Spring 5-11-2013

Effects of herbivory as an ecological constraint of willow growth at a restored riparian corridor

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This Master's Thesis

EFFECTS OF HERBIVORY AS AN ECOLOGICAL CONSTRAINT OF WILLOW GROWTH AT A RESTORED RIPARIAN CORRIDOR

by

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is submitted in partial fulfillment of the requirements

for the degree of:

Master of Science

in

Environmental Management

at the

University of San Francisco

Submitted:		Received:	
12/1/2014		12/9/14	
Jacqueline A. McCrory	Date	Gretchen C. Coffman, PhD	Date

Abstract

A critical component of nearly all riparian restoration projects is the rapid successful recovery of native vegetation. The dynamic conditions and diverse biotic community supported by riparian ecosystems can present numerous constraints to restoration efforts. This study investigated stunted growth of arroyo willow (*Salix lasiolepis*) cuttings planted along the banks of Redwood Creek as part of the National Park Service's Muir Beach Restoration Project to restore habitat for special status species in California. Based on observations of deer browsing, as well as signs of extensive biomass removal, I designed a field experiment using exclusionary fencing to test the significance of deer browse on growth of recently planted willows. My study design consisted of measuring the difference in growth (height, mean canopy diameter, estimated aerial percent cover, and volume) in relation to three factors (exclusionary deer fencing, side of bank, and willow age) during the 2013 growing season. Results of my study indicate that deer herbivory was a critical stressor contributing to limited growth of recently planted willow cuttings along the restored banks of Redwood Creek. The main effect of exclusionary fencing was very highly significant for all four growth metrics; however, it had the greatest beneficial effect on younger willows in their second growing season along the right bank. Exclusionary fencing can be used as a cost-efficient method for restricting browsing by wild herbivores at riparian restoration sites, most effective when implemented for protecting willows during their first two growing seasons or until they are resilient to the effects of herbivory.

Key words: exclusionary fencing, deer, herbivory, Redwood Creek, *Salix lasiolepis*

Introduction

Riparian systems in the western United States have undergone widespread, intense modification and degradation due to land-use change, extraction of surface water and groundwater, and river impoundment (Naiman et al. 2002; Postel and Richter 2003; Revenga et al. 2005; Pearce 2007). The physical alteration of these habitat types has largely contributed to the loss of native riparian forests, such as willow (*Salix* spp.) communities, to the extent that they are considered one of the most threatened forest types in the United States (Swift 1984; Busch and Smith 1995). While native riparian vegetation accounts for less than one percent of land in the western United States (Knopf et al. 1988), it is essential for supporting species diversity and ecosystem function throughout the surrounding ecosystems (Gregory et al. 1991; Naiman et al. 1993). Due to loss of critical ecosystem services, habitat and special status species that rely on these habitats, riparian ecosystems have increasingly become the focus of restoration throughout the United States in the past 40 years, especially along the Pacific coast in California (Palmer et al. 2007; Heinrick et al. 2014).

Successful, expeditious re-vegetation of native riparian species is a critical component of most riparian restoration projects. Native woody riparian species typically grow quickly and support the ecosystem by stabilizing streambanks (Johnson 2003; Gray & Barker 2004), increasing root density for erosion prevention (Wynn et al. 2004), and establishing channel vegetation structure for faunal habitats (Copeland et al. 1996; Young & Clements 2003). Woody riparian species also provide valuable ecosystem services by increasing retention of flood water, reducing sedimentation, regulating temperature by providing shade, and improving water quality (Karle & Densmore 1994; Hupp & Osterkamp 1996; Bernhardt et al. 2007; Corenblit et al. 2007; Sudduth et al. 2007; Dosskey et al. 2010). Willow species in particular are valuable in the re-vegetation of riparian ecosystems in the United States (Kuzovkina and Quigley 2005). However, restoring riparian vegetation can be a challenging process. The dynamic nature and diverse assemblage of plants and animals typically present in riparian ecosystems can pose site-specific ecological challenges for successfully restoring riparian vegetation.

When restoring riparian ecosystems, it is important to consider not only anthropogenic constraints, but natural constraints as well. Plant-animal interactions for example, while naturally-occurring, can have significant detrimental effects on riparian ecosystems. Excessive grazing by livestock and wild herbivores in particular, has contributed to the worldwide degradation of riparian ecosystems (Robertson & Rowling 2000; Jansen & Robertson 2001). Browsing by large herbivores can degrade aquatic habitats to the extent that they are no longer capable of supporting the fish and amphibious species that rely on them by altering stream morphology, reducing the density of vegetation which regulates water temperature, and increasing sedimentation through bank erosion (Armour et al. 1991; Platts 1991; Belsky et al. 1999; Kauffman et al. 2001; Brookshire et al. 2002). In some cases, intense grazing by wild herbivores during the summer season has been shown to completely eradicate populations of woody plants (Maschinski 2001; Olofsson et al. 2001).

Grazing by wild herbivores is not exclusively detrimental to the growth and survivorship of riparian vegetation. Several studies have demonstrated the ability of plants to tolerate the stress of browsing and overcompensate by increasing photosynthesis (Poveda et al. 2010; Fornoni 2011). However, the majority of the existing research indicates herbivory has a negative effect on plant growth and reproduction (Morris et al. 2007; Chun et al. 2010; Oduor et al. 2010). Frequent removal of woody stems and foliage by herbivores over time can result in the reduction of the carbon reserves below the ground surface, thereby preventing natural defense mechanisms including chemical resistance and rapid vertical growth, rendering the plants more susceptible to browsing (Wagner et al. 1995). Morphological and physiological responses to browsing by plants can vary depending on the type of herbivore as well as the frequency, intensity, and season by which browsing occurs (Danell, Huss-Danell & Bergström 1985; Danell, Bergström & Edenius 1994).

The species, age, and physical stature of plants can also influence the effects of herbivory (Edenius, Danell & Bergström 1993; Baker and Walford 1995). Willows for example, typically demonstrate early rapid growth and grow to a maximum of approximately 10 meters in height, with most branches suitable for browsing being inaccessible to most large herbivores after only a single growing season (Shields et al. 1995; Bergström & Guillet 2002). While their rapid growth makes willows resistant to browsing, cuttings are highly susceptible to intense browsing during the first few years after being planted (Bergström & Guillet 2002). Recently planted willow cuttings are typically small in size with the majority of their biomass physically accessible to large herbivores, and are typically high in nutritional content as they prioritize rapid production of photosynthetic material over chemical defense mechanisms (Driebe & Whitham 1998; Ball, Danell, & Sunesson 2000). Therefore, while willows are frequently used when restoring riparian vegetation, there are many factors to consider when herbivory is a potential stressor.

