behavioral responses of elk to predation risk. These studies did not observe significant shifts in elk spatial patterns or foraging behavior that would result in meaningful changes in herbivory pressure. Thus, there is no direct empirical evidence for elk behavior that would suggest the occurrence of a BMTC with aspen in the MHSA. In consideration of the theory that large cursorial predators are unlikely to initiate a BMTC (Schmitz 2005), and supporting evidence of this theory from studies of elk behavior in the MHSA (Gower et al. 2009a, 2009b, 2009c, and White et al. 2009) and other areas of the GYE (Creel and Christianson 2009, Kauffman et al. 2010), a BMTC among wolves, elk and aspen in the MHSA is not supported.

The primary objectives of this study were to test hypotheses relating changes in elk abundance and distribution to browse conditions and plant growth within identified aspen stands. This study directly links changes in browse pressure on aspen to an extensive dataset detailing the effects of recolonizing wolves on elk (Garrott et al. 2009b).

Woody plants provide a record of historical browse conditions in their annual tree rings and morphological architecture that allow for the detection and dating of shifts in browsing regimes (Keigley et al. 2003). A browse history was constructed for aspen stands in the MHSA as a means of assessing changes in browse pressure from wintering ungulates. Aspen are a preferred winter browse species of elk (Kufeld 1973) and served as an indicator species for changes in historical browse conditions related to changes in

elk use. Young regenerative aspen, accessible to browsing, were found to be widely spread throughout the study area (Chapter 2, this volume). The unique arrangement of isolated elk population responses to wolf predation allowed for a direct test for the occurrence of a DMTC in a wolf-elk-aspen system where aspen were hypothesized to exhibit reduced browsing pressure and increased growth in areas where elk numbers have declined significantly.

This research integrates a vegetative component to a long-term ecology study and contributes to a growing body of literature attempting to gain a better understanding of trophic interactions among large mammals and their habitat in the Greater Yellowstone. Additionally, this study investigates trophic cascades in an area of the GYE not yet reported on in the literature, broadening our understanding of the impacts of wolf reintroduction on the ecosystem across a heterogeneous landscape.

Study Area

The Madison headwaters study area (Figure 4.1) spans ~36,190 ha encompassing portions of the Central Plateau and Madison Plateau in west-central YNP and the associated Firehole, Madison, and Gibbon river drainages (Garrott et al. 2003). The boundaries of the study area are defined by elk winter home ranges estimated by Gower et al. (2009c). Elevation in the MHSA ranges from ~2048-2560 m and the topography is comprised of relatively flat undulating terrain dissected by steep canyons. Climate in central YNP is characterized by long cold winters and short cool summers with snowpack persisting typically 6-7 months of the year (8-9 mo/yr. on the Madison Plateau) (Newman

and Watson 2009). The mean annual temperature for the period 1997-2007 was 3° C (Newman and Watson 2009). Mean annual snowpack depth was ~1 m for the same period, but could reach several meters at higher elevations. Mean annual precipitation varies greatly (Newman and Watson 2009). Complex landscape patterns arising from the combined influences of climate, geology, soils, hydrology, terrain, vegetation, and human impacts dictate wildlife ranges and spatial use (Newman and Watson 2009).

The study area is composed of large tracts of forests with interspersed meadow complexes. The non-forested areas consist of wet meadows, dry meadows, talus slopes, and geothermal areas. Wet and dry meadow complexes comprise ~20% of the landscape and occur on the fertile soils of alluvial plains deposited between adjacent lava flows (Newman and Watson 2009). Forested land covers ~80% of the study area, of which approximately ~53% was burned in the fires of 1988 (Newman and Watson 2009), which created a mosaic of burned and unburned forest across the landscape (Romme and Despain 1989). Approximately 95% of forested land in the MHSA is dominated by lodgepole pine (*Pinus contorta*). These large expanses of lodgepole pine occur on poorly developed rhyolitic soils from lava flows and are differentiated by varying stages of stand succession (Newman and Watson 2009). Other tree species that occur, but are less common in the study area are: whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*) (Newman and Watson 2009). Aspen are rare in the study area and are typically found in talus and at low elevations in the ecotone between conifer forests and meadow complexes (Newman and Watson 2009).

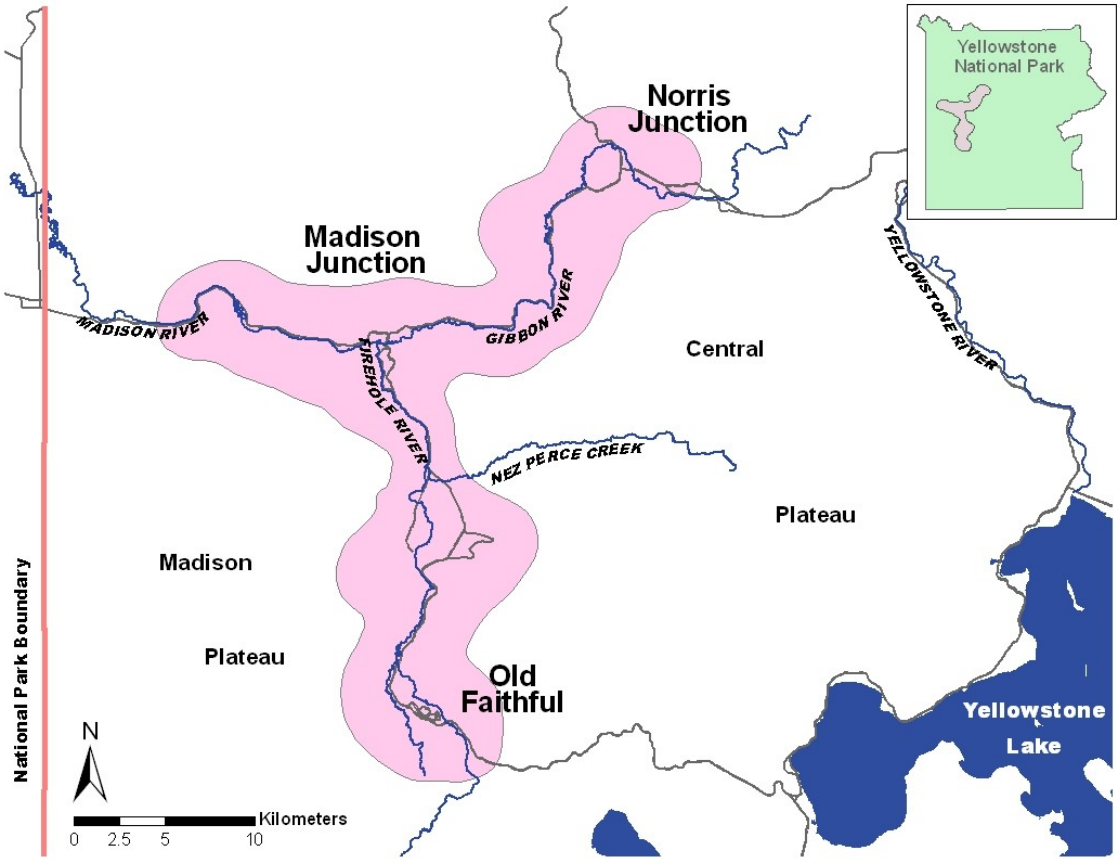

Figure 4.1: Map of the MHSA, west-central Yellowstone National Park, Wyoming, USA, including the Gibbon River, the Firehole River, and the Madison River drainages. The study area boundaries are defined by estimated winter home ranges for the resident elk herd (Gower et al. 2009c).

History of the Madison Headwaters

Elk Herd: Pre-wolf to Post-wolf

Changes in Abundance and Distribution*:* Observations on the Madison headwaters elk herd were initiated in 1991, seven years before wolves colonized the study area. The elk population remained relatively stable for over 30 years, varying from 400-800 animals (Craighead et al. 1973, Aune 1981) and was evenly distributed

throughout the study area. Wolves recolonized the study area in 1996, with the first pack (Nez Perce pack) establishing during the winter of 1998-1999, primarily using the Firehole and Gibbon drainages. By 1999 the elk numbers in the Gibbon had begun to decline substantially (Figure 4.2). Elk in the Gibbon drainage were heavily predated upon, with elk numbers declining approximately 50% by 2001. The Gibbon drainage was essentially elk free by 2004, the same year peak wolf use was documented in the study system and six years following the establishment of the first pack in the MHSA. The Firehole drainage also experienced a significant decline in elk, but much more gradually than the Gibbon drainage. The elk population in the Firehole did not experience significant decline until around 2004, but fell dramatically by the end of the study (Figure 4.2). The Madison drainage experienced an anomalous peak in the elk population (see White et al. 2009 for an explanation), but remained relatively stable throughout the study, with current estimates not dramatically lower than the pre-wolf era (Figure 4.2). By the end of the study the total elk population in the MHSA was estimated at ~74 elk (R.A. Garrott, Montana State University – *unpublished* data) with over 92% of the population residing in the Madison drainage, a dramatic shift from the pre-wolf era (Figure 4.2). The shift in elk distribution in the MHSA was the result of elk being removed by wolves from certain areas on the landscape, rather than a redistribution of animals, as collared elk in the system maintained strong site fidelity throughout the duration of the study (Gower et al. 2009c).

