THESIS

WILLOW GROWTH RESPONSE TO ALTERED DISTURBANCE REGIMES IN ROCKY MOUNTAIN NATIONAL PARK: HERBIVORY, WATER LEVELS, AND HAY PRODUCTION

Submitted by

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ABSTRACT

WILLOW GROWTH RESPONSE TO ALTERED DISTURBANCE REGIMES IN ROCKY MOUNTAIN NATIONAL PARK: HERBIVORY, WATER LEVELS, AND HAY PRODUCTION

Disturbances are essential to the perpetuation of functioning riparian areas. However, with westward expansion, riparian areas, with access to water, fertile soils, and abundant vegetation, have been the target of heavy human use and alteration. Disturbance regimes in riparian areas have been modified, and, as a result, riparian systems and their associated vegetation have been in decline across the United States. The west side of Rocky Mountain National Park (RMNP) in the Kawuneeche Valley has a history of human use and landscape level modification ranging from altered elk and moose populations, hydrological modification from trans basin diversions, and a history of vegetation removal from hay production. This study sampled willow growth (height, cover, and annual growth) response to these overlapping altered disturbances in the Kawuneeche Valley. We found that the largest influence on willow growth was a high level of herbivory that could be attenuated by exclosures. Depth to water level did not significantly relate to willow growth, but a possible -100 cm water level threshold could explain conditions below which water levels would influence growth. Lastly, hay production decreased the overall presence of willows and therefore cover. Future research is needed to explain mechanisms behind these trends but the high levels of browse and decreased overall vigor of willows in the Kawuneeche Valley indicate increased management needs.

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CHAPTER ONE – INTRODUCTION: RIPARIAN AREAS, FUNCTION, AND DECLINE

1. Introduction

Riparian areas make up just 1% of the land in the Western United States (US) but provide habitat, food, and ecosystem functions that are disproportionate to their total land surface area (USDA 1996). Riparian areas are found in the low-lying areas along waterways and are uniquely situated as a transition zone between aquatic and terrestrial systems (Naiman, Decamps, & Pollock, 1993). Consequently, they exist under conditions indicative of both systems including high water levels and regular disturbances. As a result, riparian areas support diverse plant and animal communities (Naiman et al., 1993). Although these plant communities contain species such as sedges (*Carex, Eleocharis)*, rushes (J*uncus, Scirpus)*, and grasses (*Poa)*, many of the functions and features of this system can be attributed to the woody vegetation. The woody vegetation that defines riparian areas includes willows (*Salix),* aspen (*Populus),* alders (*Alnus)* and cottonwood (*Populus),* although exact composition is location dependent.

Periods of high-water levels alters the soil upon which riparian vegetation grows. Seasonal flooding deposits coarse sediment into floodplains while simultaneously eroding materials, resulting in heterogeneous soils that are able to retain large amounts of water (Appling, Bernhardt, & Stanford, 2014). Inundation of high-water levels in spring and the subsequent decrease in water level during summer results in redox reactions in soils. The presence of water can create anaerobic conditions that decompose plant litter more slowly. However, the fluctuation of wet periods and dry periods that occur during summer months produces high rates of decomposition (Xiong & Nilsson, 1997). The influence of high water-levels therefore leads to litter and debris decomposition that supports these productive systems and soil conditions that promote riparian vegetation adapted to these hydrologic conditions. In all, the proximity and influence of water make riparian areas diverse and productive.

The other condition that makes riparian areas diverse and productive is constant change caused by disturbance regimes. Categorized by the frequency, size, duration, and types of disturbances: a disturbance regime is a pattern of disturbances that occur across a landscape over a long period of time (Naiman et al., 1993). Historic disturbance regimes consist of seasonal flooding, debris flows, herbivory by ungulates and beavers, and beaver dams and ponds, among others (Naiman et al., 1993; Swanson, 1994). These disturbance regimes provide a large influx of outside energy and materials (nutrients, sediments, and debris) and create heterogeneous landscapes that make riparian systems productive and able to support large plant and animal community assemblages (Kominoski et al., 2013).

Flooding is one of the most influential disturbance regimes in riparian systems (Tiegs, O'Leary, Pohl, & Munill, 2005). Flooding in the mountains of the western US generally occurs seasonally in the spring in response to snow melt. The high volume of water associated with floods carries sediment, debris materials, and nutrients into the stream channel (Council, 2002). As water slows or encounters resistance, it deposits these materials onto adjacent floodplains. This deposition increases the productivity in riparian systems (Baniya et al., 2020). Flooding deposits materials while simultaneously removing vegetation and eroding streambanks, creating new areas for seedling germination and plant establishment (Riis, Baattrup-Pedersen, Poulsen, & Kronvang, 2014). The dynamic of deposition and erosion contributes to the heterogeneity of these landscapes resulting in different niche environments for various flora and fauna to thrive.

Herbivory is another naturally occurring disturbance regime in riparian systems, due to the high productivity of these sites. Herbivory can occur from an abundant number of animals such as elk, moose, deer, beaver, and muskrats (Ward, Maser, & Rodiek, 1983). Although the removal of material at high levels can be detrimental (Beschta & Ripple, 2009), low levels of plant removal can increase the heterogeneity of riparian systems (Naiman & Decamps, 1997). Additionally, variation in herbivory type can influence the response of the vegetation that is browsed. Beavers, for example, will remove part of a willow near the base of the plant, stimulating new growth (Baker, Ducharme, Mitchell, Stanley, & Peinetti, 2005).

Beavers disturb the landscape not only by cutting down vegetation for food and shelter but also through the building of dams. Beavers dam water to create safe passage through riparian areas: the resulting beaver ponds provide a location to store food and opportunity to avoid predators (Żurowski, 1992). Damming raises water levels which can result in overbank flooding that increases lateral stream connectivity (Laurel & Wohl, 2019). This results in water spreading across the landscape, around the sides of dams, creating a multi-threaded channel system. The resulting small channels spread water farther throughout a floodplain than a single larger channel could (Westbrook, Cooper, & Baker, 2006).

Riparian areas and the associated woody vegetation provide abundant ecosystem functions. Woody vegetation, in particular, provides wildlife habitat both as cover from predation and heat but also as a source of food. Vegetation shade streams serving to decrease temperatures of waterways, essential for fish spawning and rearing. The roots of woody vegetation stabilize stream banks, reduce water speed, and remove pollutants (Council, 2002; Naiman & Decamps, 1997). In some areas 80% of animal species rely on riparian areas for at least one part of their lives (Krueper, 1993). Beaver for example need access to food and building materials such as willows that grow generously in riparian areas. Although riparian areas are pivotal to many species and to ecosystem function, they are declining in response to human land use.

1.1 Altered disturbance regimes and riparian decline

For the same reasons that riparian systems are important to ecosystem function and many species of flora and fauna, they are also valuable to humans. High plant and soil productivity, access to water, and presence of abundant wildlife have drawn people to use and settle in riparian areas. Human land use along riparian systems has historically included water diversion and damming, clearing vegetation for agriculture and housing, and stream channelization (Benke, 1990; Giling, Grace, Thomson, Nally, & Thompson, 2014). The result of these human influences is altered disturbance regimes that subsequently lead to a decline in riparian systems (Brinson, Swift, Plantico, & Barclay, 1981) and the plant communities that rely on them (Fesenmyer, Dauwalter, Evans, & Allai, 2018). A realization of the importance of these systems followed by the change in the valuation of riparian areas since the 1970's has led to an increase in land management towards restoration (Goodwin, Hawkins, & Kershner, 1997).

Within the last 50 years, the goals of land management agencies in the United States (US) have pivoted from managing riparian systems for human use towards process based restoration (Elmore & Beschta, 1987). US land management agencies, such as the Bureau of Land Management, the US Fish and Wildlife Service, and the National Park Service, manage around 50 % of western lands in the US. Agencies are therefore in a unique position to manage large amounts of land occupied by riparian systems. Historically, riparian areas were seen as areas of productive human use and therefore management involved modifying these systems for use in farming, livestock grazing, and water storage (Johnson & Jones, 1977). However, along with the environmental movement of the 1970's, a change occurred in the public's interest in retaining intact ecosystems (Mcguire, 1978). The result of the change in land use goals by these agencies has led to long-term monitoring, vegetation restoration goals, and continued research of riparian systems. Some of this research had identified land use changes as a primary cause of declines in riparian systems and vegetation. The identification of the impacts of these changes is critical to inform future land management.