Frequently, maintenance activities are necessary to facilitate successful re-vegetation following the completion of restoration activities (Massingill 2003). Particularly when browsing is recognized as a potential stressor, actions for protecting restored vegetation from herbivores may be required to prevent or reduce the stress of browsing and allow unobstructed growth (Sweeney et al. 2002; Pollock et al. 2005). Methods for shielding riparian vegetation from the effects of browsing range from removing browsing entirely from the ecosystem in the case of livestock, using fencing or alternate material to restrict browsing from portions of the ecosystem, or implementing a controlled management plan which permits browsing to an extent which would not be detrimental to the establishment and growth of new vegetation (Platts 1991; Elmore 1992; Medina et al. 2005). Many studies have demonstrated increased survivorship, growth, seed production and abundance of newly planted woody cuttings following the exclusion of herbivores (Briggs et al. 1994; Briggs 1995; Cooke & Lakhani 1996; Green & Kauffman 1995; Kauffman et al. 1995; Moen & Oksanen 1998; Shaw 2006). The use and success of protective methods for excluding browsing vary based on site conditions and the form and extent of herbivory; however, most utilize the exclusionary fencing method to promote passive recovery of riparian vegetation (Roni et al. 2012).

This study evaluates the effect of browsing by wild herbivores on recently planted willow cuttings and tests the effectiveness of using exclusionary fencing as a method for restricting herbivory to facilitate plant growth at a riparian restoration site. Abnormal growth patterns were observed among willow cuttings after being planted as part of a restoration project at a riparian corridor in coastal California. Exclusionary fencing was employed as a method for restricting access to the willows by herbivores to determine if browsing was having a significant detrimental effect on the growth of recently planted willows. I hypothesized that the installation of exclusionary fencing and removal of herbivory as a stressor on the willow cuttings would yield a greater difference in growth over the growing season than unfenced willow cuttings that remained exposed to browsing by herbivores.

Methods

Study Location

In Marin County, California, a 46-acre restoration project at Big Lagoon and Redwood Creek at Muir Beach ("Restoration Project") was initiated in 2009 and completed in 2014 by the National Park Service Golden Gate National Recreation Area (GGNRA). Historically, the area had undergone extensive landscape modifications which diverted the natural flow of the creek, filled Big Lagoon, reduced water flows and altered the creek and lagoon. Critical habitat for federally listed Coho salmon, steelhead trout, and California red-legged frogs (*Rana draytonii*) was lost (Madej et al. 2006). Restoration goals included the re-establishment of self-sustaining, functional riparian and lagoon ecosystems; enhancement of viable habitat for sustainability of populations of several special status species; reduction of flooding on surrounding roadways; and facilitation of a compatible visitor experience in the coastal National Park (Jones and Stokes 2007; PWA 2003, 2004). In an effort to restore habitat for these species at Redwood Creek, off-channel habitat was created for juvenile Coho salmon, natural creek alignment and floodplain connectivity were restored, the backbeach tidal lagoon was enhanced, and the channel was revegetated with native wetland and riparian plants.

Planting woody riparian species, including *Salix lasiolepis* (arroyo willow) cuttings, along the banks of Redwood Creek was a key component for restoring ecological functioning and sustainability of the riparian ecosystem. Successfully re-vegetating the banks of Redwood Creek would help stabilize bank erosion, regulate water temperature, provide habitat for many aquatic species, and repair native riparian vegetation structure (Jones and Stokes 2007; PWA 2003, 2004). Woody vegetation planted along the banks of Redwood Creek demonstrated signs of stunted growth during the first year following initial planting, indicating the presence of a stressor in the system. Based on direct observations of mule deer (*Odocoileus hemionus*) browsing on willows, as well as signs of extensive biomass removal, I hypothesized that high-frequency deer herbivory was an important stressor potentially responsible for stunted growth of the arroyo willow cuttings during their first years of growth after being planted along the restored banks of Redwood Creek. I designed a field experiment using exclusionary fencing to test the significance of deer browsing on growth of recently planted willows in their second and third growing seasons over the course of the 2013 growing season, with sampling dates on May 4-5, 2013 and on September 28-29, 2013. I chose not to study the effects of herbivory among willows in their first growing season because I suspected that willows in their first growing season could potentially be exhibiting a stunted growth response due to residual stress from being recently planted. I chose not to study the effects of herbivory among willows in their fourth growing season because they appeared to be demonstrating signs of healthy growth and fewer signs of biomass removal.

The study area for this experiment is located along a 366-meter lower reach of Redwood Creek at Muir Beach in Marin County, California (Figure 1) (Jones and Stokes 2007; PWA 2003, 2004). The study area is characteristic of a Mediterranean climate, with dry summers and mild, moist winters. Annual temperature in the vicinity of the study area ranges from an average minimum of 7.2° Celsius (C) to an average maximum of 21.4°C (Western Regional Climate Center; WRCC 2013). Average annual precipitation in the vicinity of the study area is approximately 120.4 centimeters (cm) per year, with a peak of approximately 26.5 cm in the month of January (WRCC 2013). The Redwood Creek Watershed is located within the Golden Gate Natural Recreation Area (GGNRA) and the Golden Gate Biosphere Reserve designated by the United Nations and is one of the 25 global biodiversity hot spots recognized by the Nature Conservancy. Redwood Creek is the southernmost watershed in North America with a persistent runs of anadromous Coho salmon (*Oncorhynchus kisutch*) (Pacific Fishery Management Council 2014).

Willow Growth Study Design

To determine whether or not deer herbivory was a factor limiting growth of arroyo willows at Redwood Creek, I examined willow cuttings for evidence of biomass removal and stunted growth. Based on these observations, I selected 160 arroyo willow cuttings in their second and third growing seasons, planted on the banks of both sides of Redwood Creek in 2010 and 2011 as part of the Restoration Project. I measured the difference in growth over the 2013 growing season. 80 cuttings were selected on the right bank and 80 on the left bank to determine if angle sun exposure had any effect on herbivory on the willows (Figure 1; Table 1). Exclusionary fencing was installed around half of the cuttings on both banks to compare differences in willow growth when exposed to versus protected from natural browsing by large herbivores. I created eight fenced plots and eight unfenced study plots with 10 willows in each in two study areas located along the restored riparian corridor of Redwood Creek. These plots were selected based on the age of the willow cuttings (second or third growing season), side of bank (left or right) and exclusionary fencing (fenced or unfenced), according to the design shown in Figure 1 and described in Table 1. Plots of exclusionary fencing were constructed using 3-meter tall polypropylene mesh fencing material, steel posts, and plastic zip ties. Fencing was installed using hand tools at the beginning of the 2013 growing season in April and remained in place for six months during the growing season before being removed in September. Fenced and unfenced study plots were located immediately adjacent to one another to insure all other conditions were similar.

I collected growth data for each of the 160 willow cuttings immediately following the installation of the exclusionary fencing and at the end of the growing season before fencing was removed. For each cutting, I took measurements for height of the tallest branch (cm); diameter of the canopy in two perpendicular directions (cm); and estimated aerial percent cover (%). I used mean volume (cm^3) of willow cuttings as a nondestructive estimate of aboveground biomass. Volume was calculated as the product of total percent aerial cover, height, and my quadrat sample size (1 m^2). I calculated the difference in growth between April and September for each growth metric to understand the effect of deer browse on willow growth between factors during the 2013 growing season.

Wildlife Camera Trapping Study

In addition to collecting willow growth data, I used a Bushnell NatureView remote, motion and heat sensor camera trap to confirm that deer were browsing on newly planted willows along the banks of Redwood Creek where signs of stunted growth were observed. I installed the camera facing a plot of unfenced willows in their second growing season (Figure 1). The camera was deployed for eight months, the duration of the willow growth study, between May and December of 2013. The camera was checked and photos were downloaded on a weekly basis during this time.