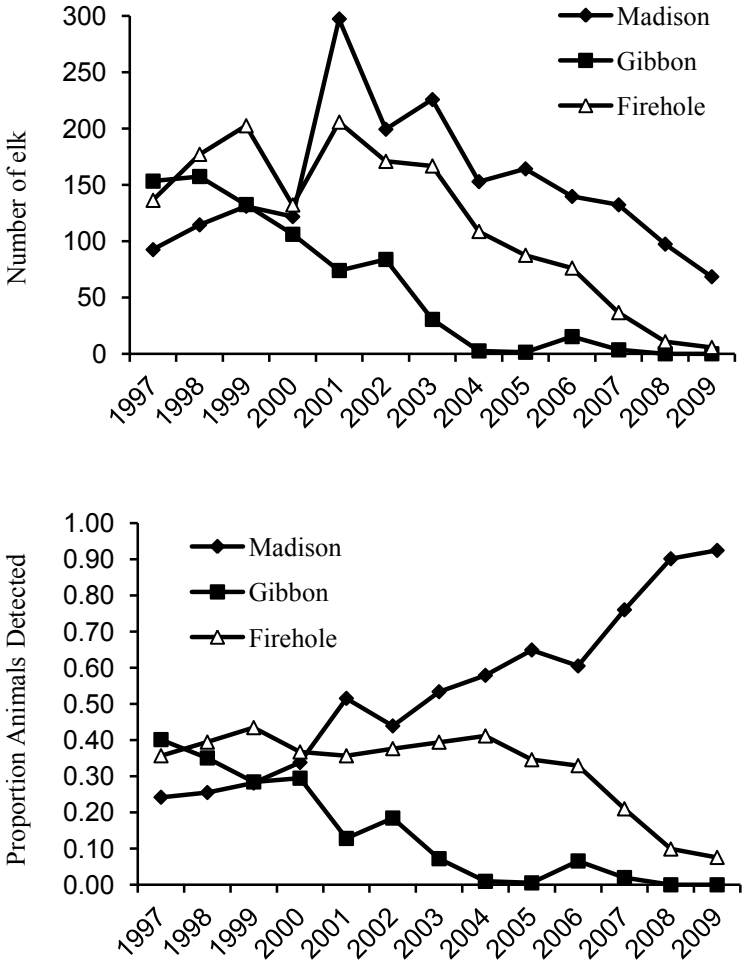

Figure 4.2: Estimated changes in the proportion of the elk population and the total number of the elk occupying the Madison, Gibbon, and Firehole River drainages from 1997 through 2009. Estimates were based on replicate mark-resight surveys (Garrott et al. 2009a).

Elk Spatial Responses Following Wolf Reestablishment: Gower et al. (2009c) revealed modest – although statistically significant – spatial responses of elk to wolf presence in the MHSA. Elk increased the area of their home ranges following wolf establishment, exhibiting a positive correlation between home range size and the presence of wolves in all three drainages (Gower et al. 2009c). Elk in the MHSA also

demonstrated a reduction in site fidelity following wolf establishment in the system. While elk generally exhibited philopatric behavior for their winter range within a particular drainage from year-to-year, they became less faithful to a particular site between successive years as wolf presence in the system increased (Gower et al. 2009c). These results indicate that elk in the MHSA demonstrated a departure from their traditional spatial patterns and adopted more dynamic spatial behaviors in response to increased wolf presence and activity within a given drainage (Gower et al. 2009c). However, habitat shifts and altered resource selection as a behavioral response to wolf presence were not observed for wintering elk in the MHSA (White et al. 2009). These studies interpreted the observed shift in spatial use of elk within their home ranges to be a result of wolves displacing elk during a predation event to avoid further imminent threat, rather than elk adopting preemptive predation avoidance strategies (Gower et al. 2009c).

Elk Group Size and Wolf Predation: Elk in the MHSA modified their aggregation patterns following wolf reestablishment as a behavioral response for managing predation risk in this newly established predator-prey system. Elk group sizes were more variable following wolf recolonization and there was a positive correlation between larger group sizes and wolf presence, activity, and the number of kills within a respective drainage (Gower et al. 2009b). Gower et al. (2009b) also found that as the elk population declined the typical individual group size increased. The observed changes in aggregation patterns in the Madison headwaters elk herd may be altering browsing pressure in areas where elk are persisting in the study tract. However, the magnitude of the observed increase in

mean group size from 5.58 elk pre-wolf to 7.55 elk post-wolf is not likely to be meaningful with respect to the relative browse pressure. Additionally, the temporal nature of the observed relationship suggests that changes in group size occurred in response to wolf presence and that this aggregation pattern does not persist when wolves are not in the system. Thus, any potential impacts on the vegetation are not consistent through time and may not occur on timescales that would result in significant changes in browse pressure at a given site.

Elk Foraging Behavior: Gower et al. (2009a) studied the foraging behavior of the Madison headwaters elk herd both pre and post-wolf reintroduction. While a modest increase in vigilance was detected when wolves were present within a given drainage, overall there were no significant changes in scanning behavior or reductions in foraging efforts. Therefore, increased vigilance as a behavioral response to the threat of wolf predation should not be expected to have any indirect effects on the associated plant community within the MHSA and will be excluded as a variable from this analysis.

Methods

Browse condition and trend of aspen were evaluated for each stand in the MHSA. Methods for evaluating browse condition and trend were adapted from a field manual developed for Montana Fish Wildlife & Parks (Keigley and Frisina 1998) based on methods developed by Keigley (1997) for assessing the impact of ungulates on browse species by analyzing plant architecture. “Architectural analysis is the process of

reconstructing past browsing conditions based on the dendrochronologic dating of morphologic features; some features are produced by light browsing, others by intense browsing" (Keigley et al. 2003). An in-depth examination of annual tree-rings (dendrochronology) of selected plants can lend insight into the actual years for which a specific level of browsing began or ceased. The year in which a specific segment of a live shoot was a terminal leader can be determined by counting the annual rings at a given height on the stem. Detailed methods for this process are described in Keigley and Frisina (1998, pgs. 96-108). For this study, "stem" is defined as the primary axis of an aspen representing an individual plant, and "shoot" is defined as either a lateral branch or terminal leader elongating from the stem.

The methods outlined by Keigley and Frisina (1998) were decomposed for this study to address two questions: 1) Is there evidence for a shift in browse pressure on woody plants in the MHSA and, if so, 2) Is there a detectable morphological response where aspen are experiencing a "release" from a dominant limiting factor (browse pressure), escaping the browse zone, and trending towards successful recruitment? Definitions of architecture type described by Keigley (1997) were modified for this study and recognize two growth forms:

Uninterrupted growth-type (UN): Produced under light-to-moderate browse conditions. The terminal leader originates each year from the previous year's growth as it passes through the browse zone. There are no signs of intense browsing (e.g. clusters of dead browsed shoots).

Intensely Browsed growth-type (IB): Produced under intense browse conditions. The stem exhibits signs of previous intense browsing (e.g. clusters of dead browsed shoots, bark stripping). The stem may or may not have recently experienced intense browsing, but needs only have been intensely browsed at some point in its life.

Each stem selected for observations was classified into one of these two categories and subject to measurement and sampling (as described below) according to its classification to characterize browsing history and aspen growth in the MHSA.

Observations and Sampling

Linear transects were surveyed in the MHSA to locate aspen stands throughout the study area. Once an aspen stand was found, the perimeter was mapped and sample plots were established. The methods for locating aspen stands and establishing sample plots are described in detail in Chapter 2, this volume.

The first 20 aspen stems encountered along a belt-transect, (or in a variable-radius circular plot), that were within the browse zone (20-150 cm in height) were selected for measurement to assess height and productivity. Samples for dendrochronological analysis were collected from no more than 50% of the individuals selected for measurement within a plot, totaling no more than 10 individual stems sampled per plot. In some instances, stem densities were too low to provide for 20 stems, in which case as many stems as were available were included in the observations. In the case where there

were multiple stems emerging from the soil at the same point, the stem that appeared to be the dominant of the group was selected for observation and sampling.

Cross sections or increment cores were collected from individuals for dendrochronological analysis of browsing history and age structure for aspen in the MHSA. Stems and shoots that were > 5 cm diameter at the segment being sampled were cored using a 4 mm diameter increment borer. Cross sections were collected from stems and shoots that were ≤ 5cm diameter at the section of the stem being sampled. It was frequently necessary to collect cross sections, rather than cores, as the stem diameters were typically ≤ 5cm. In most cases, multiple samples were collected from each of the stems selected for sampling in order to date changes in morphology associated with browsing on an individual stem. Cross sections were surfaced using a razor blade to elucidate the annual rings. Increment cores were mounted and prepared following standard dendrochronology techniques (Stokes and Smiley 1968). Ages were determined using a dissecting scope to count the number of annual rings. Cross-dating methods were not employed, as the majority of trees within the browse zone were < 20 years of age and could not be reliably cross-dated due to the shortness of tree-ring series and the lack of sensitivity of tree-ring widths to environmental variability during the juvenile growth stage.

Browsing History of Aspen in the MHSA

Current Level of Browse Intensity: An assessment of the current level of browse intensity was made for each stand through an examination of terminal leaders within the

browse zone (20-150 cm) that have been recently exposed to browsing. Browse intensity was categorized as either intense or light-to-moderate following Keigley et al. (2003):

Intense (I): Browsing caused death to a complete annual segment of an aspen shoot (dieback to lower portions of the stem).