CHAPTER TWO -- WILLOW GROWTH RESPONSE TO ALTERED DISTURBANCE REGIMES IN ROCKY MOUNTAIN NATIONAL PARK: HERBIVORY, WATER LEVELS, AND HAY PRODUCTION

1. Introduction

Riparian areas have been modified by human for thousands of years but more substantially in the last 100 to 500 years (Petts, Moeller, & Roux, 1989). This has resulted in the alteration of normally functioning disturbance regimes and general riparian decline. Similar modifications have occurred in riparian areas across the world. Major modifications to these systems have included an increase in herbivory as the result of increased herbivores, altered hydrology as the result of damming, water diversions, and loss of beaver, and impacts from land modification due to agriculture such as hay production.

1.1 Altered Herbivory

Riparian vegetation is favored by ungulates and therefore highly impacted by increased levels of herbivory. Altered levels of browse are the result of introduced species such as horses and cattle, or increased numbers of native species such as elk, moose, and deer (Berger, Stacey, Bellis, & Johnson, 2001; Kay, Journal, & Mar, 1997; Opperman & Merenlender, 2000). Increased herbivory from native species is often caused by mass extinction that led to the loss of apex predators and subsequent growth of prey species population that feed on riparian vegetation (Berger et al., 2001). The impact of increased population size is compounded by decreased access to historic foraging habitats and decreased herd movement (Laundré, Hernández, & Altendorf, 2001; Theobald, Miller, & Hobbs, 1997). In multiple studies, increased browse levels have been found to lead to a decrease in riparian vegetation (Beschta & Ripple, 2016; Kaczynski & Cooper, 2015; Singer et al., 1994), seed production of riparian plants (Gage & Cooper, 2005), and therefore leading to a loss of riparian function (Beschta & Ripple, 2007; Kay, 1994). Although these studies provide insight into one part of the mechanisms affecting willow growth, more research is needed on the multiple compounding stressors affecting riparian plant communities. The influence of altered hydrology caused by water diversions, extirpation of beavers, and agriculture have also been explored as possible drivers of vegetation decrease in riparian systems (Council, 2002; Westbrook et al., 2006).

1.2 Altered Hydrology

Water developments are ubiquitous in the drier Western US to move water from areas of high precipitation to high water use. Colorado is an ideal example of this, with most of the state's population on the more arid eastern front range (Lochhead, 1987). As a result, Colorado is home to 44 trans basin water diversions, mainly located along the Continental Divide, the topographically mountainous high elevation delineation between water that flows into the Pacific and Atlantic oceans (Coleman, 2014). The ecological result of these diversions can be seen in alterations to the hydrology and plant communities along riverine systems. Among the alterations are changes in sediment flows, decreased overall flow and flooding events, increased water temperatures, and decreased plant regeneration (Ryan, 1994; Wiener et al., 2008).

Along with water diversions, the extirpation of beavers has altered hydrology across landscapes. Beavers use riparian trees and shrubs to build dams that result in overbank flooding and ponding across a landscape (Westbrook et al., 2006). The contributions to ecosystem functions from beaver and beaver dams is immense. Ponding created by dams promotes nutrient and sediment deposition, builds floodplains up higher than they would be otherwise, releases water slowly during droughts, and creates wetlands (Brazier, Puttock, Auster, Davies, & Graham, 2021; Puttock, Graham, Carless, & Brazier, 2018). Beavers also increase the connection of floodplains via canals (Pollock et al., 2014). Beavers were extirpated from most of the U.S. in the 1800's as the result of beaver trapping and eradication. Beavers were seen as a nuisance, with their dams often blocking waterway diversions and drainages (Goldfarb, 2019). A strong industry of fur trapping for fashion wear also contributed to their decline. Without the presence of beavers, dams begin to breach from lack of maintenance and streams incise and banks erode. As a result, floodplain groundwater levels go down, channels simplify, and water increases in speed (Green & Westbrook, 2009; Wolf, Cooper, & Hobbs, 2007).

As a result of both diversion and loss of beaver, water tables have declined, prompting studies on the connection between riparian vegetation and water depth. However, while two studies from Yellowstone National Park (YNP) found a relationship between water tables and willow growth (Bilyeu, Cooper, & Hobbs, 2008; Marshall, Hobbs, & Cooper, 2013), another study from Rocky Mountain National Park found no relationship (Zeigenfuss, Singer, Williams, & Johnson, 2002). A lack of consensus on the influence of hydrologic alterations could be the result of the complexity of water alterations and site-specific conditions, therefore requiring more extensive research.

1.3 Agricultural Alterations

The alteration of riparian areas for agricultural use has modified both the hydrology and vegetation of these systems. Agriculture is prevalent in riparian areas in valley bottoms due to fertile soils and water access. The conversion of riparian areas for agricultural use has occurred ubiquitously across the U.S., although conversions frequently occur along large streams (i.e. Colorado, Missouri, Mississippi rivers) (Swift, 1984). Agriculture along waterways changes hydrology through drainages and ditches causing decreased water in both minimum and maximum flow periods as well as decreasing the variation of flows in streams (Council, 2002; Poff, Bledsoe, & Cuhaciyan, 2006). Lowland farming has also led to the removal of riparian vegetation. Riparian vegetation loss, as a result of agriculture, leads to increased erosion, decreased aquatic habitat, increased low water flow periods, higher temperature, and increased water pollution (Micheli, Kirchner, & Larsen, 2004). Although research exists around the impacts of active agricultural sites, or the restoration of old sites, few studies have looked at the long-term impacts of historic willow conversion.

1.4 Research Objectives

Riparian systems are, and have historically been, in decline across the US, but recent change in agency land management goals are directing resources to improve them. The loss of riparian areas and the resulting loss of ecosystem functions have a profound impact on plant and animal communities. In response, researchers have spent considerable time and effort exploring the contributing factors that have led to this decline (Jones, Slonecker, Wade, & Hamann, 2010; Obedzinski et al., 2001; Swift, 1984). Specifically, land management agencies need research to inform management decisions. However, each locality, ecosystem, and riparian area have different historic management and a variety of site-specific factors that determine management needs. Rocky Mountain National Park (RMNP) is one of the most popular National Parks in the United States, visited by over four million people a year. However, due to decades of human influence has seen declines in riparian vegetation. In response the RMNP created *The Elk Vegetation and Management Plan*, with the goal of willow and aspen recovery and dedicated resources to explore the factors limiting riparian vegetation growth (Zeigenfuss, Johnson, & Wiebe, 2011).

This research project will examine the influence of altered disturbance regimes on riparian vegetation, specifically willows, in the Kawuneeche Valley inside Rocky Mountain National Park (RMNP). The Kawuneeche Valley is the headwaters of the Colorado River and is an ideal location for investigating altered disturbance regimes due to its long history of land use management. Reflecting the patterns of disturbances to riparian areas across the West, the Kawuneeche Valley has been impacted by increased herbivory, hay production, and altered hydrology caused by the trans-basin water diversions, loss of beaver, and agriculture. Indicative of most altered disturbances, within the Kawuneeche Valley these disturbances overlap spatially. As water levels are altered by diversions, willows are over browsed by elk and (non-native) moose. Where willows were once cleared from the land for hay production, loss of beaver dams also resulted in less suitable areas for willow revegetation. Using the Kawuneeche Valley in RMNP as a study site this research aims to analyze the effect each disturbance has on willow growth and to provide insights into management for willow recovery.

Our research objectives were to investigate:

(1) Herbivory impacts on willow growth. We hypothesized that herbivory would be negatively correlated to willow growth. In plots within exclosures (tall fenced in areas built to exclude ungulates), every willow growth metric would be greater than in the presence of herbivory.

(2) Relationship between willow growth and water table depth. We hypothesized that July average water tables would positively correlate with willow growth.

(3) The influence of past hay production on willow cover. We hypothesized that there would be a negative correlation between hay production and willow growth.

2. Methods

2.1 Project location

This study was conducted in the Kawuneeche Valley in RMNP, west of the continental divide, at the headwaters of the Colorado River. All the study sites were located in a montane ecosystem, with elevations ranging from between 2667 and 3994 meters. Average annual precipitation is 640 millimeters, and groundwater originates from snow melt that discharges from lateral glacial moraines into the Kawuneeche Valley.