Statistical Analysis

I organized my statistical analysis as a full factorial design for the factors of side of bank (left and right), location of study plots (1 and 2), age of willows (2^{nd} and 3^{rd} growing season), and exclusionary fencing treatment (fenced and unfenced). First, I conducted a one-way Analysis of Variance (ANOVA) of growth metric data for study plots (Figure 1) and a one-way ANOVA for side of bank, to determine if these factors needed to be included in a multi-factorial ANOVA. I found that growth did not differ significantly between study plots, but was significantly different between the right bank and the left banks. Thus, I included side of bank in my three-way ANOVAs to analyze the interactions between three factors (side of bank, age of willows, and exclusionary fencing) and four growth metrics (difference in mean height, difference in mean canopy diameter, difference in mean estimated aerial percent cover, and difference in mean volume). All growth metric data were log transformed prior to analysis to meet assumptions of normality and homogeneity of variance.

Following each ANOVA test, I conducted pairwise comparison of means using Tukey’s Honestly Significant Difference test to analyze differences between group means. All ANOVAs were run using Systat Software (Version 13) (Systat Software, a subsidiary of Cranes Software International Ltd.).

Results

Willow Height

Overall, fenced willow cuttings in their second growing season had an approximately 61% greater increase in mean height than unfenced willows in their second growing season for all factors (Figures 2 and 3). Fenced willow cuttings in their third growing season also greater change in height than unfenced willows in their third growing season, but it was much less significant with only a 6% greater change in mean height.

Based on the results of the Tukey’s Honestly-Significant-Difference Test for growth metric mean height on the right bank, there was a very highly significant difference ($P < 0.001$) between fenced and unfenced second season willows. Fenced willows in their second growing season demonstrated a significantly greater change in height than unfenced second season willows. There was no significant difference between fenced and unfenced third season willows ($P = 0.727$) (Figure 2a). There was also a very highly significant difference in mean height between unfenced second season and fenced third season willows on the right bank (P <0.001). Fenced willows in their third growing season demonstrated a significantly greater change in height than unfenced second season willows. There was no significant difference in mean height between fenced second and third season willows on the right bank (P = 0.160).

Based on the results of the Tukey's Honestly-Significant-Difference Test for growth metric mean height on the left bank, there was no significant difference between fenced and unfenced second season willows (P = 0.636) and no significant difference between fenced and unfenced third season willows (P = 0.982) (Figure 3a). There was a very highly significant difference in mean height between unfenced second and third season willows on the left bank (P <0.001). Unfenced willows in their third growing season demonstrated a significantly greater change in height than unfenced second season willows. There was no significant difference in mean height between fenced second and third season willows on the left bank (P = 0.566).

Willow Canopy Diameter

In their second growing season, fenced willow cuttings had an approximately 58% greater increase in mean canopy diameter compared to unfenced willows for all factors (Figures 2 and 3). Similarly, fenced willow cuttings in their third growing season had an approximately 32% greater change in mean canopy diameter than unfenced willows in their third growing season (Figure 2 and 3).

Based on the results of the Tukey's Honestly-Significant-Difference Test for growth metric mean canopy diameter on the right bank, there was a very highly significant difference between fenced and unfenced second season willows (P <0.001) (Figure 2b). Fenced willows in their second growing season demonstrated a significantly greater change in canopy diameter than unfenced willows. There was no significant difference between fenced and unfenced third season willows (P = 0.464) (Figure 2b). There was a very highly significant difference in mean canopy diameter between unfenced second and unfenced third season willows on the right bank (P <0.001) (Figure 2b). Unfenced willows in their third growing season demonstrated a significantly greater change in canopy diameter than unfenced second season willows. There was no significant difference in mean height between fenced second and fenced third season willows on the right bank (P = 0.557) (Figure 2b).

Based on the results of the Tukey's Honestly-Significant-Difference Test for growth metric mean canopy diameter on the left bank, there was no significant difference between fenced and unfenced second season willows (P = 0.767) (Figure 3b). Fenced willows in their second growing season demonstrated a significantly greater change in canopy diameter than unfenced second season willows. There was no significant difference between fenced and unfenced third season willows (P = 0.070) (Figure 3b). There was no significant difference in mean canopy diameter between unfenced second and unfenced third season willows on the left bank (P = 0.993) (Figure 3b). There was no significant difference in mean height between fenced second and fenced third season willows on the left bank (P = 1.000) (Figure 3b).

Willow Aerial Cover

Fenced willow cuttings in their second growing season had an approximately 77% greater increase in mean percent cover than unfenced willows in their second growing season (Figure 2 and 3). Similarly, fenced willow cuttings in their third growing season had an approximately 25% greater increase in mean percent cover than unfenced willows in their third growing season (Figure 2 and 3).

Based on the results of the Tukey's Honestly-Significant-Difference Test for growth metric mean aerial percent cover on the right bank, there was a very highly significant difference between fenced and unfenced second season willows (P <0.001) (Figure 2c). Fenced willows in their second growing season demonstrated a significantly greater change in aerial cover than unfenced second season willows. There was no significant difference between fenced and unfenced third season willows (P = 0.992) (Figure 2c). There was a significant difference in mean aerial percent cover between unfenced second and unfenced third season willows on the right bank (P = 0.030) (Figure 2c). Unfenced willows in their third growing season demonstrated a significantly greater change in aerial cover than unfenced second season willows. There was no significant difference in mean aerial percent cover between fenced second and fenced third season willows on the right bank (P = 0.760) (Figure 2c).

Based on the results of the Tukey's Honestly-Significant-Difference Test for growth metric mean aerial percent cover on the left bank, there was no significant difference between fenced and unfenced second season willows (P = 0.888) and no significant difference between fenced and unfenced third season willows (P = 1.000) (Figure 3c). There was no significant difference in mean aerial percent cover between unfenced second and unfenced third season willows on the left bank (P = 0.840) (Figure 3c). There was no significant difference in mean aerial percent cover between fenced second and fenced third season willows on the left bank (P = 0.998) (Figure 3c).

Willow Volume

Fenced willow cuttings in their second growing season had an approximately 87% greater increase in mean volume than unfenced willows in their second growing season (Figure 2 and 3). Similarly, fenced willow cuttings in their third growing season had an approximately 35% greater change in mean volume than unfenced willows in their third growing season (Figure 2 and 3).

Based on the results of the Tukey's Honestly-Significant-Difference Test for growth metric mean volume on the right bank, there was a very highly significant difference between fenced and unfenced second season willows ($P < 0.001$) (Figure 2d). Fenced willows in their second growing season demonstrated a significantly greater change in volume than unfenced second season willows. There was no significant difference between fenced and unfenced third season willows ($P = 0.992$) (Figure 2d). There was a very highly significant difference in mean volume between unfenced second and unfenced third season willows on the right bank ($P < 0.001$) (Figure 2d). Unfenced willows in their third growing season demonstrated a significantly greater change in volume than unfenced second season willows. There was no significant difference in mean volume between fenced second and fenced third season willows on the right bank ($P = 0.972$) (Figure 2d).