Light-to-Moderate (LM): Ungulate browsing was not intense enough to cause death to a complete annual shoot segment

Current browse level was determined for the 20 aspen stems selected for measurement in each plot. Methods for selecting and classifying a primary stem are detailed in Keigley and Frisina (1998 pgs. 75-77).

Detecting a Shift in Browse Regimes: To detect a potential shift in browse regimes, (from an era of intense browsing prior to wolf reintroduction to a subsequent era of light-to-moderate browsing), the age of current terminal leaders was compared to the age of dead clusters that were formerly terminal leaders on the same plant. Dead clusters are formed when a segment of the aspen shoot that bears the terminal leader is continuously intensely browsed each winter, leaving behind a cluster of dead woody stubs, and eventually causing significant dieback to lower portions of the main stem. The plant then initiates a new apically dominant leader from a dormant adventitious bud on some portion of the lower stem or shifts dominance to a previously initiated lateral shoot. If heavy browsing conditions persist, the plant will continue to form dead clusters as its leader growth is continually clipped (Keigley 2003). The comparison of the longevity of terminal leaders allows for the determination of whether or not current leaders are living

longer before experiencing significant dieback than did former leaders (now dead clusters) under intense browsing conditions. It was assumed that, if there has been a significant reduction in browsing pressure on aspen, then current leaders should have experienced a period of recent uninterrupted growth. That is, the majority of current leaders in areas where browse pressure has declined significantly should not exhibit signs of intense herbivory (death of a complete annual segment). If the longevity of the recent uninterrupted growth (RUG) is greater than the longevity of dead clusters, then, all else being equal, there is evidence that historical intense browse pressure was alleviated sometime in recent history. If a shift in browse regimes is evident, the timing of this shift can be approximated by the average date of shoot elongation of the RUG. This is accomplished by subtracting the age of the RUG from the year it was sampled (2009).

The difference in longevity between the RUG and dead clusters (Δ_L) was calculated by subtracting the average age of dead clusters from the age of the RUG from the same plant. Samples for the calculation of Δ_L were paired by individual aspen to provide a relative difference and to avoid issues of individual heterogeneity in growth form, productivity, or injury response. A sample was collected from the base of multiple dead clusters (1–5 depending on the number available for sampling) on each aspen selected for sampling and exhibiting signs of historical intense browsing. Ages of dead clusters were averaged per individual aspen stem to represent the average age at which terminal leaders succumbed to browsing pressure and experienced significant dieback. A single sample was collected from the base of the RUG of the current leader, as aspen typically develop a single leader stem. These samples were prepared and aged according

to the dendrochronology methods described above. Δ_L was averaged across all individuals within a stand to characterize the difference in longevity at the stand level (the stand was the sampling unit).

Age Structure

A sample was collected from the base of each aspen stem selected for sampling to determine total age of the stem and date its origination. For IB stems, a sample was taken from the live portion of the stem just below the lowest cluster of dead stems (H_{BBD}, see next section) as a means of determining the age at which the plant was initially browsed. For UN stems, a section was taken at 20 cm in height to determine the age at which the plant entered the browse zone. Determining the age at which a plant was initially browsed or initially entered the browse zone lends insight into how long plants have historically been intensely browsed in the MHSA and, for UN stems, how long aspen have experienced light-to-moderate browse conditions. Cross sections were collected from up to three dead aspen stems (< 150 cm in height) per plot in order to evaluate the average age of death for a regenerative aspen stem that was unable to grow beyond the browse zone. These samples were prepared and examined in the same manner as live cross sections.

Aspen Height Growth and Productivity

A series of measurements was recorded for each of the 20 stems selected for observation to characterize the overall height of regenerative aspen, productivity, and vertical gains relative to historical browse conditions:

H_{BCYG}: Height from the base of the plant to the base of the current year's growth, as an indication of net height gain prior to the current growing season. (Accounts for offtake from winter ungulate browsing on shoots).

H_D: Height from the base of the plant to the tip of the tallest dead stem that exhibits obvious signs of intense browsing, as an indication of the upper bound of the browse zone of that plant.

H_{AD}: Height of current leaders above the H_D, (H_{AD}= H_{BCYG} - H_D), as an indication of whether or not an individual stem is growing beyond the height at which it has been historically browsed.

H_{BBD}: Height to the base of the browsed dead: Height from the base of the plant to the tip of the lowest dead stem that exhibits obvious signs of intense browsing, as an indication of the lower bound of the browse zone of that plant.

L_{PYG}: Length of the previous year's growth as an indicator of site productivity relative to aspen shoot elongation. Measured as the length of the shoot (cm) between where the previous year's growth originated (bud scar) and terminated (either at the bud scar from which the current year's growth elongated or where the shoot was clipped).

Analysis Methods

The dramatic shift in abundance and distribution of elk following wolf establishment created a clear dichotomy of elk presence/absence, facilitating the evaluation of DMTC's among wolves, elk and aspen in the MHSA. Wintering elk, and thus browsing pressure, were previously distributed evenly throughout the study tract and are currently restricted almost entirely to the Madison drainage (Figure 4.2, White et al. 2009). Drainage was used as a proxy for changes in elk abundance and distribution in the MHSA and so changes in aspen growth relating to DMTC's were assumed to occur at the drainage level following the observed changes in elk. Each stand was assigned to a drainage (Firehole, Gibbon, or Madison) based on the winter home ranges of the elk that used them (estimated for the period 1991–2007 by Gower et al. 2009c) and the drainage that each group of elk is associated with. Elk in the MHSA exhibit strong site fidelity with very localized movement patterns and infrequent movements outside the drainage of their affiliation (Gower et al. 2009c). Two stands located in the Gibbon drainage (according to geomorphology) were assigned to the Madison drainage, based on elk home ranges. Another stand found in the Gibbon drainage could not be assigned to any one elk group, due to overlap in home ranges, and was excluded from all drainage-wise analyses.

The stand was the sampling unit and so all measurements and observations within a stand were averaged to characterize the stand-level response. Diagnostics plots and tests were performed to reveal any deviations from normality. Parametric tests were used where possible and data transformations or non-parametric tests were used where

departures from normality were discovered. One-sample t-tests were used to determine if Δ_L was significantly different from zero (H_a: $\Delta_L \neq 0$) for each drainage. ANOVA's and Kruskal Wallis Rank sum tests (dependent upon normality of the data) were used in all drainage-wise comparisons (Δ_L, age of the RUG, age of dead clusters, H_{AD}, H_{BCYG}, L_{PYG}) and were followed by *post hoc* multiple comparisons tests (Tukey's Honest Significant Difference or Tukey-type non-parametric multiple comparison procedure, Zar 1984) where significant differences were detected. All statistical analyses were performed using program R (R Development Core Team, 2011).

It was predicted that, in the Gibbon drainage where the elk population declined precipitously, aspen would be taller and exhibit significantly reduced browsing pressure relative to the Madison drainage, where 92% of the remaining elk herd winters. That is, Δ_L and ln(age) of the RUG for aspen stands in the Gibbon drainage would be significantly greater than for stands in the Madison drainage. The Madison Drainage was predicted to experience continued intense browsing pressure ($\Delta_L \approx 0$) with current leaders exhibiting recent intense browsing (small RUG) and suppressed height ($H_{AD} \approx 0$). The Firehole drainage was predicted to exhibit reduced browsing pressure and increased height growth, but to a lesser degree than in the Gibbon drainage, as changes in elk abundance in the Firehole drainage occurred later and more gradually than in the Gibbon drainage. Values for Δ_L and ln(age) of the RUG in the Firehole may not be significantly different from the other two drainages.

Results

During the summer of 2009 forty eight transects were surveyed in the MHSA for a total distance of 226 km. Thirty one aspen stands were located and mapped and assigned to a drainage; 11 in the Firehole River drainage, 12 in the Madison Canyon, and 8 in the Gibbon River drainage. (Only 30 of the 31 stands were included in drainage-wise analyses. Stand 9 was censored from the Gibbon drainage due to overlap in elk winter home ranges; see Methods section for details on assignment of stands to drainage). For each identified stand, 1-3 plots were sampled totaling to 69 plots for the entire study area (66 excluding Stand 9 for drainage-wise analyses). Observations of plant morphology and browse condition were recorded for 1,327 individual live aspen stems and 2,532 samples (cross sections and increment cores) were collected from 636 individual live stems selected for sampling. Cross sections were collected from 56 dead stems within the browse zone. In total, for all sample types, 2,583 samples were collected to reconstruct historical browse conditions and evaluate the occurrence of a change in ungulate browsing pressure on aspen in the MHSA following wolf reintroduction.

The spatial arrangement of aspen stands on the landscape differed across drainages with respect to their associated environmental attributes. In the Gibbon and Madison drainages, aspen tended to be confined to small stands found on steep (~40°) southerly aspects in scree or talus fields at the convex break in the slope near the plateau edge. Very few aspen exist in the Gibbon River drainage, where the regenerative

lodgepole forest is very dense with post-burn saplings and deadfall. No aspen were found north of the Gibbon Canyon, except for the rare discovery of small groups of stems (1-6) found interspersed with the lodgepole saplings. Aspen in the Firehole drainage were found to be diffuse throughout the burned forest, occurring primarily on southerly aspects, favoring no particular slope steepness (median= 18, range: 0 – 40). The geology throughout the study area is fairly homogenous; all but one of the aspen stands considered in this study were growing on glacial till derived from rhyolitic ash and lava flows. (See Chapter 2, this volume, for more detailed description of aspen distribution and morphology in the MHSA).