Grand Ditch is a trans basin water diversion that transfers water from the west side of the continental divide from tributaries at the headwaters of the Colorado River. Built between 1896 and 1936, and approximately 14 miles long, the Grand Ditch diverts 50 % of water otherwise destined for the Kawuneeche Valley and ultimately the Colorado River (Woods, 2000). There have been multiple breaches in the ditch with the most recent in 2003 and that deposited ~36,000m^3 of sediment into the Colorado River (Rubin, Rathburn, Wohl, & Harry, 2012).

2.2 Site selection

Sites selected for this project ran the length of the Kawuneeche Valley and corresponded to altered disturbance regimes represented by increased herbivory, changes in water depth, and hay production (Figure 1). Monitoring plots were chosen from within each disturbance area

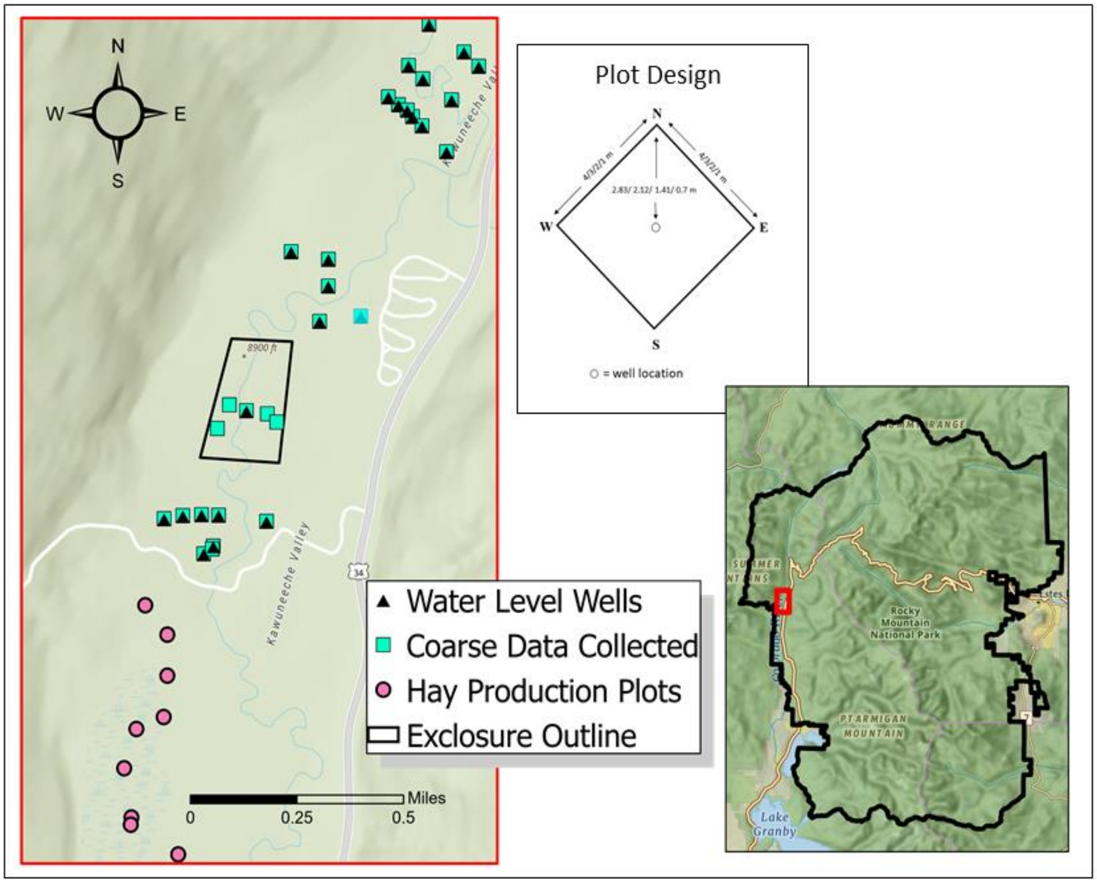

Figure 1: Section of plot locations along Kawuneeche Valley. The hay production plots identified in this section were related to historic clearing and farming by Holzwarth Ranch. The exclosure outlined is Timber Creek. Turquoise squares are coarse level plots, fine level plots were selected from among coarse plots. Wells were used as the center of plot, when available.

based on existing monitoring infrastructure from past research (such as groundwater monitoring wells or herbivore exclosures), or randomly to ensure spread of plots across the study area.

2.2.1 Herbivory

Herbivory from elk and moose is found throughout the valley, but decreased levels of browse are limited to four exclosures that were established to exclude browse. The exclosures are referred to from north to south as Colorado, Timber Creek, Onahu, and Buckaroo. Timber

Creek is the largest and most recently established exclosure built in 2011 while the other exclosures were built in the late 1990's (Kaczynski, 2013). Due to high browse levels outside of exclosures, the plots inside of exclosures were the only locations of low browse. Some browse was the result of moose and elk that could enter and exit the exclosures with high snowpack or temporarily broken fences. Sites to measure herbivory were therefore selected inside exclosures and, due to the prevalence of herbivory outside exclosures, plots to represent high levels of herbivory were chosen based on sites of other disturbances.

2.2.2 Altered Hydrology

To assess water levels, plot locations were selected from wells already established for prior research projects with coordinates supplied by RMNP research staff. Water level depths were taken throughout the month of July (n= 56 wells). Wells consisted of 1-to-2-inch diameter PVC that were drilled with holes or horizontal slots to allow water exchange between the surrounding soil and the inside of the pipe.

2.2.3 Hay Production

Active agriculture in the Kawuneeche Valley started as soon as homesteaders began to inhabit the Valley and continued into the mid 1980's. After the 1980's, hay production ceased in the Valley (Andrews, 2011). National Register of Historic Places, Grand Lake Area Historical Society, and aerial imagery provided by the United State Geological Survey were used to identify site locations of former hay production (USGS, n.d.). These sites correlated to hay production activities that occurred on former ranches and dude ranches. They included Holzwarth Ranch, Little Buckaroo, and Green Mountain Ranch/Onahu Ranch.

2.3 Data Collection

Data were collected at each plot on different scales, referred to as coarse and fine level. Coarse-level measurements represented broader plant and plot-level growth attributes (height and cover), and fine plot level measurements represented plant and stem-level growth attributes (number of shoots per stem, annual shoot growth lengths, and stem counts). All willows were measured in coarse plots, but only the three most abundant plant species were measured in fine plots: *S. monticola, S. planifolia, and S. geyeriana.* Protocols used for monitoring were modified from the Monitoring Plan for Vegetation Responses to Elk Management in Rocky Mountain National Park (MPVR) and Rocky Mountain Network Wetland Ecological Integrity Monitoring Protocol (SOP) (Schweiger, O'Gran, Borgman, & Britten, 2015; Zeigenfuss, Johnson, Wiebe, & Survey, 2015).

As defined in the MPVR protocol, plots were four by four-meter squares with the corners placed at the cardinal directions, centered around existing groundwater monitoring wells, if available (Figure 1). To maximize time, plots that had over 30 plants per 4x4 m plot were scaled down to include 30 plants or less, resulting in 3m x 3m, 2m x 2m, and 1m x 1m plots. This plot design was used across all study sites.

Percent browse followed SOP protocols, where evidence of browse was estimated over the number of total stems per plant. For example, if 10 stems of a plant with a total of 20 stems had evidence of browse, then the browse rate was 50 %.

Annual shoot growth measurements are the most robust response variable and modified from the protocols established in Bilyeu et al. (2007). Stems that represented 10 % of the plant biomass were randomly selected (usually this was represented by ~3 stems). For each of these stems the number of new shoot growths, starting from the base of the stem and moving upwards, was counted. Shoot length was subsequently measured on ten % of the new shoots. New growth was determined by terminal bud scale scars.

2.4 Statistical Analysis

All analysis was done using R software version R-4.0.3 including univariate, multivariate linear regressions, and analysis of variance (ANOVA). Growth metric dependent variables in the analysis were average height per plant per plot in centimeters, cover per plant (square centimeters) as a %age of total plot area, and annual growth per plant per plot in meters. Independent variables represented the altered disturbance regimes: presence or absence of exclosure, water level depth in centimeters, and presence or absence of historic hay production. The confidence interval for all regressions was 95 %.

The data on heights, cover, and annual growth was inherently heavily tailed as a result of the percent browse, averaging closer to 0% in exclosures and nearly 100% outside of exclosures. Data was transformed to adjust for normality and equal variance, using a log transformation where appropriate. All transformations were done on the willow growth response variable.