Based on the results of the Tukey's Honestly-Significant-Difference Test for growth metric mean volume on the left bank, there was no significant difference between fenced and unfenced second season willows ($P = 0.888$) and no significant difference between fenced and unfenced third season willows ($P = 1.000$) (Figure 3d). There was a highly significant difference in mean volume between unfenced second and unfenced third season willows on the left bank ($P = 0.004$) (Figure 3d). Unfenced willows in their third growing season demonstrated a significantly greater change in volume than unfenced second season willows. There was no significant difference in mean volume between fenced second and fenced third season willows on the left bank ($P = 0.600$) (Figure 3d).

Wildlife Camera Trapping

Photo-documentation collected from the wildlife camera trap confirmed that mule deer were browsing on willow cuttings planted along the banks of Redwood Creek. Photo-documentation also indicated that deer were successfully restricted from browsing on fenced willow cuttings but continued browsing on unfenced willow cuttings. Based on the findings of this eight-month camera trapping study, deer consistently browsed on unfenced willows throughout the length of the study, with between a mean of two and six visits per day (Figure 4).

Discussion

In this study, I found a clear response to the restriction of browsing by deer through the use of exclusionary fencing on arroyo willow cuttings along the banks of Redwood Creek. Fenced willow cuttings generally demonstrated increased growth and increased biomass retention compared to cuttings located outside of fenced plots that were exposed to unrestricted browsing during the 2013 growing season. These results indicate that over-grazing by deer resulted in significant adverse effects to growth of newly planted willow cuttings within this restored riparian corridor. Observations of increased growth among willows protected from browsing in this study are consistent with other studies which have demonstrated improved survivorship and growth among willow communities following the removal of large herbivores (Elmore & Beschta 1987; Myers & Swanson 1995; Clary et al. 1996; Peineti et al. 2001; Dormann & Skarpe 2002; O'Grady et al 2002; Carline & Walsh 2007). The findings of my study at Redwood Creek were unique however, in that the effect of fencing was different between two willow ages and the sides of the bank on which they were located.

It is common for willows to be the preferred food source for a variety of herbivores in riparian ecosystems (Tolvanen et al. 2002; Meiman et al. 2009); therefore, it was not surprising to confirm herbivory as a stressor influencing growth of willows at Redwood Creek. Studies have shown that the nutritional value of leaves and shoots of willows in their first two years of growth is valuable to large herbivores (Rea and Gillingham 2001). Additionally, juvenile willows are likely to be more accessible to herbivores due to their smaller stature than mature willows, and they may have reduced chemical defenses as they prioritize early rapid growth (Julkunen-Tiitto 1989; Martinsen, Driebe, & Whitham 1998; Ball, Danell, & Sunesson 2000; Ruuhola et al. 2001; Massad 2013). Although willows evaluated in this study were in their second and third growing seasons, frequent browsing kept their size small. Therefore, it may be possible that willows at Redwood Creek were not only more accessible to herbivores, but may have also been higher in nutritional quality if they continued to prioritize the production of photosynthetic material over chemical defenses.

Overall, most willows in their second growing season located within the fenced plots demonstrated a much higher change in growth for all metrics (height, canopy diameter, aerial percent cover, and volume) compared to unfenced willows. However, willows in their third growing season located within the fenced plots demonstrated no significant difference in growth metrics compared to unfenced willows in their third growing season. These results suggest that the effects of browsing by large herbivores have a greater detrimental effect on younger willows in their second growing season than older willows in their third growing season. This finding is consistent with other studies which have found the effects of herbivory to depend on the age of the willows (Weltzin et al. 1998; Del-Val and Crawley 2005; Guillet and Bergstrom 2006; Massad 2013). Specifically, this finding is consistent with studies which have found a negative correlation between the abundance of large herbivores and the successful establishment of willows during the first year after they were established (Marshall, Cooper & Hobbs 2014). The difference in effectiveness of protective fencing between second and third season willows suggests that the ability to combat the effects of herbivory and compensate for lost biomass was different between the two age groups. These results differ from studies which conclude that younger trees may demonstrate increased compensatory responses to herbivory than older plants due to greater accumulation of stored reserves (Boege 2005; Boege and Marquis 2005). However, some studies have found that younger willows are more susceptible to the detrimental effects of herbivory since biomass removal can largely impact the reserves necessary for compensatory responses such as production of photosynthetic material (Hanley and Fegan 2007). Therefore, young willows which have less biomass to begin with, may have an even lower ability to rapidly compensate and recover under conditions of unrestricted browsing without some form of protection and relief. These results suggest that protective fencing had a greater beneficial effect for younger willows in their second growing season than older willows in their third growing season, indicating that willow cuttings at this site become more resistant to the effects of herbivory by the third growing season after being established.

Results of my study confirmed that fencing had the greatest beneficial effect among second season willows on the right bank specifically. As discussed previously, the increased growth trend observed among younger willows is consistent with studies that have found deer herbivory to have more detrimental effects on younger, juvenile willows compared to more mature willows (Den Herder, Virtanen, & Roininen 2004); however, this does not explain the differences observed between sides of bank. In other studies, the ability of plants to tolerate or compensate for herbivory has been shown to vary based on conditions of the surrounding environment such as nutrient availability, water availability, and soil conditions (Bryant et al. 1983; Olson & Richards 1988; Maschinski &Whitham 1989). For example, experimental studies at Yellowstone National Park found that the ability of willows to compensate for herbivory is directly related to whether or not access to water resources is adequate (Johnson, Cooper & Hobbs 2007; Bilyeu, Cooper & Hobbs 2008; Marshall, Hobbs & Cooper 2013). Additionally, studies at Yellowstone indicated that willow height was typically greater among plants that relied primarily on groundwater compared with willows which relied more directly on water within the upper soil layers (Johnston, Cooper & Hobbs 2011). If access to water resources or sun exposure based on the differing angles varies significantly between the right and left banks of Redwood Creek, it could be a factor contributing to the differences in growth observed between banks. The positive correlation between the ability of willows to compensate for herbivory and access to adequate water resources may explain why the difference in growth was very highly significant for all growth metrics for fenced second season willows on the right bank, but was not significant for growth metrics of fenced second season willows on the left bank. Additional studies would be required to confirm whether or not water availability is a significant factor limiting willow growth at Redwood Creek.

The effects of herbivory are variable because plant survivorship and growth are dependent on many interrelated factors (Li 2005). Responses to herbivory may vary based on the age of the plant, the existing stature of the plant prior to herbivory, time and duration of herbivory in relation to the growing season (Maschinski & Whitham, 1989; Olson & Richards 1988), and conditions of the surrounding environment such as nutrient availability, water availability, and soil conditions (Bryant et al. 1983; Olson & Richards 1988). Assessing growth of plants in riparian ecosystems is particularly difficult because they are exposed to both herbivory stressors and a dynamic hydrologic regime which can affect soil conditions. Based on the differences in growth observed among second season fenced willows between the two banks of Redwood Creek, it is likely that herbivory is not the only stressor limiting willow growth in this system. Therefore, when analyzing the effects of herbivory, it is important to assess the interrelated ecosystem factors which may influence those effects.