Age Structure

The year of origination was determined for 636 individual regenerative aspen stems within the browse zone. The median age of stems observed in this study is 11 yrs and ranged from 2 to 47 years. Figure 4.3 indicates that there was a pulse of stem origination in the years immediately following the 1988 fires, peaking between 1990 – 1991, with a subsequent pulse peaking between 1998 – 2001. The majority (70%) of stems originated sometime after 1995, with the greatest frequency of origination occuring during the second pulse. Stems observed to have an UN architecture type (n=257) primarily originated during the second pulse of stem origination, and have a bimodal distribution with peaks at 2001 and 2005. The median age for UN type stems was 8 years and ranged from 2 to 21. Stems greater than 20 years of age (predating the 1988 fires) made up only 2.4% of all live stems sampled, suggesting that recent aspen regeneration

was stimulated by the 1988 fires and that young regenerative aspen originating prior to the fires were either scarce on the landscape or were burned in the fire.

The median age at death for dead stems sampled in this study is 10 years and ranged from 5 to 21 years. If these stems belonged to the cohort of stems that originated immediately following the 1988 fires, they would have died on average between 1998 and 2000; just prior to the beginning of the second pulse of stem initiation and the establishment of wolves in the MHSA (Figure 2.16, Chapter 2, this volume).

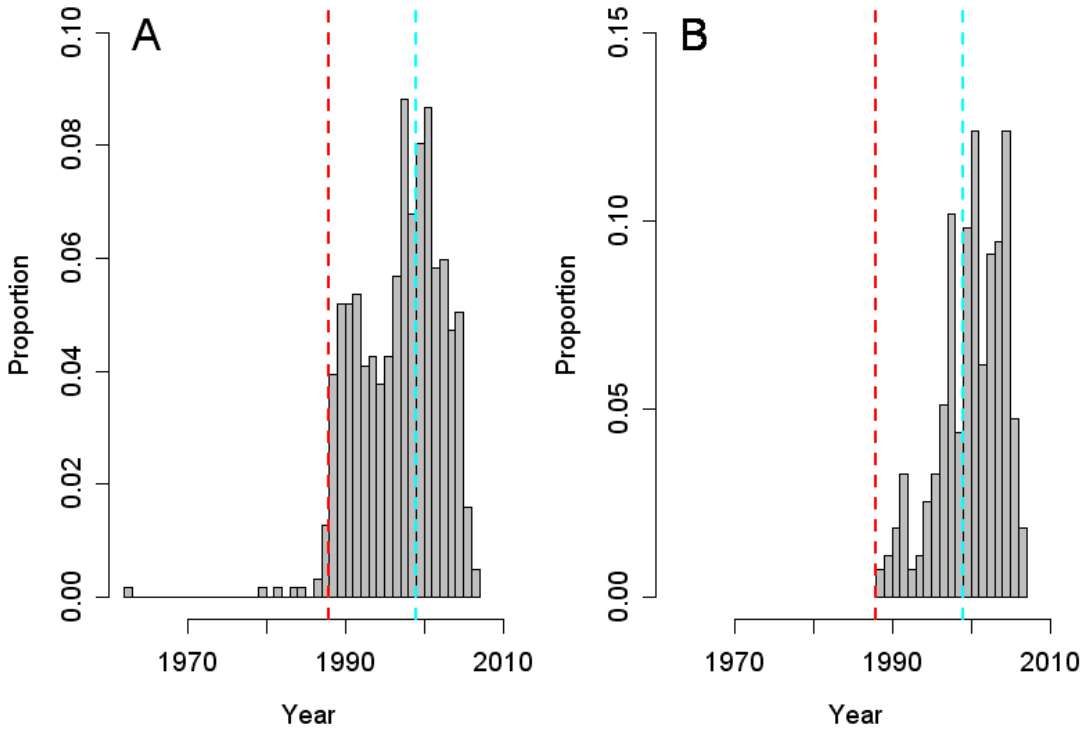

Figure 4.3: Age structure for regenerative aspen in the MHSA. Proportion of stems originating each year for all stems (A), and UN type stems (B). The dashed vertical lines demarcate the 1988 fires in YNP (red) and the growing season following the first winter with an established wolf pack in the MHSA (1999, blue line – Smith et al. 2009).

Browsing History of Aspen in the MHSA

Only 6% of aspen stems in the MHSA had been intensely browsed during the winter prior to sampling (winter 2008−2009). However, this varied across drainages. The Firehole drainage experienced the greatest frequency of current intense browsing with 9.96% of observed stems exhibiting signs of intense ungulate herbivory (death of a complete annual segment). Most of these intensely browsed stems occurred in a single stand that is not representative of the current browse conditions throughout the Firehole drainage. The Madison and Gibbon drainages experienced a minimal amount of intense browsing with only 0.8% and 1%, respectively, of stems being intensely browsed during the prior winter. Stem density was not significantly different across drainages (χ^2= 3.28, df = 2, p-value = 0.194, Kruskal-Wallis rank sum test), and so could not explain the observed difference in the percent of stems intensely browsed. That is, the number of stems available for elk to browse did not differ across stands and did not bias the relative proportion of stems browsed. Although there was some disparity across drainages, overall, the percentage of stems intensely browsed was very low throughout the study area. This would suggest that browsing was not limiting aspen growth in the MHSA during the year of sampling

Δ_L was calculated for 381 individual stems and was averaged across individuals to assess the average difference in longevity between current leaders and dead clusters at the stand level (the stand was the sampling unit). Drainage-wise averages for Δ_L were positive for all three drainages, indicating that current leaders are living longer than their predecessors had before succumbing to browsing pressure and experiencing significant

dieback (Table 4.1). This runs counter to the prediction that the Madison drainage would experience continued intense herbivory. The magnitude of the response differed across drainages (F= 4.27, df= 2 and 27, p= 0.025, from a one-way ANOVA) (Figure 4.4). As predicted, mean Δ_L was greatest in the Gibbon drainage where elk declined precipitously following wolf reintroduction. However, the difference in Δ_L was not significantly different between the Gibbon and Madison drainages as predicted. The Madison drainage had the greatest variation in Δ_L, where some stands showed no difference in longevity between the RUG and dead clusters and others had a relatively large Δ_L (Table 4.2). Figure 4.4 indicates that the lack of a significant difference in Δ_L between the Gibbon and Madison drainages is due to a small number of relatively large values and that Δ_L in the Madison drainage is more similar to that observed in the Firehole drainage.

Table 4.1: Descriptive statistics for the comparison of longevity between current leaders and dead clusters for aspen in the MHSA. (Standard deviations in parentheses). p-values are from one-sample t-tests (H_a: $\Delta_L \neq 0$).

Drainage	**Mean Δ_L**		**Mean age of dead clusters**		**Mean age of RUG**		**No. of Stands**	**No. of Stems**	**p**
Firehole	1.10	(1.35)	4.23	(1.26)	5.69	(1.89)	11	154	0.022
Gibbon	3.22	(1.24)	5.36	(1.60)	8.58	(2.08)	7	85	<0.001
Madison	1.69	(1.78)	4.67	(1.42)	6.41	(1.54)	12	142	0.007

Table 4.2: Results from a Tukey's Honest Significant Difference *post hoc* multiple comparison procedure assessing the statistical significance of drainage-wise differences in Δ_L and the ln(age) of the RUG (95% family-wise confidence level).

Drainage	diff. in mean	lower conf. int.	upper conf. int.	p-adj
Drainage-wise difference in Δ_L				
Gibbon-Firehole	2.12	0.30	3.95	0.020
Madison-Firehole	0.59	-0.98	2.16	0.626
Madison-Gibbon	-1.54	-3.31	0.26	0.104
Drainage-wise difference in ln(age) of RUG				
Gibbon-Firehole	0.43	0.11	0.76	0.008
Madison-Firehole	0.14	-0.14	0.43	0.432
Madison-Gibbon	-0.29	-0.61	0.03	0.081

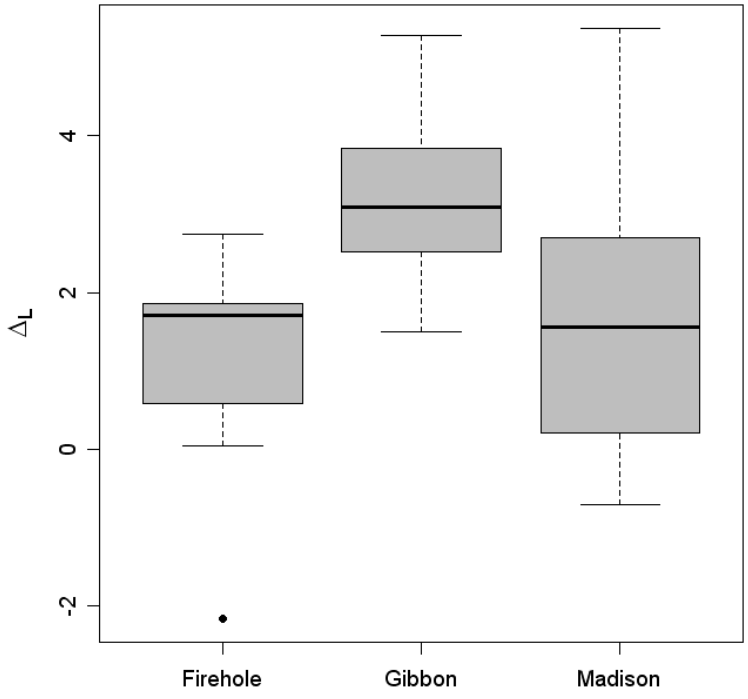

Figure 4.4: Drainage-wise comparison of the difference in longevity between current terminal leaders and dead clusters as an indicator for a change in browse pressure (Δ_L= age of the RUG – age of the dead clusters). Drainage was used as a proxy for observed changes in elk abundance and distribution (White et al. 2009).