Height, cover, and annual growth were the independent variables in a univariate regression to relate to the presence or absence of hay production. The hay production analysis was constrained by locations in the Kawuneeche Valley that did not overlap with exclosures or well locations. There were not enough willows plants present in hay production plots to compare height and annual growth metrics. ANOVA was used to test the difference between cover inside and outside of exclosures.

A multiple regression between each growth metric (height, cover, and annual growth) was used to compare growth to the presence or absence of exclosures and depth to water table. Percent browse was not used as a metric of comparison due to the lack of independence in plots within each of the four exclosures. Instead exclosures were used as a proxy for low browse and outside of exclosure plots used to represent high levels of browse.

Willow growth measurements were taken on a plant level (plant height, plant level cover, and annual growth per plant). However, to standardize the growth metrics on each plot, plant age and species growth metrics were transformed into average plant per plot measurements. Annual growth was calculated using the average 2020 annual shoot growth multiplied by the average number of shoots on an individual stem. This stem level growth metric was then multiplied by the number of stems on that same plant. The average growth per plant across the plot was used as the comparison metric. Cover was calculated using the extents of each plant (length multiplied by the width) over the area of each plot, as a percentage. Height was averaged over each plant per plot.

3. Results

3.1 Conditions inside and outside of exclosures

Browse rates were over four times lower inside the four exclosures in the Kawuneeche Valley (Colorado, Timber Creek, Buckaroo, and Onahu) than outside (Table 1). Browse rates outside of exclosures were 93±0.46 % compared to 24±1.8 % inside. Browse was determined to be the result of moose and elk, with most plants browsed by both elk and moose together, at 59 %, while 28 % of plants were browsed by moose alone, and 2.9 % by elk alone. Differences in browse from outside of exclosures to inside explained 70 % (p-value = <0.0001) of height, 60 % of cover (p-value = <0.0001), and 50 % (p-value = <0.0001) of annual growth.

Table 1: Average and median growth metrics along the Kawuneeche Valley. Growth metrics are all greater inside of exclosures, as are water levels. Browse levels are lower inside of exclosures. The average and median browse, water level, height, and annual growth are not reported for hay production sites due to the lack of data for those metrics present on the hay production sites.

		Browse (% / plot)	**Water Level (cm / plot)**	**Height (cm / plot)**	**Cover (% / plot)**	**Annual Growth (m / plot)**
Average	Inside no hay production	24±1.8	-95±19	217±16	123±14	137±29
	Outside no hay production	93±0.46	-64±4.4	47±3.0	21±2.7	35±15
	Outside Hay Production				0.28±0.27	
Median	Inside no hay production	7.4	-104	220	123	128
	Outside no hay production	98	-63	40	13	10
	Outside Hay Production				0	

Willows growing inside exclosures were taller and larger with more growth than their counterparts not protected by fencing (Figure 2). The difference in height between willows protected by exclosures or open to browse was 170 cm, with willows inside exclosures averaging 217±16 cm tall and willows outside averaging 47±3.0 cm in height. The range of heights inside of exclosures was between 116 and 327 cm and outside exclosures was between 20 and 119 cm. Plant cover averaged 123±14 % inside exclosures and 21±2.7 % outside, a difference of about 100 %. Cover ranged from 44 to 241 % inside but did not exceed 100 outside of exclosures (0 to 94 %). There was 102 m less annual growth per plant outside of exclosures (137±29 m inside compared to 35±15 m outside). The range of annual growth was between 29 to 301 m inside exclosures and 1.5 to 401 m outside of exclosures.

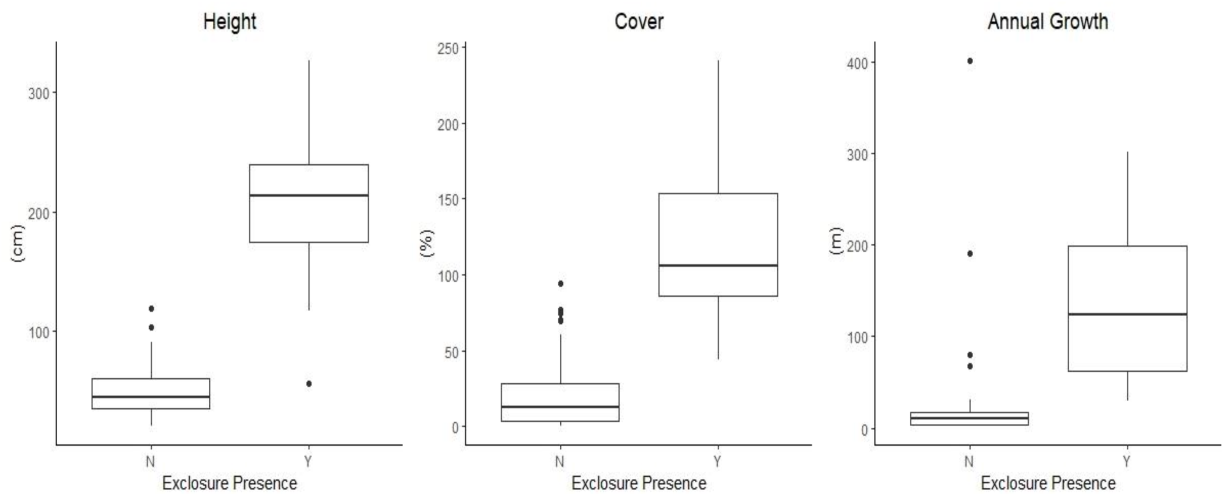

Figure 2: Comparison of average height, cover, and annual growth inside and outside of exclosures. All growth metrics were on average higher inside exclosures.

All four of the exclosures in the Valley have historically kept out large levels of browse. However, Timber Creek, the largest and most recently built exclosure (2011 compared to early 2000's for Colorado, Buckaroo, and Onahu), had the most browse (Figure 3). This is due to ungulates that have occasionally been able to enter the exclosure during periods of high snow in the winter when moose can clear the fences. Two adult moose and a calf were present inside the exclosure for the duration of the summer of 2020. As a result, Timber Creek exclosure had the highest average browse at 46±3.7 % per plant compared to Buckaroo 1.1±0.83 %, Onahu 0 %, or Colorado 25±6.7%. Timber Creek also had a higher range of browse, 0-100%, than Buckaroo (0-40%) and Onahu (0-0%). Despite this, each exclosure had higher levels of each growth metric than outside (Figure 4). Colorado and Buckaroo had the tallest average heights (279±14 cm and 223±11 cm, respectively) and Buckaroo and Onahu had the greatest cover (180±5 % and 136±8%, respectively). Colorado and Timber Creek had the greatest yearly growth (256±58 and 152±32 m, respectively).

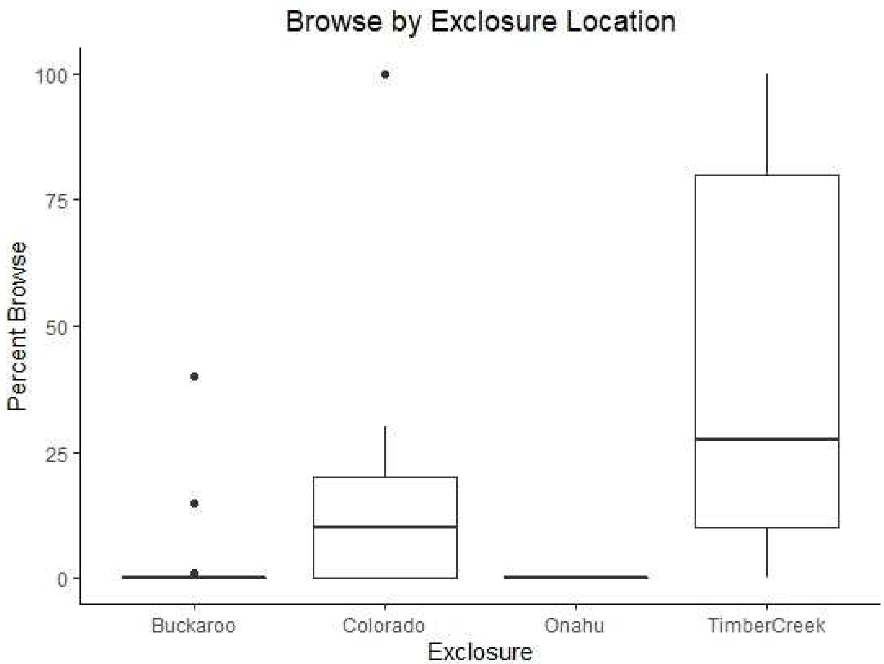

Figure 3: Variation in browse by exclosure. Timber Creek Exclosure had the highest average and largest range of browse. Onahu had no evidence of browse.