In this study, use of exclusionary fencing resulted in higher growth among willows in their second growing season which indicates that the implementation of exclusionary fencing may be an effective method for facilitating the passive recovery of riparian vegetation. The successful use of exclusionary fencing in this study is consistent with other projects which have found this technique to be a successful solution to reducing the stress of herbivory; however, many of these studies used fencing to restrict access by livestock, not wild herbivores. This study corroborates findings from other studies which conclude that the use of exclusionary fencing can be a successful tool for protecting restored vegetation from herbivory by populations of wild herbivores in addition to livestock (Briggs et al. 1994; Kauffman et al. 1995; Guillaume et al. 2012; Opperman 2000).

While the use of exclusionary fencing to restrict access by large herbivores and reduce the stress of browsing proved to be an effective method for protecting newly planted willow cuttings in this study, it is not a universally applicable solution and may not be appropriate for all projects. In some cases, the implementation of exclusionary fencing as a method for preventing herbivory has been shown to pose additional consequences (Keesing 1998; Shaw et al. 2010). Depending on site conditions, fencing vegetation could potentially have negative impacts such as inadvertently trapping wildlife, restricting use of wildlife corridors, or influencing changes in the way different species use a given area. In this study, fenced plots were originally intended to remain in place for at least two consecutive years; however, during the winter season of 2012, water levels rose substantially in the channel of Redwood Creek. Due to concerns that fencing could inadvertently trap fish using the riparian corridor, fencing was removed for the remainder of the wet season and re-installed in April 2013. While the removal of exclusionary fencing was not anticipated, it was a necessary action and should be taken into consideration for similar riparian restoration projects. In addition to potentially affecting the passage of other animals in the ecosystem, the use of exclusionary fencing can have other indirect detrimental effects such as enabling browsing by other herbivores such as small mammals and slugs (Keesing 1998; Hitchmough 2003; Medina et al. 2005) and increases in populations of invasive species (Roni et al. 2012). Therefore, while the use of exclusionary fencing can be effective for restricting browsing by large herbivores, it is important to consider the potential indirect effects of implementing this method.

Camera trapping results suggest that the frequency of deer browsing at this site is highest during the months of May, July and December. Herbivory is expected to be higher during the spring and summer months due to the fact that new growth among willows susceptible to browsing is highest during this time of year (Martinsen, Driebe & Whitham 1998). The peak in frequency of deer browsing during December may have been due to the lack of alternate food sources at the site during that time of year. The timing of browsing may influence the effect and response of willows. For example, studies have found that browsing on willow species could be more detrimental during the summer because the tearing of leaves directly affects the ability of the plant to photosynthesize during the growing season, whereas during the winter, browsed willow shoots and stems demonstrated increased shoot growth, branch frequency and bud formation (Bergström & Danell 1987; Bryant et al. 1991; Bergman 2002; Den Herder, Virtanen & Roininen 2004). The timing and frequency of deer browsing activities is particularly valuable information for riparian restoration sites such as this one, which require exclusionary fencing to be removed during the wet season, leaving willows exposed to unrestricted browsing.

The results of this study affirm the importance of both monitoring and documenting the progress of restoration projects during and following their completion (Bash & Ryan 2002; Shields et al. 2003). It is essential to identify potential stressors or problems as early as possible to create and implement remediation plans, which can be better accomplished through long-term monitoring (Bell et al. 2014). Few projects evaluate revegetation activities after a few years of establishment (Taylor et al. 2006). Some studies which conducted longer-term monitoring did not observe stabilized growth until after four seasons of growth after establishment (Bunting et al. 2013). If vegetation monitoring had not been a component of the Restoration Project studied, the stunted growth behavior among restored vegetation may have not been identified and growth would have proceeded more slowly, prolonging the restoration of suitable fish habitat. Even for an aspect of restoration as common as the planting of willow cuttings, a successful outcome is not guaranteed. Given the complexity and variation of riparian ecosystems, it is useful to understand the various challenges that have surfaced during previous projects and the successes and failures of previously implemented methodologies. While the restoration of riparian ecosystems is becoming more common, the effectiveness of applied methodologies is not always documented (Kondolf et al. 2007; Miller & Hobbs 2007; Palmer et al. 2007; Lennox et al. 2009). To further the field of restoration ecology and contribute to the understanding and success of riparian restoration, it is particularly important to document restoration projects that faced complications and implemented a course of action to combat those complications, regardless of their success, so they may benefit future projects.

Implications for Practice

- While herbivory was found to be a key stressor on the restoration of riparian vegetation at Redwood Creek, it is not unusual for multiple factors to be stressors in restoration projects due to the dynamic complexity of riparian ecosystems. When considering the site in terms of restoration, it is important to identify the most prevalent stressor with the most realistic option for remediation.
- Herbivory can directly impede the growth of newly planted willow cuttings in riparian restoration projects. Exclusionary fencing is a low cost, low maintenance, and effective solution to mitigate the effects of herbivory and promote plant establishment and growth. However, consideration must be given to winter flows in the stream system and fencing may have to be taken out along the banks before the rainy season to prevent trapping of fish.
- Newly planted, smaller vegetation is more susceptible to herbivory than larger plants. Following the second year of growth post-establishment, new willow growth begins to become less accessible to most herbivores. Exclusionary fencing has a greater impact if implemented during the first two years following planting, when foliage is most accessible to deer browsing due to height, or until plants demonstrate sufficient tolerance to the effects of browsing.
- While exclusionary fencing proved effective for mitigating the effects of herbivory for this study, it is not universally applicable for preventing herbivory for all riparian restoration projects. As discussed previously, many other factors such as soil characteristics, soil moisture, and access to groundwater must be considered.

Acknowledgements

I gratefully acknowledge the National Parks Service and Golden Gate National Recreation Area for allowing me to conduct this study at Redwood Creek throughout the course of ongoing construction and restoration efforts and for constructing the fenced plots. I would like to personally thank NPS staff Chris Friedel, Kristen Ward, Naomi LeBeau of GGNPC, and any and all additional staff and volunteer support along the way. I greatly appreciate the University of San Francisco, Environmental Science Department and Masters of Science in Environmental Management Program, specifically Professors Gretchen Coffman, John Callaway and Stephanie Ohshita, for logistical support, critiquing manuscript drafts, and funding. I would also like to thank all University of San Francisco undergraduate volunteers, including

Brett Marquette and others that assisted with the construction of exclusionary fencing, and Matthew Richter for assisting in camera trap data collection and analysis.

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Tables

Table 1. Study design for collecting growth metric data for arroyo willow cuttings planted along the restored banks of Redwood Creek organized by factors of interest.

Year Willows were Planted (Growing Season)	*Bank*	*Plot Number*	*Total Number of Unfenced Replicates per Plot*	*Total Number of Fenced Replicates per Plot*
2011 (2^{nd})	Right	1	10	10
2011 (2^{nd})	Right	2	10	10
2011 (2^{nd})	Left	1	10	10
2011 (2^{nd})	Left	2	10	10
2010 (3^{rd})	Right	1	10	10
2010 (3^{rd})	Right	2	10	10
2010 (3^{rd})	Left	1	10	10
2010 (3^{rd})	Left	2	10	10
		Total number of cuttings	80	80

Table 2. Results of 3-Way ANOVA for factors of interest and growth metrics collected for arroyo willow cuttings along the restored banks of Redwood Creek over the course of the 2013 growing season. Factors of interest include the age of the willow cuttings (second or third growing season), side of bank they were located on (left or right) and exclusionary fencing (fenced or unfenced). Growth metrics include height of the tallest branch (cm), diameter of the canopy in two perpendicular directions (cm), estimated aerial percent cover (%), and mean volume (cm^3) of willow cuttings as a nondestructive estimate of aboveground biomass.