The relatively small Δ_L observed for aspen in the Firehole drainage may be a result of elk densities remaining high for a longer period of time and browse pressure being reduced only recently. Elk densities in the Firehole drainage did not begin to decline significantly until 2004, which corresponds well with timing of origination for the average RUG in the Firehole (2003-2004) (Figure 4.2).

The ln(age) of the RUG (stand averages) was found to differ significantly across drainages (F= 5.47, df= 2 and 27, p= 0.010, from a one-way ANOVA), where the mean RUG was older in the Gibbon drainage (mean= 8.58 years) than in the other two drainages (Madison= 6.41, Firehole= 5.69 years) (Table 4.2, Figure 4.5). However, the difference in the age of the RUG between the Madison and Gibbon drainages was not significantly different. Similar to the results for Δ_L, the variability in age for the RUG in the Madison drainage was influenced by a few relatively large observations. All three drainages exhibit uninterrupted leader growth for greater than 5 years, suggesting that the browse intensity in recent years has been light-to-moderate. The age of the RUG corresponds to a decline in browse intensity between 2000 and 2001 in the Gibbon drainage, 2002 to 2003 in the Madison drainage, and 2003 to 2004 in the Firehole drainage. This suggests that the Gibbon drainage has experienced reduced browsing pressure for a longer period of time, as evidenced by a longer period of uninterrupted leader growth.

The ln(age) of the of dead clusters was not different across drainages (F= 1.50, df= 2 and 27, p= 0.242, from a one-way ANOVA), indicating that aspen throughout the

MHSA were able to endure heavy browsing for approximately the same number of years before major dieback of leader stems occurred (Figure 4.5).

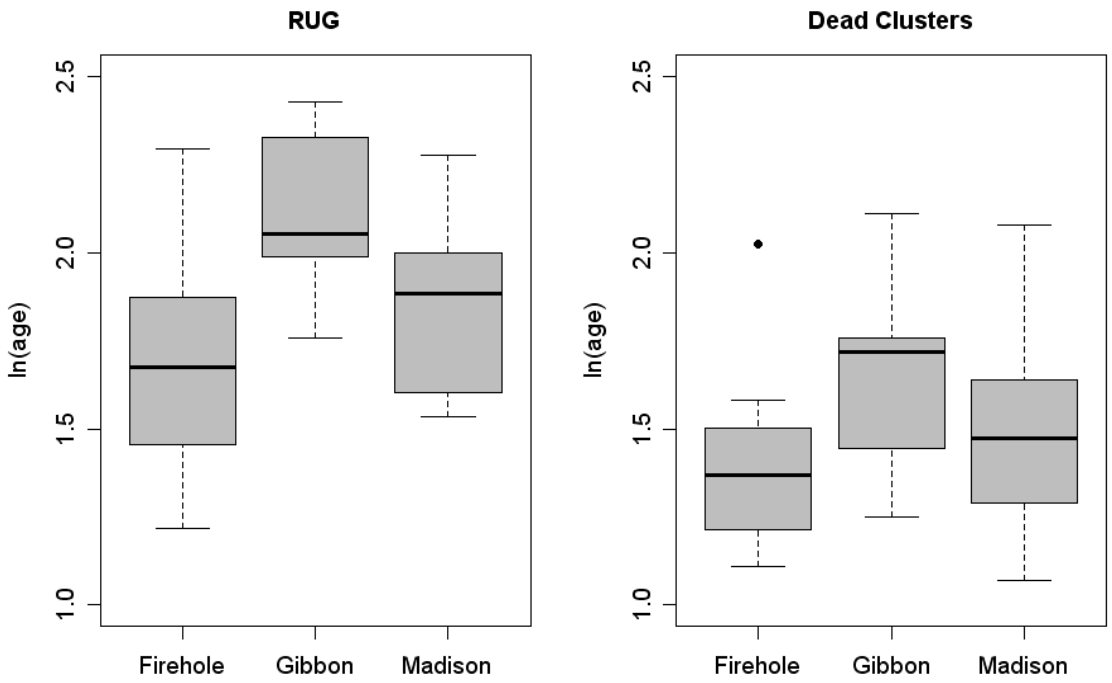

Figure 4.5: Difference in ln(age) by drainage for recent uninterrupted growth (RUG) and dead clusters.

Aspen Height Growth and Productivity

H_{AD} was significantly different across drainages ($F= 10.30$, $df= 2$, $p < 0.001$, from a one-way ANOVA), where aspen in the Gibbon and Madison drainages were growing beyond the maximum height at which they had been previously browsed, indicating that aspen have been making modest vertical gains in recent years (Figure 4.6, Table 4.3). Counter to the predicted response, H_{AD} was not significantly different between the Madison and Gibbon drainages. Aspen in the Firehole exhibited relatively insignificant

growth beyond H_D. Aspen in the Gibbon and Madison drainages have achieved an average net height above the H_D of 46.8 cm (13.0 to 76.4) and 33.1 cm (1.9 to 59.2), respectively, whereas aspen in the Firehole grew only 5.5 cm (-13.0 to 51.3) of H_D on average, with some terminal leaders growing below the height of the tallest dead clusters.

Table 4.3: Results from a Tukey's Honest Significant Difference *post hoc* multiple comparison procedure assessing the statistical significance of drainage-wise differences in H_{AD} (95% family-wise confidence level).

Drainage	diff. in mean	lower conf. int.	upper conf. int.	p-adj
Drainage-wise difference in H_{AD}				
Gibbon-Firehole	41.25	17.28	65.23	0.001
Madison-Firehole	27.59	6.89	48.29	0.007
Madison-Gibbon	-13.66	-37.24	9.92	0.337

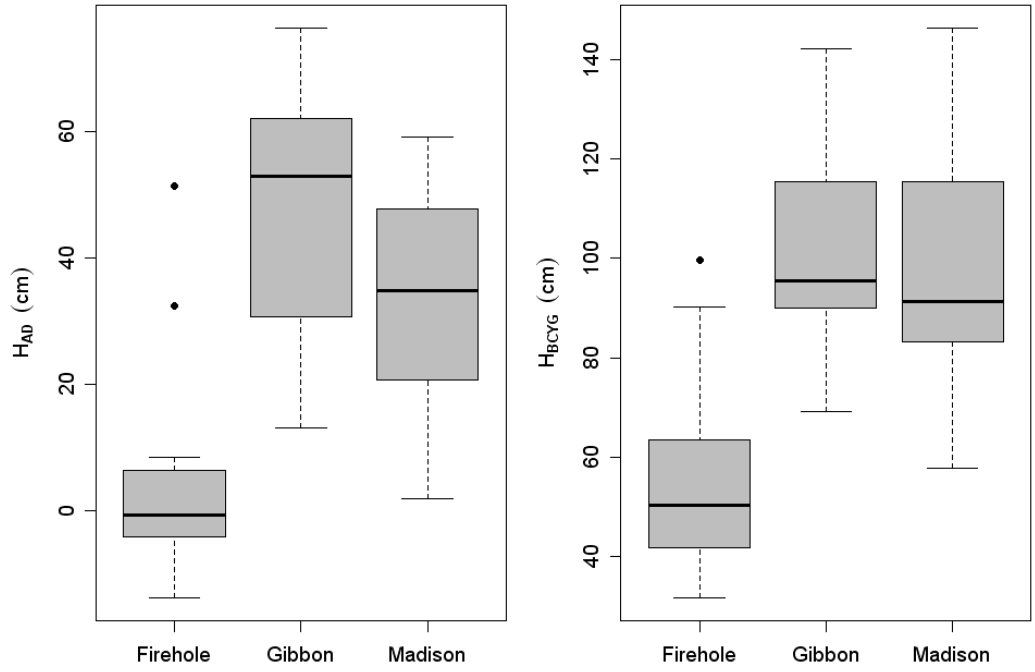

Figure 4.6: Height relative to height of the tallest dead clusters (H_D) and height to the base of the current year's growth (H_{BCYG}) by drainage (based on stand averages).