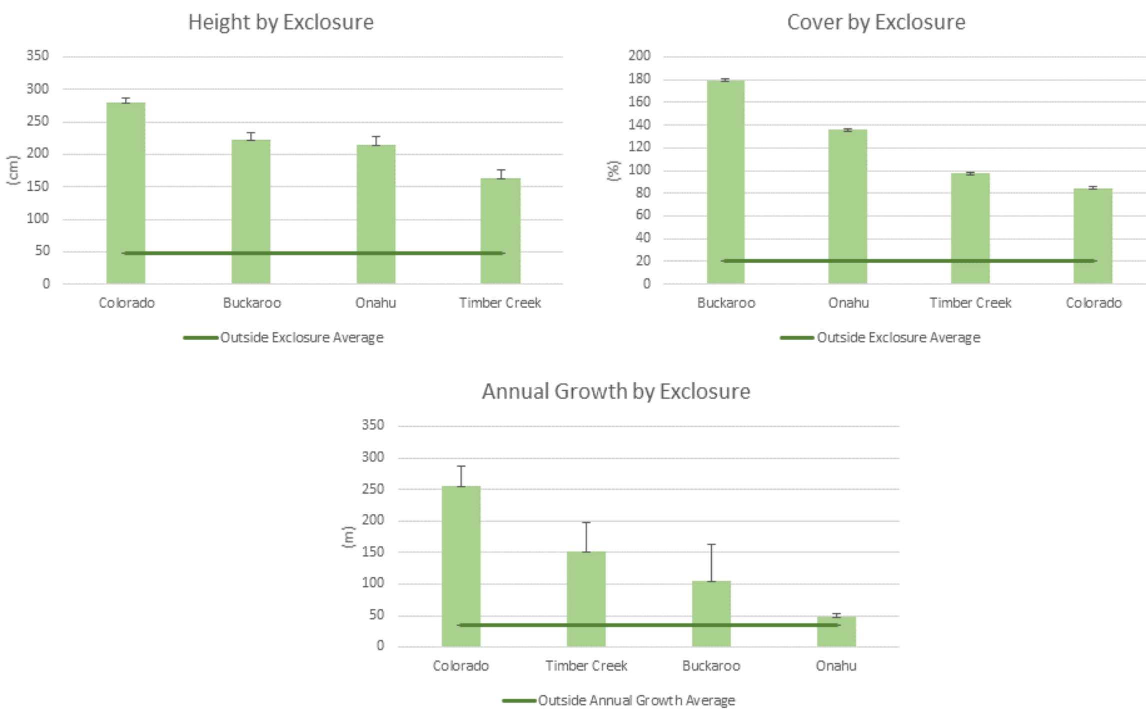

Figure 4: The difference in height, cover, and annual growth by exclosure compared to the average growth outside of exclosures. (dark green line). All willow growth metrics are higher inside every exclosure, however the annual growth inside the Onahu exclosure is the closest to the outside average.

3.2 Water Level

The average water level across the Kawuneeche Valley in the month of July was -68±4.8 cm. The variation in water levels ranged from -170 cm at the deepest to 5 cm above ground level at the most shallow. Comparing water levels to growth both inside and outside of exclosures, water level was not a significant predictor of height or annual growth. Water level did explain 60% of cover (p-value = <0.0001); however, the amount of influence was small (regression coefficient = 0.28). Although height and cover inside exclosures appears to relate to water level (Figure 5), the relation was not a statistically significant (p-values > 0.24). Annual growth and water levels were not significant at the p-value = 0.05 level overall. Water levels inside the exclosures suggested a possible trend (p-value = 0.06) but were not significant outside of exclosures (p-value = 0.25).

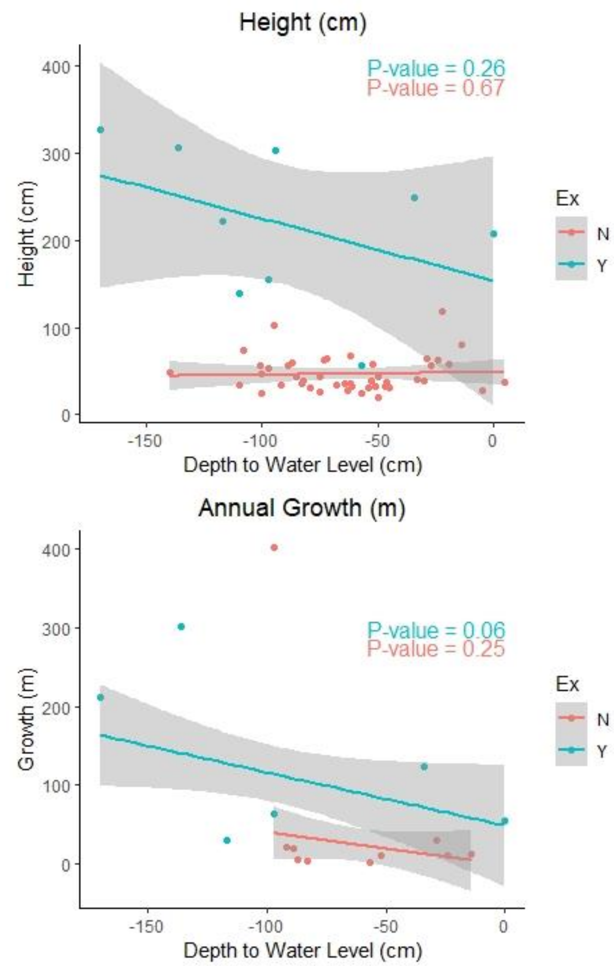

Figure 3: Depth to water level comparison for each willow growth metric. No relationships are statistically significant, although the annual growth and water level comparison shows a potential trend.

3.3 Hay Production

Hay production sites only occurred outside of exclosures and did not include enough plants to make comparisons across the Kawuneeche Valley between height and annual growth metrics. Only two of the 24 hay production plots surveyed had any willows present, totaling seven plants across all plots. Including the seven plants, the average cover across all hay production plots was 0.28±0.27%, compared to 21±2.7% in areas outside of exclosures that were not historically farmed, and 123±14% inside exclosures that had not been historically hayed. The high amount of error was due to the high occurrence of zero cover in 22 of the 24 plots. The average height of the seven plants was 52±3.2 cm, slightly above the average height outside of exclosures with no hay production (47±3.0 cm). The two plants with annual growth collected had an annual growth of 1.09 m and 13 m. 40% of cover was explained by hay production (p-value = <0.0001).

3.4 Willow Species

The highest proportion of willow species found in the Valley was of Salix geyeriana (n = 363 plants), Salix planifolia (n =279 plants), and Salix monticola (n = 170 plants), from a total of 907 plants (Figure 6). The growth forms of the three most abundant plants were similar: *S. geyeriana* height: 0.6 - 5 m, *S. planifolia* height: 0.1-9 m, and *S. monticola* height: 1.5 - 6 m (Ackerfield, 2015).