Growth Metrics	*Factors of Interest*						
	Bank	*Year*	*Fenced*	*Bank*Year*	*Bank*Fenced*	*Year*Fenced*	*Bank*Year*Fenced*
Height	$F_{[1,150]} = 2.536$ P = 0.113	$F_{[1,150]} = 97.115$ P = 0.000***	$F_{[1,150]} = 37.351$ P = 0.000***	$F_{[1,150]} = 11.572$ P = 0.001***	$F_{[1,150]} = 27.631$ P = 0.000***	$F_{[1,150]} = 29.345$ P = 0.000***	$F_{[1,150]} = 7.27$ P = 0.008**
Canopy Diameter	$F_{[1,150]} = 10.943$ P = 0.001***	$F_{[1,150]} = 28.587$ P = 0.000***	$F_{[1,150]} = 62.105$ P = 0.000***	$F_{[1,150]} = 31.721$ P = 0.000***	$F_{[1,150]} = 11.335$ P = 0.001***	$F_{[1,150]} = 8.624$ P = 0.004**	$F_{[1,150]} = 18.368$ P = 0.000***
Percent Cover	$F_{[1,125]} = 11.861$ P = 0.001***	$F_{[1,125]} = 4.705$ P = 0.032*	$F_{[1,125]} = 16.974$ P = 0.000***	$F_{[1,125]} = 0.004$ P = 0.952	$F_{[1,125]} = 5.671$ P = 0.019*	$F_{[1,125]} = 8.969$ P = 0.003**	$F_{[1,125]} = 4.059$ P = 0.046*
Volume	$F_{[1,123]} = 13.655$ P = 0.000***	$F_{[1,123]} = 54.811$ P = 0.000***	$F_{[1,123]} = 26.469$ P = 0.000***	$F_{[1,123]} = 3.055$ P = 0.083	$F_{[1,123]} = 18.674$ P = 0.000***	$F_{[1,123]} = 24.370$ P = 0.000***	$F_{[1,123]} = 6.093$ P = 0.015*

Legend: * = 0.05 ≥ P > 0.01 = significant, ** = 0.01 ≥ P > 0.001 = highly significant, *** = P ≤ 0.001 = very highly significant

Figures

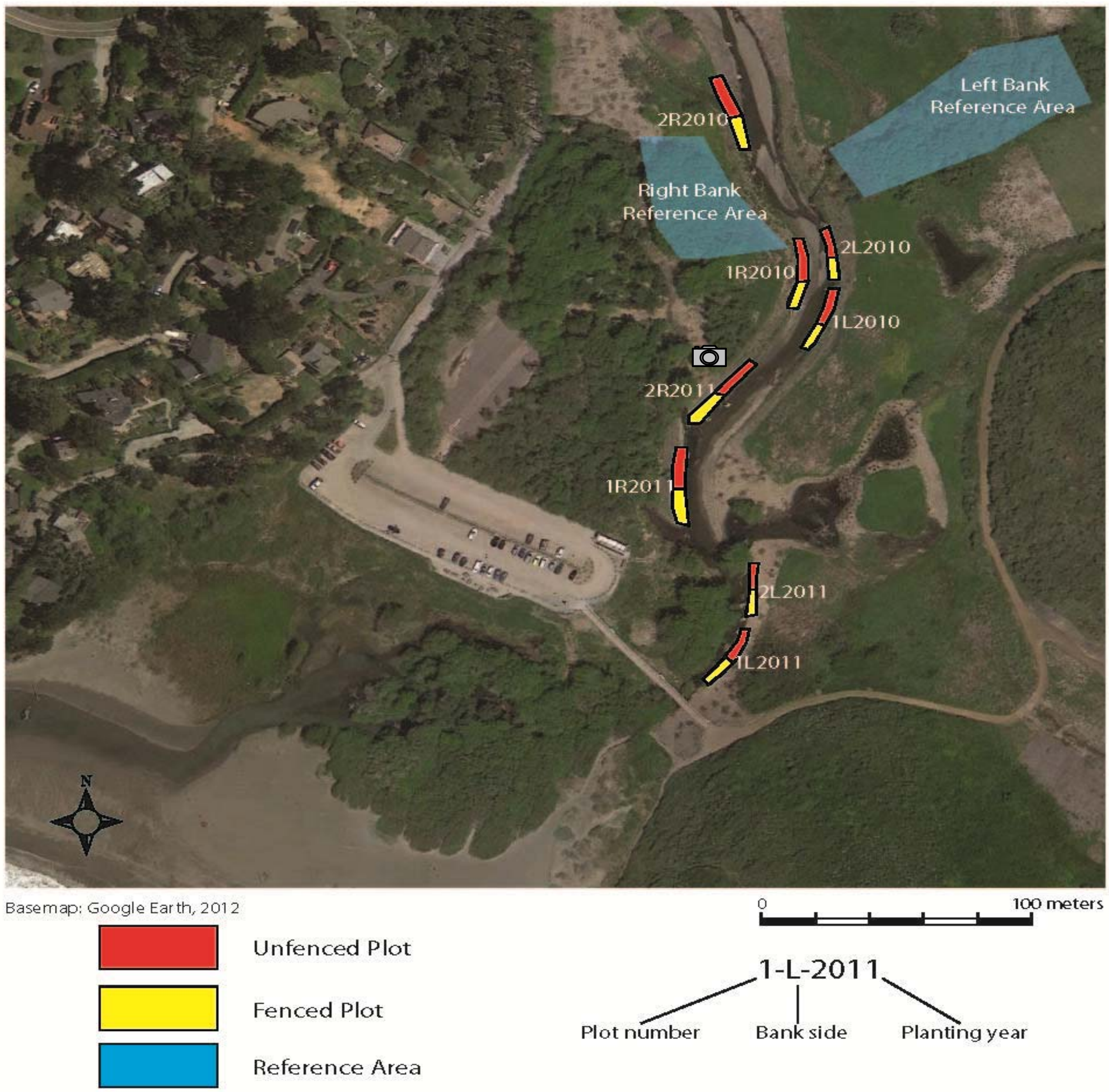
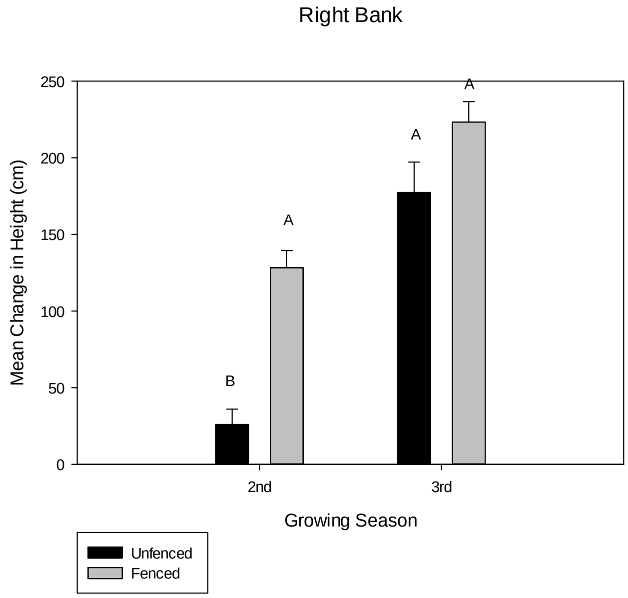
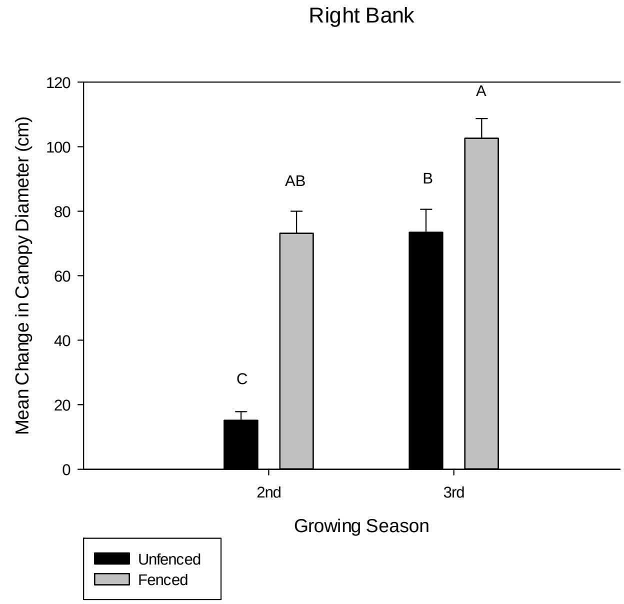