H_{BCYG} was significantly different across drainages (F= 11.96, df= 2, $p < 0.001$, from a one-way ANOVA), where aspen in the Firehole drainage were significantly shorter than aspen in the Madison and Gibbon drainages (Figure 4.6, Table 4.4). H_{BCYG} was not significantly different between the Madison and Gibbon drainages. Median H_{BCYG} of stems was well within the defined browse zone (20 – 150 cm) in all three drainages (Firehole= 50.4 cm, Gibbon= 95.4 cm, Madison= 91.2 cm). However, these heights were derived from average stand values and do not represent variability at the individual stem level. Eighteen of the 31 stands had at least one stem with $H_{BCYG} > 150$ cm, and 15 of the 31 stands had individual stems with $H_{BCYG} > 200$ cm (Figure 4.7). Thus, while the average height indicates that aspen are not escaping the browse zone and are still susceptible to suppression from ungulate herbivory, there is a number of young aspen stems throughout the study area that have escaped the browse zone and have the potential to reach canopy height and achieve successful recruitment.

Table 4.4: Results from a Tukey's Honest Significant Difference *post hoc* multiple comparison procedure assessing the statistical significance of drainage-wise differences in H_{BCYG} (95% family-wise confidence level).

Drainage	**diff. in mean**	**lower conf. int.**	**upper conf. int.**	**p-adj**
Gibbon-Firehole	45.79	18.05	73.52	0.001
Madison-Firehole	40.90	16.95	64.84	0.001
Madison-Gibbon	-4.89	-32.17	22.39	0.897

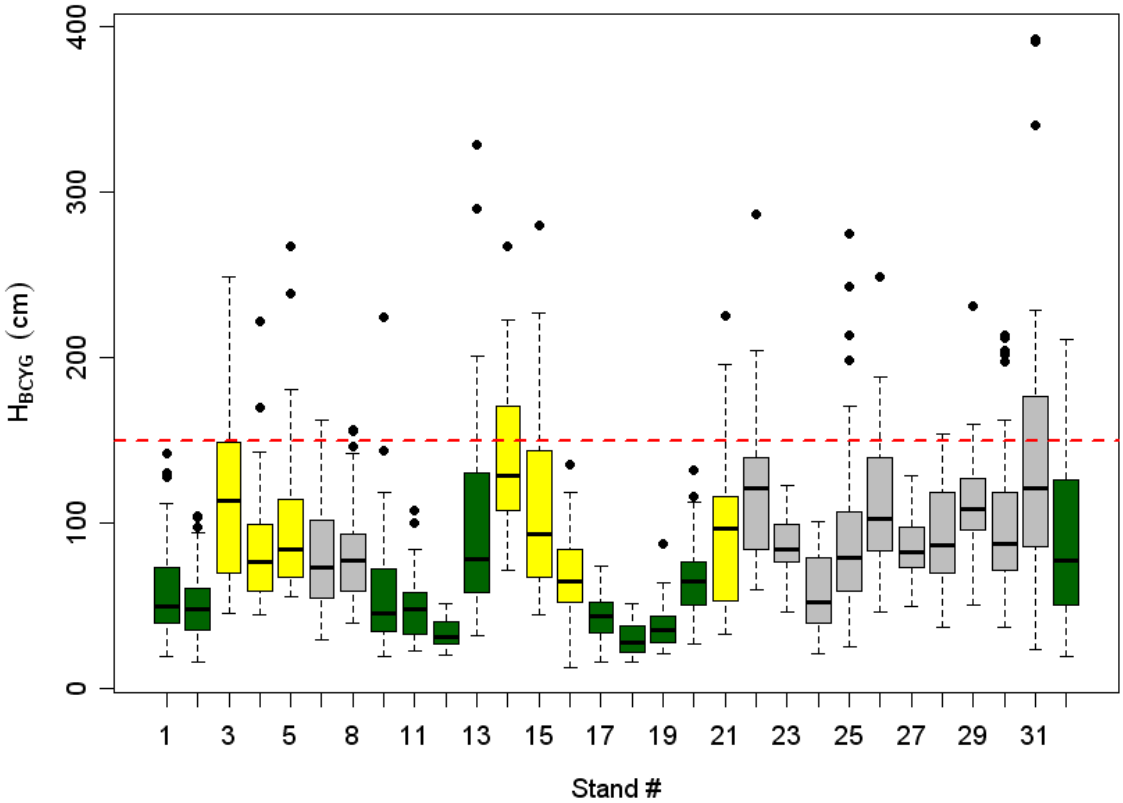

Figure 4.7: Height to the base of the current year's growth by stand. A small number of individual aspen stems, occurring throughout the study area, have escaped the browse zone. This may be an indication of ongoing recruitment. Drainage assignment coded by color: Firehole (green), Gibbon (yellow), Madison (gray). The dashed red line represents the upper boundary of the defined browse zone (150 cm).

L_{pyg} was not significantly different across drainages (F=1.03, df= 2 and 27, p= 0.371, from a one-way ANOVA), indicating that productivity relative to leader growth was similar throughout the study area (Figure 4.8). The previous year's growth was measured during the current growing season and could potentially have been browsed during the winter prior to measurement, affecting net shoot elongation. However, it is not likely that the net L_{pyg} was significantly biased due to offtake from browsing during

the prior winter given that only 6% of current leaders were browsed during the winter of 2008-2009. Mean L_{pyg} was 11.7 cm (3.6 – 30.2 cm) for the entire study area.

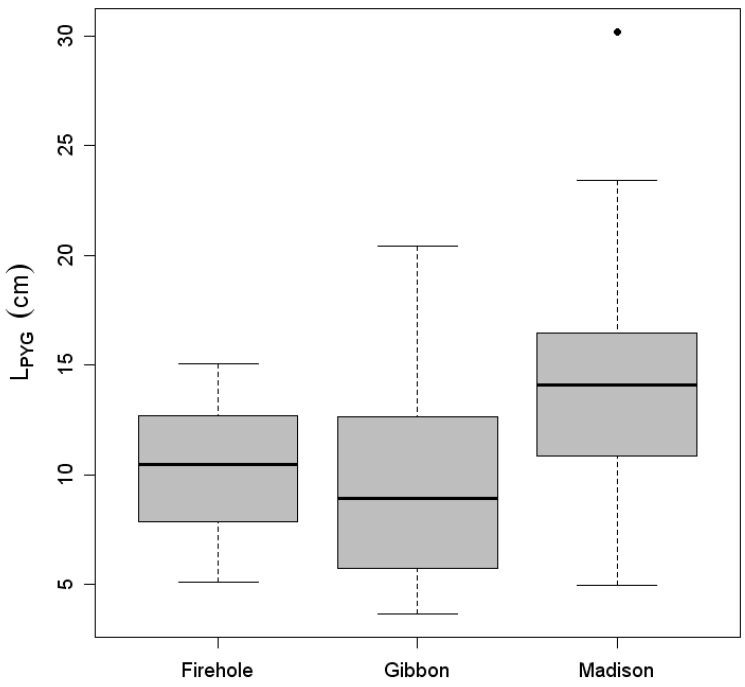

Figure 4.8: Stand-level averages of the length of the previous year's growth (L_{PYG}) by drainage.

Discussion

This study was designed to address two primary questions relating to trophic cascades: 1) was there a marked decrease in browsing pressure on aspen, and 2) was there a corresponding plant-growth response indicating that aspen were "released" from browsing pressure and are now growing vertically through the browse zone? The answer to the first question is, yes, a significant reduction in browse pressure directly related to predator offtake was detected in areas where the elk population declined dramatically.

Aspen in the Gibbon drainage had a relatively large Δ_L compared to the Madison and Firehole drainages with almost no terminal leaders browsed (2%) the previous winter. Although the difference was not statistically significant between the Madison and the Gibbon drainages, Δ_L was a conservative estimate of the difference in longevity of terminal leaders, as the RUG was still alive when sampled. As the current terminal leaders continue to grow, Δ_L will likewise increase with the age of the RUG. Additionally, the mean Δ_L in the Madison drainage was influenced significantly by one particular aspen stand that may not have been representative of changes in elk abundance/distribution for the Madison headwaters elk herd (see following discussion of Madison drainage). As further evidence that the observed decrease in browsing pressure was related to the elk population decline in the Gibbon drainage, the average year of origination of the RUG for aspen in the Gibbon drainage was between 2000-2001, the timing of which corresponds well with the establishment of the first wolf pack in the study system and the subsequent elk population decline in the Gibbon (Figure 4.9).