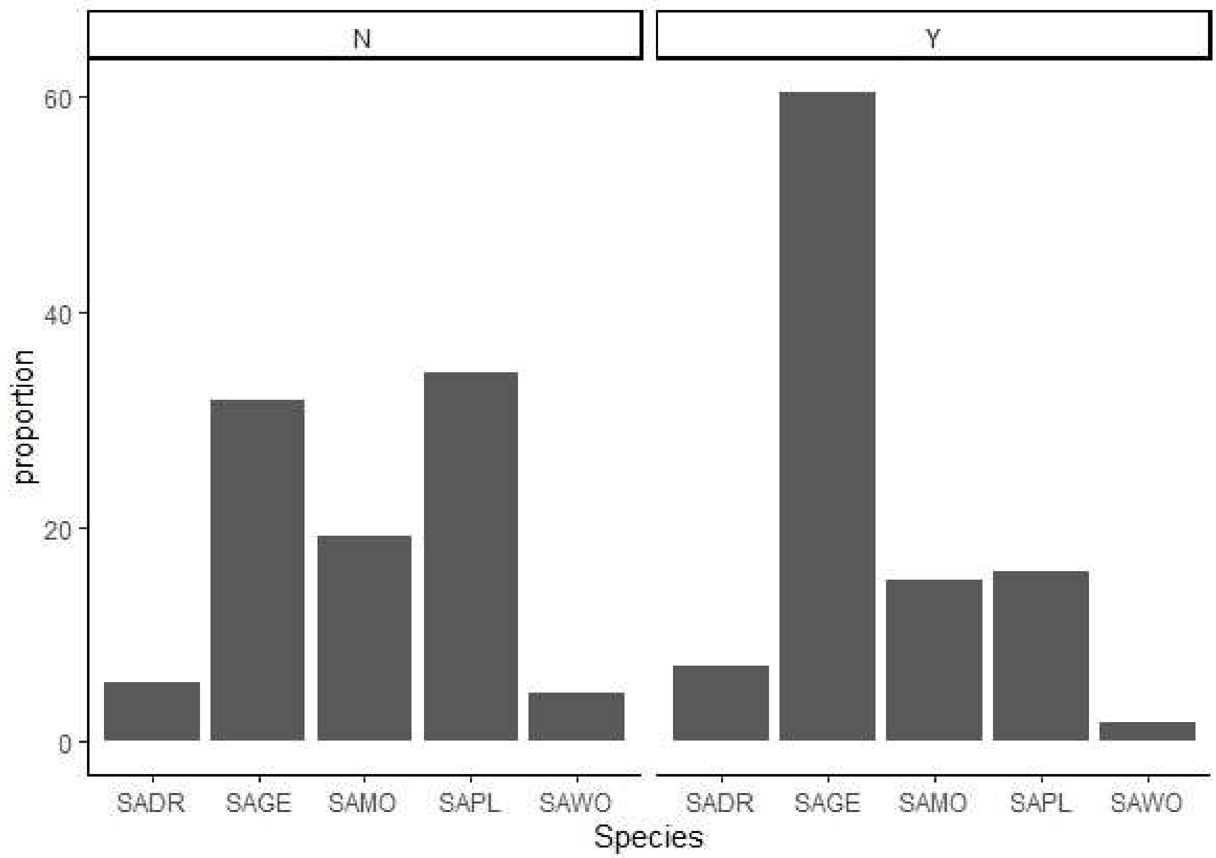

Figure 4: Proportion of species present inside and outside of exclosures. S. geyeriana is the most prevalent, by far, inside exclosures but the second most prevalent outside of exclosures. The top three species found inside and outside exclosures were the same: S. geyeriana, S. planifolia and S. monticola.

High levels of herbivory cause a decrease in height, cover, and annual growth. Willow height, cover, and annual growth both inside and outside of exclosures were not significantly explained by the depth to water, although the relationship between willows and water inside the exclosures may be stronger than outside the exclosures. Historic hay production negatively impacted total willow presence, potentially adding another consideration for willow restoration in the future.

4. Discussion

4.1 Browse

Of the three altered disturbances assessed in this study, browse was the most impactful to willow growth. High levels of browse resulted in decreased height, cover, and annual growth. The evidence of decreased growth is found in the difference in growth inside and outside of exclosures. Inside the exclosures, annual growth was 119% higher, cover was 142% higher, height was 129% higher, and overall browse rates were 118% lower. Not only were growth rates higher inside of exclosures but the relationship between browse and each growth metric was substantial. In a broader context, exclosures, which mitigated against high levels of browse, are an effective restoration treatment that result in taller, broader, and relatively well growing willows. This study faced limitations of browse gradients, with only four exclosures in the Kawuneeche Valley. However, this provides opportunities for future research around browse thresholds to willow recovery.

The influence of decreased browse and increased willow growth inside exclosures is not surprising based on prior research on exclosures and browse. The positive influence of exclosures on willow growth is well known (Brookshire et al. 2002; Dauwalter, Fesenmyer, and Miller 2018; Tucker, Schulz, and Leininger 1990). Studies done in YNP and RMNP, found that willows grew taller and with more cover inside of exclosures (Chadde and Kay n.d.; Gysel 1960; Kay and Chadde 1992; Stevens 1980). The negative influence of browse on willow growth is also well researched and confirms the large role that browse plays in this study (Beschta & Ripple, 2016). In RMNP, Zeigenfuss et al. (2002) found herbivory to have the largest impact on productivity of willow communities.

Singer et al. (1998) and Stevens (1980) provide a historic take on the influence of browse on willow growth that highlights the changing conditions of these systems. Singer et al. (1998) experimentally compared the influence of browse levels on willow height, abundance, and seed production in YNP and RMNP. They found that elk browse alone did not account for the willow declines experienced in RMNP due to better growing conditions that allowed willow plants to compensate for high levels of offtake. Favorable conditions were described by adequate access to water as the result of more precipitation, the presence of beaver and beaver dams, and, the authors concluded, probably higher water tables. In the second study, with data collected in the 1960's, Stevens et al. (1980) found increased elk were not impacting the cover and browse levels of willows in the Kawuneeche Valley, but that willows were in decline in the rest of RMNP. In the context of these two studies, in is important to consider the historic change that has occurred in RMNP. Beavers and beaver dams that might have created favorable conditions for riparian vegetation in the past, are not present in the Kawuneeche Valley. Willows that experienced low impact from browse in the 1960's have spent 40 years under pressure from increasing elk and moose populations.

Even with the shared increase in height and cover inside all exclosures, differences existed between exclosures. The most important difference could be the condition of the willow communities prior to exclosure construction. An exclosure constructed around a willow population that has already significantly declined may take longer for willows to recover than inside an exclosure that was built around a healthy willow population. The condition of the willows prior to exclosure construction is therefore important in determining whether exclosures aid in short term willow growth or maintain willow stature over time. This is especially pertinent in the Kawuneeche Valley because willows outside of current exclosures are, on average, 129%

shorter and 142% less broad. It is also important for land managers that have certain restoration goals in mind and want to know which restoration techniques will allow them to achieve their management goals. A positive outcome of creating exclosures around willows would therefore be determined by a willows ability to grow larger inside the protection of fencing in both the short and long term. Westbrook et al. (2011) cites heavy browse in the Kawuneeche Valley during the duration of their study (2003-2009). Andrews (2011) describes a history of the Kawuneeche Valley that includes concerns of over browsing from elk and moose in the Kawuneeche Valley in the 1990's (Zeigenfuss, Singer, & Bowden, 1999). Even without height and cover data from before exclosures were erected, it can be assumed that high browse pressure was present in the Valley before the late 1990's when Onahu, Colorado, and Buckaroo exclosures were erected and before 2011 when the Timber Creek exclosure was erected.

The results of this study indicate that inside exclosures height and cover growth levels are higher, and that growth is maintained over time. Annual growth represents a change in growth over a year. Even though data is limited to 2020, the elevated amount of growth inside of exclosures indicates that plants are growing taller and larger inside exclosures (growth inside 137±29 m and outside 35±15 m). This is potentially in response to decreased stress caused by browse or that willows can maintain new growth without loss from browse.

Even if the higher growth rates inside exclosures in 2020 are not indicative of a trend across all years, the higher average height and cover inside exclosures indicate that fencing protects new growth. The height and cover metrics each represent the culmination of growth over many years. It is likely that willows now enclosed were browsed prior to being protected. So, it can be assumed that, regardless of growth rate, they have grown larger since the time they were fenced in. The ability of exclosures to protect new growth from browse is relevant to the restoration of willow currently outside of exclosures. Willows outside exclosures, regardless of growth amount, cannot increase their height and cover under the current browse levels.

There are additional considerations that impact growth in relation to exclosures such as differences in exclosure location, size, year since construction, and the occasional ungulate intrusion. For example, even though Onahu had the lowest browse rate of all the exclosures, it had the lowest annual growth in 2020 (48±6 m). Suggesting that additional factors are determining growth rate. Despite this, Onahu's current height (214±13 cm) and cover (136±6%) support the idea that growth, even if small, has been maintained. Overall, the trends of this study suggest that exclosures result in net growth by both protecting willows from browse resulting in increased growth year to year and by protecting past growth over many years.