Figure 1. Location of study plots and reference areas along Redwood Creek at Muir Beach, California. Study sites are labeled as follows: plot number (1 or 2), right or left bank (R or L), and age of willow cuttings (2011 represents second growing season and 2010 represents third growing season). The camera symbol represents the location where the camera trap study was located.

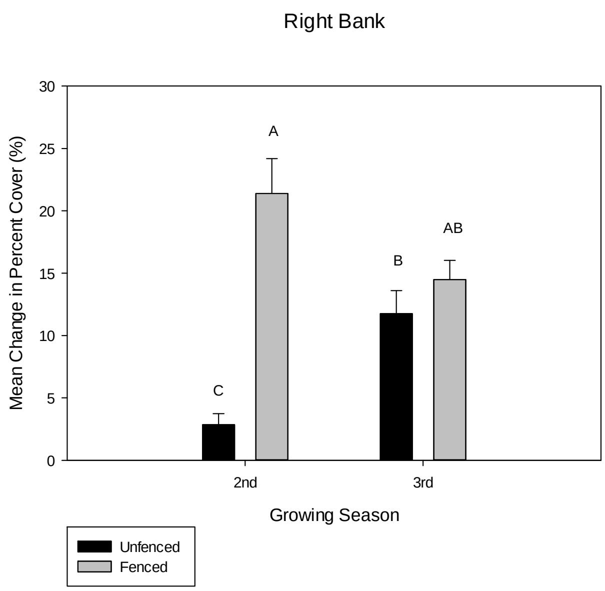
a) Difference in mean height (cm)



b) Difference in mean canopy diameter (cm)



c) Difference in mean aerial percent cover (%)



d) Difference in mean volume (cm^3)

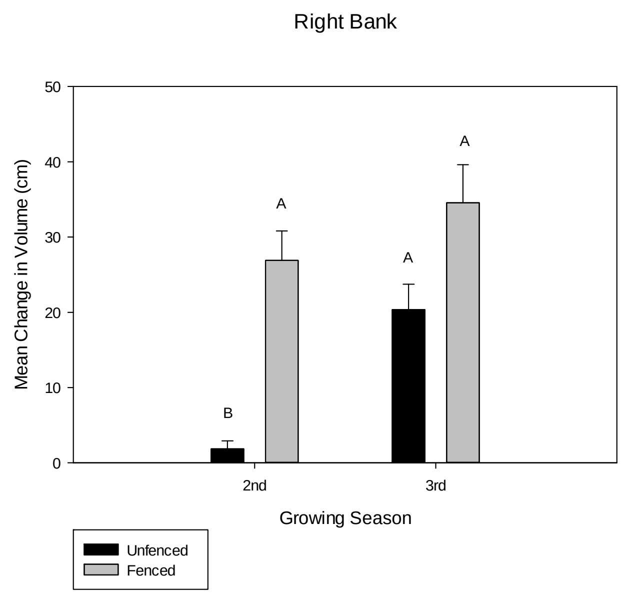
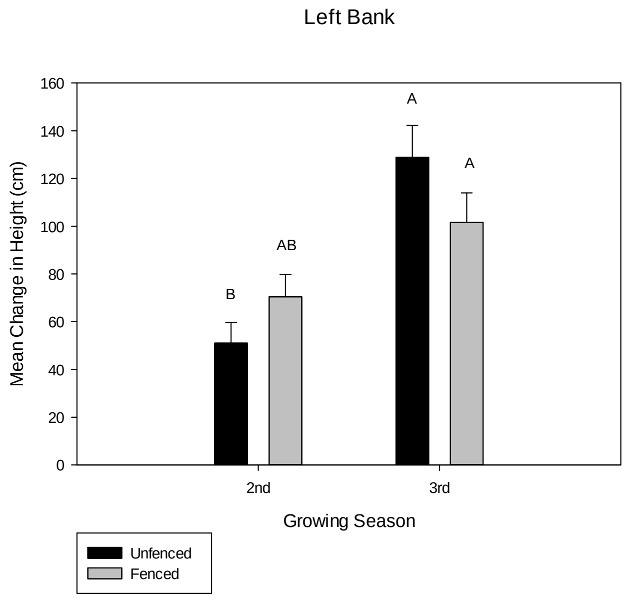
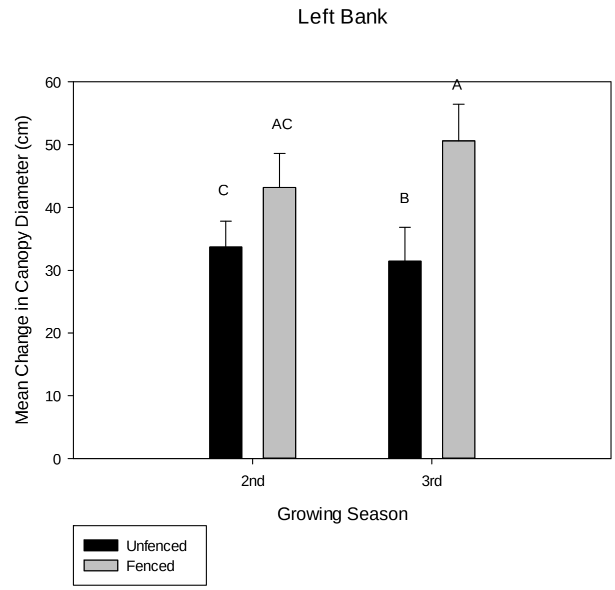


Figure 2a-d: Difference in willow growth during 2013 growing season (May-September 2013) between fenced and unfenced treatment and younger (2nd growing season) versus older willow cuttings (3rd growing season) on the right bank. Results for various growth metrics are show in a) mean height, b) mean canopy diameter, c) mean percent cover, and d) mean volume.