Whether or not a decline in browsing pressure resulted in a DMTC, whereby increasing numbers of aspen are growing through the browse zone, is not yet known. While the results provide evidence for modest increases in aspen height due to a decline in browsing pressure, aspen in the Gibbon drainage did not exhibit profuse leader growth in response to a release from intense browsing pressure, as was observed in other trophic cascade studies in the GYE involving aspen (Ripple and Beschta 2007, Halofsky et al. 2008), willow (Ripple and Beschta 2006, Beschta and Ripple 2010), and cottonwood (Beschta 2005). H_{BCYG} for aspen in the Gibbon remained well within the browse zone

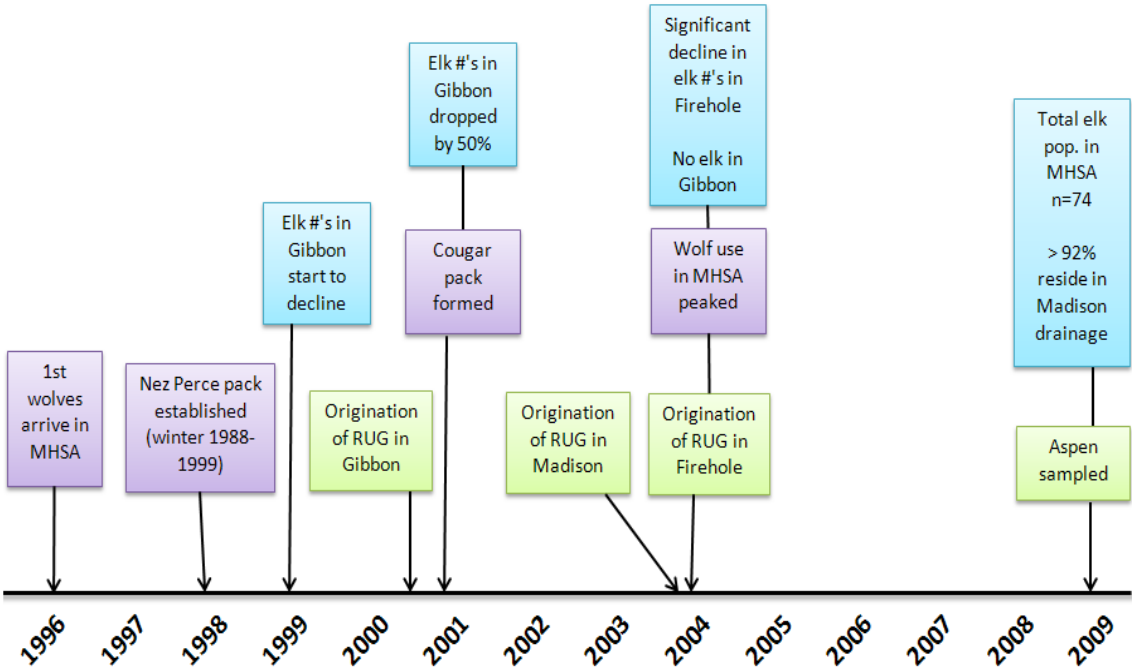

Figure 4.9: Timeline depicting the temporal relationship of wolf use (Smith et al. 2009), change in elk abundance and distribution (Garrott et al. 2009a, White et al. 2009), and the average year of origination for the RUG of aspen in each of the three river drainages (Firehole, Gibbon, Madison) following wolf recolonization of the MHSA.

(mean= 102.5 cm), increasing its height above the tallest dead cluster by only 46.8 cm, on average, over a period of eight to nine years since browse pressure declined (Figure 4.9). This is a relatively slow growth rate for aspen (Despain 1990). At the current growth rate of 11 cm/yr (mean L_{PYG} for aspen in the Gibbon drainage, Summer 2009), it would take another 10 years, approximately, for the current leaders to grow > 200 cm. Additionally, the drainage-wise difference in plant height does not correspond with predictions for a DMTC, for which you would expect aspen heights in the Gibbon drainage to be significantly taller than those in the Madison drainage. There was no significant difference in height between the Madison and Gibbon drainages (Figure 4.6) and productivity was similar across drainages, with regards to shoot elongation (Figure 4.8).

Rather, drainage-wise height differences were better explained by stand origins. Most of the aspen stands in the Firehole drainage originated from a seedling establishment event following the 1988 fires in YNP, while the majority of stands in Madison and Gibbon drainages were primarily clonal in origin, predating the fires. The superior height growth observed for aspen suckers in the clonal stands is likely a result of parent roots subsidizing productivity (see Chapter 2, this volume).

According to trophic cascade theory (Lima 1998, Schmitz et al. 2000, Schmitz 2004), if aspen height growth and recruitment is primarily limited by intense ungulate browsing, as is suggested by much of the scientific literature surrounding historic aspen recruitment in the GYE, then aspen should increase in height, trending towards recruitment, in response to a decline in browsing pressure. Why then did aspen in the MHSA not exhibit significant height growth in response to a major reduction in browse pressure? One possible explanation is that browsing is not the dominant limiting factor and that aspen in the MHSA are bottom-up regulated, most likely as a function of site productivity. Browsing is certainly not the only factor regulating plant growth and the dominance of top-down versus bottom-up controls for a given species assemblage likely varies with environmental conditions (Hunter and Price 1992). In a factorial experiment on post-fire aspen growth, Renkin and Despain (1996) found that aspen root biomass differed significantly between wet and dry sites and was a good predictor of post-fire growth responses. They reported the height of aspen suckers 5-7 years following a burn treatment to be 30 cm for the tallest suckers growing at sites with the lowest root biomass, whereas sites with the greatest root biomass produced suckers up to 4 m. The

authors commented that prolific aspen growth at marginal sites was dubious, even if elk densities were extremely low. This is a relevant consideration for aspen in the MHSA.

Aspen in the MHSA were found to occupy a relatively narrow landscape position where growing conditions are likely in the margins of this species' ecological amplitude. Long severe winters with short growing seasons that are hot and dry are typical in the MHSA. Additionally, the majority of the forested area is dominated by lodgepole pine growing in rhyolitic soils that are poor in nutrients and water holding capacity (Despain 1990 – See Chapter 2 this volume for a more detailed description of environmental attributes associates with aspen stands in the MHSA). L_{PYG} for aspen in the MHSA was very small (mean= 11.7 cm) for a species known to grow > 1m in a single growing season (Despain 1990, Renkin and Despain 1996, Chapter 2, this volume), and did not vary significantly across drainages. Thus, aspen in the MHSA may not have had the available resources for profuse growth in response to a release from intense browsing as would aspen growing in a highly productive site.

It is possible that climate may have negatively affected aspen productivity, attenuating any profuse growth response to a release from browsing pressure. Climate studies have demonstrated a trend towards a warmer drier climate in YNP (Balling et al. 1992a, 1992b) and a major decline in snowpack in the Rocky Mountain West over the past 30 years (Pederson et al. 2011), a trend that may induce environmental stress for plant communities. However, a dendrochronology study of the climate-growth response for mature aspen trees in the MHSA revealed that productivity increased modestly over the past 70 years with the period of greatest productivity (1994 – 2001) occurring

concurrently with wolf reintroduction (Chapter 3, this volume). Given that the MHSA occurs at relatively high elevations and experiences severe winter conditions and a short growing season, a warming trend may be more likely to enhance aspen productivity by extending the growing season.

The results from this research are consistent with the hypothesis of a DMTC, in that a dramatic decline in elk abundance resulted in increased longevity of current terminal leaders and modest increases in height. However, these results provide only weak support for a DMTC, whereby predators indirectly alter the distribution and composition of vegetation on the landscape through direct interactions with their prey (Polis 1999). The magnitude of the growth response for aspen in the MHSA was such that the reduction in browse pressure is not likely to elicit significant changes in the amount or quality of aspen habitat in the MHSA in the near term. Although aspen are rare in the study system, they provide an important habitat on the Rocky Mountain landscape for a diversity of wildlife and understory vegetation (Mueggler 1988, DeByle 1985). Aspen in the MHSA appear to be more strongly regulated by factors related to site productivity than by ungulate browsing, and are more likely to persist in the form of a perennial shrub (Despain 1990), rather than develop a significant canopy structure.

The results from this study are consistent with the theory that plants growing in highly productive sites are more likely to respond to a release from herbivory than plants growing in marginal sites (Fraser 1998). Recent studies of willow on the NWR have demonstrated a greater tolerance for herbivory with an increased ability to compensate for tissue loss on sites with greater access to water, and concluded that the patchy

distribution of willow recovery on the NWR is a result of an interaction between top-down controls (herbivory) and bottom-up regulation (water, in this case) on plant growth (Johnston et al. 2007, Bilyeu et al. 2008, Tercek et al. 2010, Johnston et al. 2011). A similar relationship was observed for aspen tolerance to defoliation across a gradient of nutrient availability, where aspen with greater access to nutrients were better able to compensate for tissue loss (Stevens et al. 2008). Bilyeu et al. (2008) posited that the landscape exists as "a mosaic of areas differing in recovery potential" with the greatest potential occurring where browsing pressure is the lowest and access to resources is greatest. The threshold at which declining browse pressure (be it mediated through behavioral or density effects) elicits a growth response in woody vegetation is likely to vary among stands along a gradient of abiotic factors. If this concept is realized in the GYE, where individual stands are responding differently to the same density of herbivores, then the differential rate of woody plant recovery across multiple sites may be mistaken for a BMTC related to landscape attributes. This interaction between bottom-up and top-down controls is likely to be operating in the MHSA. While the present study did not directly test for plant growth responses across a gradient of productivity, a virtual elimination of elk from the Gibbon drainage did not elicit a substantial plant growth response, suggesting that the growth potential for aspen throughout the MHSA is more strongly regulated by bottom-up forces. Further investigation would be required to identify the suite of abiotic limiting factors, as this study did not adequately account for bottom-up controls to detect this interaction.