For land managers to improve riparian health and function across the western US there is a need to verify successful restoration techniques. This need is compounded by the high cost and logistical constraints of restoration that necessitate efficient restoration tools. It is therefore important for restoration of riparian areas to identify the hierarchy of restoration need across landscapes. Although past research indicates that browse is an element in riparian decline, this study identifies browse as the foremost influence and therefore directs where restoration efforts should begin. In turn, without addressing heigh levels of browse the efficacy of other restoration techniques (i.e. plantings or simulated beaver structures) might decline or become altogether nonviable. Ultimately, effective restoration should result in willows accumulating growth over time. Recovery goals are often set for willow heights at around two meters (Painter & Tercek, 2020), with the effect that tall willows also result in increased cover. Therefore, if a restoration tool allows willows to grow above two meters, it is a successful restoration technique. With average heights inside of exclosures in this study at above two meters and cover above 100%, exclosures allow willows to achieve restoration goals. Exclosures alone, and the low levels of browse that they facilitate, are therefore a singular restoration technique that can be implemented to improve riparian vegetation. Addressing the impacts of browse at the onset of willow restoration can potentially be the difference between successful and unsuccessful restoration.

Although there is strong evidence that decreasing browse results in positive willow growth, limitations of this study center around low browse gradients and exclosure infrastructure. Due to the observational nature of this study, there was a limitation in the gradient of browse levels across the valley. The only browse levels represented across the Kawuneeche Valley were high browse outside exclosures and low browse inside of exclosures, facilitated by the historic exclusion of ungulates. This low browse gradient was limited to four exclosures and did not allow for comparison of browse above the low browse (~24%) and below high levels of browse (~93%). Additionally, the size of the exclosures meant low browse represented a comparatively low percent of the total area of the valley. Three of the four exclosures in the Kawuneeche Valley were less than 3,500 sq meters while the largest exclosures, Timber Creek measured ~116,000 sq meters. The small size of these exclosures limited the sample size of low browse but also excluded observations of the larger functionality that might result from improved vegetation growth. For example, large willows should facilitate the return of beavers and the cascade of processes that results from beavers and beaver dams. However, during the duration of this study, no beaver activity was seen inside of an exclosures. This study therefore looked at the impacts of overlapping altered disturbances in the Kawuneeche Valley but not necessarily the overlapping positive impacts of browse removal.

Future research on the relationship between browse and willow growth should be centered around restoration goals. While decreasing browse was shown and has been known to increase woody riparian vegetation growth, a question that remains is how much of a decrease in browse is needed to restore riparian vegetation. Exclosures, in this study for example, historically excluded all browse (with an exception in Timber Creek in the year of data collection). This begs the question: is the complete removal of herbivory necessary for willow restoration or is there a range of decreased browse that would allow for normal growth? Expanding upon this line of reasoning, one could ask: if decreased browse levels are needed for restoration, are there other contributing factors besides just the level of browse that influence willow growth? This could include not only browse percentage but also browse intensity. It might also include considering the amount of time browse needs to be limited on a landscape, a few years or a few decades? Overall, addressing questions around thresholds: how much restoration or change is necessary to return riparian function, should be addressed to make sure that restoration goals are centered around ecosystem function.

4.3 Water Depth

Our study found that July water levels are not significantly related to height, cover, and annual growth. When the influence of water level is viewed with browse (outside exclosures) and without (inside exclosures), a potential trend seems to emerge. Without browse, the trendlines might suggest that height decreases (slope = -0.71x), cover increases (slope = 0.51x), and annual growth decreases (-0.67x) with decreased water levels. Statistical analysis does not support the significance of these trends, potentially due to a lack of real relationship between the growth metrics and water level or low sample size. The influence of water levels may be muted by the heavy browse, with any positive influence on growth from water levels removed by browse (height outside slope = 0.04x, cover outside slope = 0.05x, and annual growth outside slope = 0.41x). Even disregarding the high p-values and viewing the trends of height, cover, and annual growth in response to water level shows conflicting growth responses to decreased water levels. Surprisingly, the trends would suggest decreasing height and annual growth with increased water levels.

The complexity of water levels and willow growth in this study falls in the middle of conflicting past research. The relationship between willow growth and depth to water level has been studied in YNP and RMNP. Bilyeu et. al. (2008) found that an increase in YNP water levels improved willow height in both browsed and non-browsed sites in their four-year study. Marshall et al. (2013) elaborated on this work and found that removing browse *and* increasing water levels resulted in the largest increase in willow height and biomass over the duration of their 10-year study. In contrast, Ziegenfuss et. al. (2002) found that increasing water levels in RMNP did not have an impact on willow growth. While all these studies noted the additional roles water plays in riparian systems, each might have overlooked the importance of baseline water level depth.

Baseline water level conditions at each location in this study suggests a threshold at which water can limit willow growth when it is deeper than 100 cm. Bilyeu et al. (2008) did a manipulative study that compared a combination of browsed and unbrowsed, dammed and undammed sites. The water level across their four sites in a five-year period, averaged over May through September, ranged between -1.08 and -1.3 meters (Table 2). Dams increased water levels to between -0.71 and -1.22m. Only in 2001, the first year of the study, were water levels deeper than 1 meter (-1.22 m) after the increase in water table caused by damming. Marshall et al. (2013) completed a similar experimental study with dammed and undammed sites. Their July average water levels were -121+6 cm with dams increasing the water level to -88 + 6 cm. In both these studies, water levels were generally raised from below 100 cm to above it with damming, and both studies found the influence of water to be beneficial to willow height growth.

Ziegenfuss et al. (2002) completed a water impoundment study on the east side of RMNP in Moraine and Horseshoe Park. They had baseline conditions with water levels all above 1 m between 1995 and 1998 in their 12-site study. The average water level in the growing season (April through October) across all four years was above 1 m for both dammed and undammed sites with July water levels ranged between -0.2 and -0.8 m. Their study found water impoundments did not increase height or production of willows, citing the potentially elevated water depth as a reason for the lack of a relationship.

It is possible then that the lack of relationship between willows and water in the Ziegenfuss et al. (2002) and the complexity of the relationship between water and growth in this study is because the willows in RMNP are not water-limited due to baseline conditions of relatively high groundwater levels. Simply, the water level conditions in RMNP study are higher than those in YNP studies. Bilyeu et al. (2013) and Marshall et al. (2008), with water limited willows, observed an influence of raised water levels and willow growth because water levels were raised above a threshold with the damming treatment (Table 2). This idea is supported by Singer et al. (1998) in their study comparing RMNP and YNP, suggesting that RMNP had better growing conditions as a result of better access to water.

Table 2: Water table levels in different studies comparing growth to groundwater levels.

Study	**Location**	**Water Level Undammed (cm)**	**Water Level Dammed (cm)**	**Notes**
Bilyeu et al. (2008)	YNP	-108 to -130	-71 to -122	Water level averaged over May-Sept.
Marshall et al. (2013)	YNP	-121	-88	Water level in July
Ziegenfuss et al. (2002)	RMNP	above -100	above -100	Water level April - Oct.
Contento et al.	RMNP	-64	N/A	Water Level in July
Unpublished	RMNP	-59.4±8.46	N/A	Water Level Average in July

The study completed by Ziegenfuss et al. in 2002 was done on the east side of the continental divide. To compare similar locations, unpublished data from a pre-treatment simulated beaver dam (SBS) study in RMNP was used to provide further evidence of a willow-water threshold. In 2019, data was collected in exclosures in Horseshoe Park, Upper Beaver Meadow, and Cow Creek on the East side of RMNP. The height, cover, and annual growth data were collected according to the Bilyeu et al. (2007) protocol. Water levels in the SBS study averaged -59.4±8.46 across all the sites and ranged from -117 to 28 cm, with only one water level falling below the 100 cm threshold. The relationship between height and cover to water levels were non-significant, supporting the trends of the other three studies analyzed in this study and supporting the threshold theory.

There were two circumstances, cover in this study and annual growth in the SBS study, where water levels related to different growth metrics (coefficients 0.29 and 0.11, respectively). Water level is a point of consideration for management as a potential tool for restoration of willow communities. Therefore, the amount of influence caused by water level is best conceptualized in the context of what could happen if water levels were raised with SBS or the return of beaver to a landscape. The largest water level increase in the research considered above was 40 cm, from Bilyeu et al. (2008) in YNP. In the context of a 40 cm increase, cover in RMNP would increase cover by 10% per plant. It would also equate to a 4.4 m increase in annual growth per plant in the SBS study done on the east side of RMNP in 2019 (unpublished data). However, with the overall higher water tables in RMNP, it is not certain that water levels could rise to the same degree as in YNP. In the YNP example, water levels were raised from -1.24 cm to -0.84 cm (40 cm total). Water table averages in this study were -68±4.8 cm and on the east side were -59.4±8.46. Water levels could potentially have some influence on willow growth, but likely to a lesser degree if water levels are already high in RMNP.