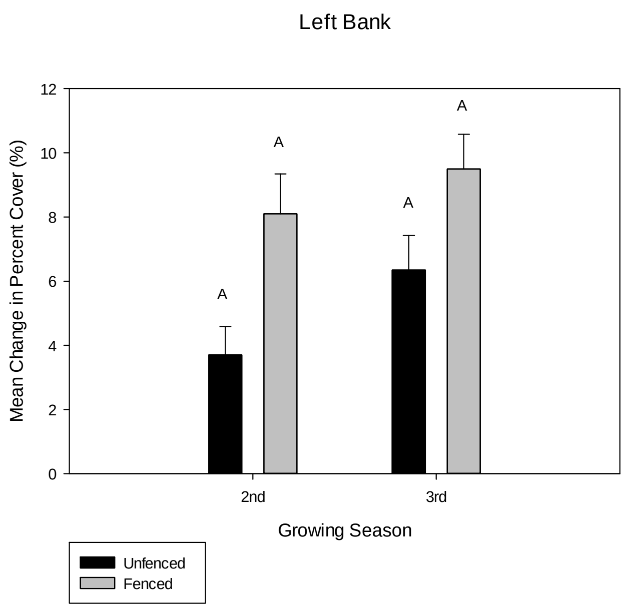
a) Difference in mean height (cm)



b) Difference in mean canopy diameter (cm)



c) Difference in mean percent cover (%)



d) Difference in mean volume (cm^3)

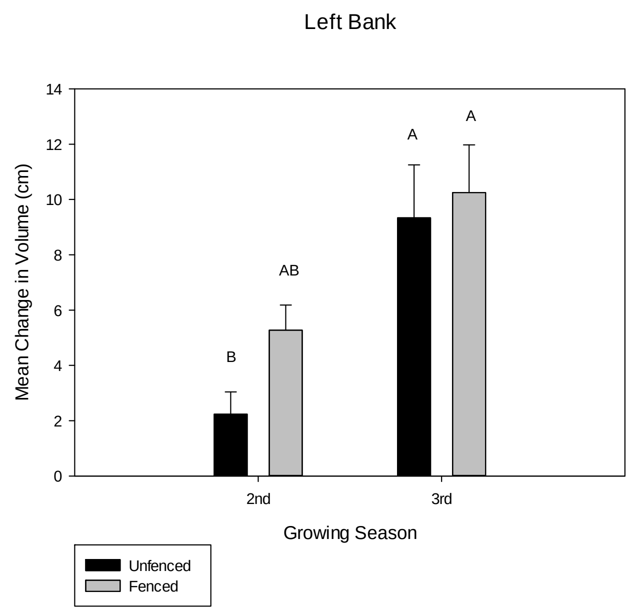


Figure 3a-d. Change in willow growth during 2013 growing season (May-September 2013) between fenced and unfenced treatment and younger (2nd growing season) versus older willow cuttings (3rd growing season) on the left bank. Results for various growth metrics are show in a) mean height, b) mean canopy diameter, c) mean percent cover, and d) mean volume.

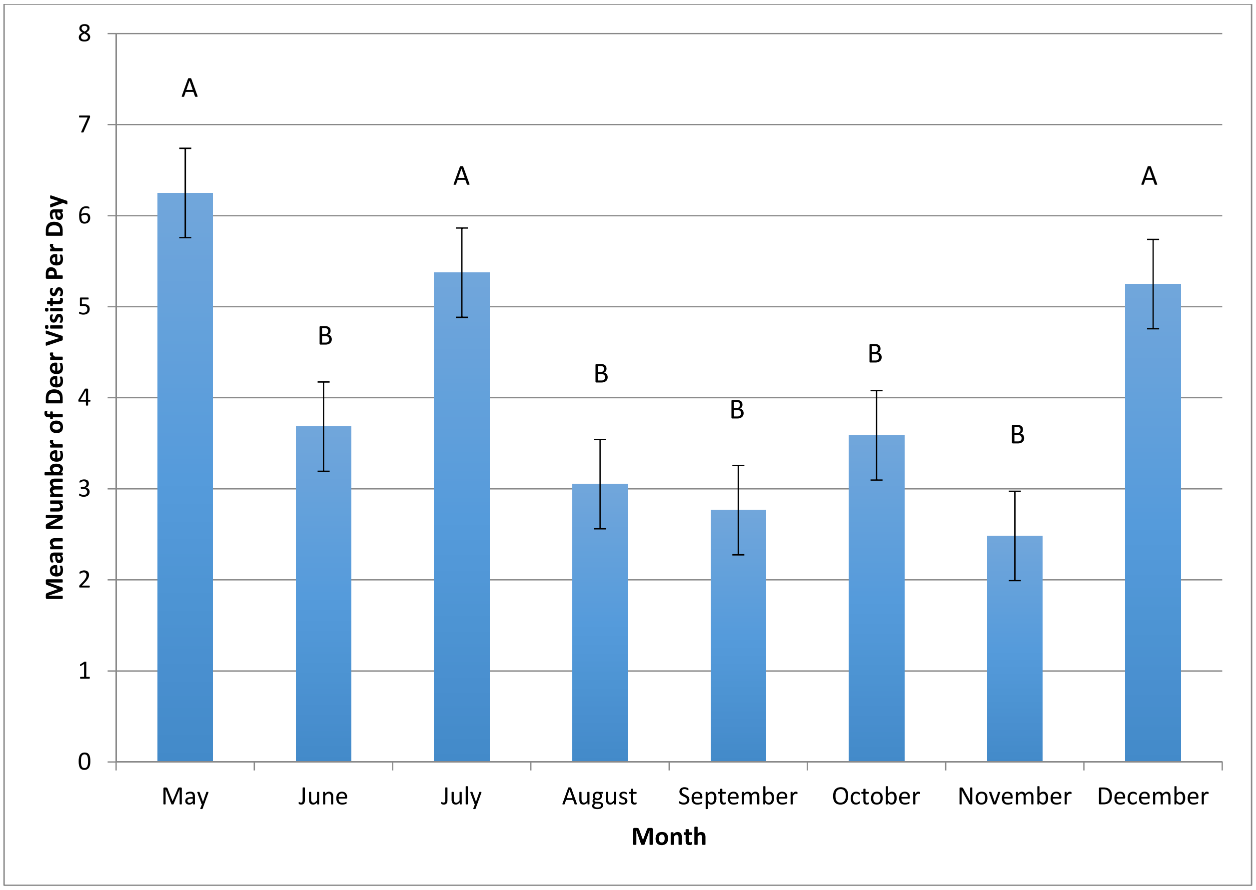


Figure 4: Mean number of deer visits per day each month at the wildlife camera trap site. The camera trap was installed facing unfenced second season willows on the right bank of Redwood Creek from May 2013 to December 2013.