It is interesting that drainage-wise averages for Δ_L were all positive. All three drainages had an average RUG of > 5 years, indicating that browsing pressure has been light-to-moderate since ~2004. Although this recent uninterrupted growth corresponds well with the timing of declines in elk abundance in the Firehole and Gibbon drainages (Figures 4.2 and 4.9), elk numbers in the Madison drainage did not decline below pre-wolf levels until much later. Browsing pressure was predicted to remain at or, near pre-wolf levels in the Madison drainage. Contrary to this prediction, aspen stands in the Madison drainage had a Δ_L significantly different from zero (p= 0.007) and had the greatest within-drainage variability in Δ_L. What explains the variability in Δ_L in the Madison drainage? It may be intuitive to suggest that, since the Madison drainage is home to the remaining elk in the study area, there may be a BMTC operating there. However, upon further investigation, it was revealed that one stand in particular had a large Δ_L, contributing significantly to the variability. This stand (Stand 23, see Table 2.1 in Chapter 2, this volume) was located at a high elevation site on top of the Madison Plateau in an area not typically occupied by cow elk from the Madison headwaters herd. This area has been observed to be used primarily by bull elk prior to wolf reintroduction (R.A. Garrott, Montana State University – *personal communication*), an observation that is consistent with the theory of ungulate sexual segregation where males and females occupy different sites outside of the breeding season (Bowyer 2004). It is likely that this site was previously occupied by bulls that either died from predation or abandoned the site in response to wolf presence, and has since remained relatively free of herbivory pressure. Given that elk in the MHSA exhibited strong site fidelity (Gower et al. 2009c)

and that no marked cow elk were ever located within 1.5 km of this stand throughout the duration of the study (pre-wolf and post-wolf, *unpublished data*), this site may not be representative of changes in elk abundance, distribution, and behavior for elk occupying the Madison drainage as they relate to aspen growth and browse pressure. However, Δ_L was still significantly different from zero with stand 23 censored (t= 3.16, p= 0.010 from a one-sample t-test), although the magnitude of the response (mean Δ_L= 1.35 years) may be biologically insignificant. A Tukey's Honest Significant Difference *post hoc* multiple comparison procedure for a drainage-wise difference in Δ_L resulted in a statistically significant difference in Δ_L between the Madison and Gibbon drainages when Stand 23 was censored (difference = -1.87, CI -3.50 to -0.25, p= 0.022).

While this discovery may explain some of the variation in Δ_L in the Madison drainage, does not account for other stands in this drainage with a higher than expected Δ_L. Two other stands with a large Δ_L were close in proximity to one another in an area characterized by dense lodgepole regeneration and deep winter snowpack. This area was located in a wide section of a predominantly narrow canyon, further away from the river than most other stands in the Madison drainage. A common defense strategy for ungulates being attacked by wolves is to run to rivers or other water bodies (Crisler 1956, Nelson and Mech 1981), a tactic commonly observed for elk in the MHSA (White et al. 2009). The combination of deep snow and being far from the only functional refuge (river) likely made elk using this area highly vulnerable to predation by wolves (Dunkley 2011). Elk may have avoided these stands following wolf establishment, resulting in decreased herbivory. Further *post hoc* analysis of radio-collared elk telemetry locations in

the Madison drainage revealed that elk locations were more concentrated near the river corridor following wolf establishment. These observations suggest that there may be fine scale behavioral shifts in elk related to proximity to refuge habitat that were not captured in previous behavioral studies. However, a more formal investigation would be required to confirm this.

Although the findings from this study run counter to other studies that found a significant growth response, the observations from this study were averaged at the stand level to characterize a stand-level response. Previous studies have focused on the tallest plants in a stand, describing them as the "leading edge" of the recovery of woody plants following wolf reintroduction (e.g. Ripple and Beschta 2007, Halofsky et al. 2008, Ripple and Beschta 2006, Beschta and Ripple 2010). A number of stems in the MHSA were found to be growing beyond the browse zone. Nearly 60% of stands had at least one current terminal leader that had been previously exposed to intense browsing that had escaped the browse zone (>150 cm, Figure 4.7, see Chapter 2, this volume, for more detailed description). Whether these stems represent the leading edge of aspen recovery in the MHSA, or are anomalies and are insufficient to replace or establish a canopy of mature trees is unknown. Kimble et al. (2011) found that the number of aspen stems successfully growing through the browse zone on the NWR was insufficient to replace the existing mature trees and that a landscape-level recovery of aspen was not evident. It is likely too soon to tell what the fate of aspen in the MHSA is, as the changes in browsing pressure have occurred only recently with respects to the scale of time on which ecological change occurs.

It should also be recognized that the scarcity of aspen in the MHSA led to small sample sizes. Additionally, the MHSA is fairly unique relative to the majority of aspen habitat in the GYE. Aspen were mostly restricted to high elevation, steep scree/talus slopes and lacked significant canopy structure that is prominent in more productive sites. Most mature aspen sampled in this study were confined to areas of coarse talus debris that likely precluded elk browsing. Although not substantial, some recruitment appeared to be occurring in these areas. Aspen growth here is likely not representative of aspen growing in other areas of the GYE. It is not surprising that plant responses to changes in herbivore pressure on the NWR are different from those in the MHSA, given that the NWR is much lower in elevation, accrues less snow, and is underlain by more fertile soils (Despain 1990).

Conclusion

This study is unique from other trophic cascade studies in the GYE in that it took advantage of data from a long-term elk demography study that was established prior to wolf reintroduction that resulted in a detailed account of how recolonizing wolves affected elk in a system where they were absent for more than 70 years prior (Garrott et al. 2009b). The data from these studies provided a well-documented gradient of elk abundance, where elk populations responded to wolf predation at the drainage level. This unique arrangement of population responses in a highly tractable study system made it possible to directly test for a density-mediated trophic cascade among wolves, elk and aspen, an unlikely scenario in natural settings. In contrast to other investigations of

trophic cascades in the GYE, a reduction in browsing did not elicit profuse aspen growth in the MHSA, although a modest increase was detected. Thus, this study provided only mild support for a DMTC following wolf reintroduction. The results from this study corroborate the conclusions of other researchers that ungulate herbivory is not the sole driver of plant-growth responses in the GYE and makes clear the need to adequately evaluate the collective influence of, and interactions between biotic and abiotic factors limiting plant growth.

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CHAPTER 5

CONCLUSIONS

This study of trophic cascades in the Madison headwaters study area (MHSA) has contributed to a growing body of literature investigating woody plant responses to the indirect effects of restoring an apex carnivore to the Greater Yellowstone Ecosystem (GYE). The results from this study have broadened our knowledge of aspen distribution and demography in Yellowstone National Park. These findings have also offered insight into how the outcome of trophic interactions can vary across the landscape by documenting aspen responses to wolf-induced changes in elk abundance/distribution in a unique area of the Park where trophic cascades have not yet been investigated.

In the second chapter, I surveyed the study area and documented the extent of aspen distribution in the MHSA for both post-fire seedling-established stands and clonal stands predating the 1988 fires in Yellowstone. These results captured a higher resolution of the distribution of seedlings on the landscape by systematically surveying the majority of the study area across environmental gradients, lending insight into what environmental conditions are associated with seedling presence and confirming the findings of previous studies. This study added another point in time to the documentation of this rare event of aspen sexual reproduction in the Rocky Mountain West. I found evidence for the initiation of vegetative reproduction among seedling-established aspen, suggesting that the new aspen colonizers may be taking hold in the MHSA and persisting. My results also suggest that aspen in the MHSA are growing in the margins of their

ecological amplitude and are likely to persist in the form of a perennial shrub, unless conditions become more favorable.

In the third chapter, I established a climate–growth relationship for mature aspen in the MHSA. I found that aspen productivity is favorable when they have experienced a cool moist summer during the prior growing season, a common trend in dendrochronology. The resulting chronosequence revealed that productivity during the last ~70 years was greatest in the decade following the 1988 fires in Yellowstone, the timing of which is concurrent with wolf reintroduction. This period of increased productivity was followed by a decline in the most recent decades, where radial growth has returned to mean levels. These results suggest that this modest increase in productivity related to climate may have acted in combination with the recent declines in elk densities to increase woody plant growth in the GYE. These results differed from other investigations of climate effects that found favorable climate growth conditions for different species in different regions of the GYE. Continued investigation will be required to adequately account for the relative influence of climate on the recent increases in woody plant growth documented in the GYE.

In Chapter 4, I was able to directly test for a density-mediated trophic cascade (DMTC). The spatial organization of elk responses in the MHSA allowed me to neatly compare aspen shoot longevity and height between sites where elk numbers remained relatively unchanged since wolf establishment and sites where elk densities declined dramatically. This was a rare and unique opportunity in that I was able to relate observations of aspen growth responses directly to a long-term data set on elk

demography spanning the pre-wolf period to wolf establishment. Having data on elk abundance/distribution/behavior with and without wolves in the system essentially created a control in what could be considered a "natural experiment". Unlike other studies of trophic cascades in the GYE that have been limited in their ability to evaluate the relative influence of density effects versus behavioral effects operating in the system, I was able to isolate the density effect in my study area. I found evidence for a significant reduction in browsing pressure in areas where elk had been virtually eliminated. This reduction in browsing pressure was accompanied by a modest increase in aspen height. However, I did not find strong support for a DMTC, whereby aspen were released from browsing pressure and are now escaping the browse zone and advancing toward recruitment. These results suggest that browsing may not be the dominant limiting factor for aspen growth in the MHSA and that aspen may be more limited by productivity. These findings agree with the hypothesis that an interplay among bottom-up and top-down forces likely results in differential plant growth responses to changes in herbivory pressure across environmental gradients. The disparity in interpretations of woody plant responses to wolf induced changes in elk abundance/distribution/behavior among different studies highlights the need for continued investigation of these interactions.

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