A lack of relationship between water levels and willow growth could be explained by a -100 cm threshold. In the experimental studies conducted in YNP by Marshall et al. in 2013 Bilyeu et al. in 2008 they found that increasing water levels relates to an increase in willow growth. However, generally, the water levels in those studies were experimentally raised from below -100 cm, to above it. Ziegenfuss et al. (2003) completed a similar experimental study in RMNP and did not find that increasing water levels related to an increase in willow growth. The water levels in their study were all above -100 cm. Finally, analyzing data from an unpublished observational study from RMNP did not find a relationship between willow growth and water level. Water levels in all but one plot in the unpublished study fell below -100 cm. A -100 cm threshold is therefore suggested from the synthesis of these four studies. A point below which, willows are water limited and active management might be needed to restore non water limited conditions.

Each riparian area is shaped by complex geomorphic, watershed, and precipitation characteristics that define the hydrology. Understanding the interaction between the hydrology and vegetation can inform land management. This study contributes to the larger understanding of the connection between ambient water levels and in situ willow growth. Providing insight into what role water plays in the context of multiple stressors in riparian systems. Additionally, synthesizing research done by Marshall et. al (2008), Bilyeu et. al (2013), and Ziegenfuss et. al (2002), identifies a potential trend that could influence when hydrologic restoration is used, when the end goal is restoring riparian vegetation. Due to the complexity of the interaction between hydrology and riparian function there is inherent limitation of defining it by a single metric. However, the insight gained into assessing the realities of multiple altered disturbances is necessary for the complete understanding of willow growth.

The limitations of assessing the impacts of altered hydrology in this study were the result of limited infrastructure, a short data collection period (one year), and limited number of water level measurements (one in July). Due to the observational nature of the study, only already established wells in RMNP were used. Although the extent of established well locations covered a large breadth of the landscape, wells did not overlap with all the other disturbances assessed in this study (i.e., hay production). The limited well infrastructure was not just limited to location but size of the well. Some wells were not deep enough to capture water levels and limited the gradient of depths that could be explored. Although July water level has been used as a metric for comparison in past studies (Marshall et al., 2013), an understanding of the hydrologic trends across an entire year would have provided additional information on water trends as they related to willow growth. Hydrology is a complex metric to observe and defining it by one attribute can limit the scope of influence hydrology plays in this system. As a response more robust research can be done to build upon the relationship between water level and willow growth seen in this study.

Future research to explore the relationship between hydrology and willow growth should center on plant physiology and further substantiating the threshold idea presented in this research. As an observational study we did not explore physiological plant response. Therefore, future studies should observe potential water stress caused by water limitations. This could be extended to the threshold water limitation theory that was presented in this study by providing evidence of water stress below the -100 cm threshold. Additionally, deeper wells in more disparate areas across the landscape could be used to identify ideal water level conditions for willow growth. Finally, studies that observe the rooting depth of willow plants could contribute to the overall understanding of willow growth patterns, hydrology, and water limitations.

4.4 Hay Production

Land use conversion to agriculture is the most direct way that humans have modified riparian landscapes. As a result, riparian areas have not just been degraded because of agriculture, but completely lost to it. RMNP is unique in that hay production sites were abandoned but no additional human land use changes occurred afterwards. This provided an opportunity to see the unaltered impacts of historic hay production. This study found the lingering influence of hay production but did not explore the compounding alterations agriculture imparts on the soil, hydrology, and microbial communities of riparian systems. The potential to explore these avenues is therefore still open to future research.

We found the impacts of a century of hay production in the Kawuneeche Valley has resulted in a permanent decrease in willows and a lack of recovery of willow communities in areas that were actively hayed. Low willow presence across hay production sites would also indicate that willows have not been able to establish in the 60 years since the last hay production stopped. With a lack of willow presence, it is difficult to compare growth patterns of those plants that were able to return or were spared in the historic removals. This could be attributed to low germination rates (Gage & Cooper, 2005) and potentially compounded by the impacts from high browse pressure that was seen across unfenced willows in the Valley. Due to the random selection of plots, this study did not capture the few willows that were seen in these areas, most notably near Onahu ranch (Contento, *personal observation*). However, the random plots were indicative of the lack of willows seen overall across these sites.

Although it is well known that agricultural sites negatively influence riparian areas and riparian vegetation, this studied clarified the long-term impacts of unrestored hay production areas. When disturbances related to agriculture have occurred in the past, they are usually framed in the amount of loss caused by these land conversions. Alternatively, these sites are being remediated to convert them back to riparian corridors. However, few studied observe the long-term impacts of removed agriculture that is left to natural conditions. This study found that active management is needed to restore areas of former agricultural use, and that without management intervention these sites do not recover to their former vigor. This solidifies the severity of change that these systems endured and highlights the need for active management in these areas.

The limitations of studying the relationship between willow growth and hay production in this study where related to the extent of land use in the former hay production sites. Although historical accounts described the historic use of different areas across the Kawuneeche Valley, the hay production practices and the exact years that hay production occurred were not mentioned in these accounts. Additional compounding disturbances also might have occurred in these areas such as grazing, topographic modifications to the landscape, and the creation of ditches. This information would have been helpful to substantiate the amount of land use change that resulted in the decline of willow growth in these areas.

Hay production usually does not occur on the landscape independently—land modification usually occurs concurrently. Understanding the impacts of not just hay production, but the extent of soil compaction, loss of microbial communities, or change in soil substate could be explored. Understanding these additional variables might help with identifying the correct restoration approach or create categories of land alteration severity for identifying where restoration is most needed. Additionally discerning what land management tools are needed to restore these areas could also be explored. Determining not only the factors that contribute to decline, but also what influences regrowth are important considerations in riparian areas.

5. Management Recommendations

RMNP implemented the *Elk and Vegetation Management Plan* to establish monitoring and long-term goals for increasing willow and aspen growth inside the park. The goals of this management plan include "at least 31% willow cover within suitable willow habitat across the winter range" and "average willow height of at least 1.1m" (Zeigenfuss et al., 2011). To achieve these goals, RMNP needs to decrease the impacts of browse in the Kawuneeche Valley. Exclosures clearly mitigate the influences of high levels of browse, not only to temporarily decrease the effects of browse but also to allow willows to maintain their growth over time. This allows even small amounts of growth to result in larger willows over years. Other methods such as raising water tables with simulated beaver dams have been suggested as a restoration option for increasing willow growth. Although beaver dams contribute additional functions besides raising water levels, this study did not find a strong influence from increasing water levels without the removal of high levels of browse. Although potentially overlooked, former hay production sites along the Kawuneeche Valley are in the most dire need of restoration, with willows barely present in those areas. Based on the research done in this study that found current average height in the Kawuneeche Valley to be 0.47 m and cover to be 21% outside of exclosures, additional measures appear to be needed to reach park goals.

6. Conclusion

Maintaining willow growth is necessary for proper riparian function and is therefore of concern for land managers in areas where willows are experiencing multiple stressors. To address this concern in the Kawuneeche Valley of RMNP, this study collected data on willows that had experienced growth under different altered disturbance regimes. This research found that exclosures are an effective treatment that protected against the effects of browse and resulted in tall, broader, and relatively well growing willows. Exclosures were also effective in decreasing browse from moose and elk and maintaining willow growth over the long term. While raising water tables has been a suggested management technique for willow restoration, this study suggests that the depth to water level does not limit willow growth above 100 cm. Although, it should be noted that raised water tables contribute more than just elevated access to water to plant roots in the broad view of ecosystem function. Lastly, the negative impacts of agriculture on native vegetation are well known but few studies observe the result of unrestored long-term historic hay production on riparian systems. This study found that hay production sites in the Kawuneeche Valley have not recovered from willow removal and landscape changes from agriculture land conversion. Overall, this study provides insights into the effects of altered disturbance regimes that can be used by land managers in RMNP specifically, but which can be applied to riparian systems across the west that are experiencing multiple stressors at once. Future research should look at the longer-term mechanisms that have created current willow communities.

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