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Research Article

Herbivory and Soil Properties as Ecological Constraints to Willow Growth in a Restored Riparian Ecosystem in Coastal California

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Abstract

This study investigated stunted arroyo willow (*Salix lasiolepis*) cuttings planted along a restored riparian corridor in Marin County, California. Restoration activities along this corridor included channel realignment, bank stabilization, and placement of streambed material and large woody debris, which required the use of heavy machinery and compacted soils. Additionally, evidence of deer browsing indicated that predation may be significantly affecting cutting growth and survivorship. In our field study, we measured effects of deer browsing and physical soil characteristics (i.e., soil moisture, compaction, texture, and total organic content) on the change in willow growth (i.e., height, mean canopy diameter, estimated aerial percent cover, and volume) of 160 recently planted willow cuttings (in their second and third year of growth following planting) to better understand stunted growth. Growth and health attributes of the cuttings were further analyzed in relation to three factors: 1) presence of exclusionary deer fencing; 2) location on left or right bank and 3) age of the cutting. Results of the study indicated deer herbivory was a critical stressor limiting survivorship and growth of willow cuttings. Exclusionary fencing resulted in significantly higher growth for all four metrics compared to unfenced willows with the greatest beneficial effect on younger willows in their second growing season. Significantly higher soil moisture and lower soil compaction were found in reference sites compared to restoration study sites. However, the influence of physical soil characteristics on willow growth revealed weak correlations. Exclusionary fencing is a cost-efficient method for restricting browsing by wild herbivores on recently planted willow cuttings, most effective when implemented during the first two growing seasons or until willow cuttings are resilient to the effects of herbivory.

Keywords: Exclusionary fencing; Herbivory; Riparian; *Salix lasiolepis*; Soil compaction; Soil moisture

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Introduction

Active revegetation 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 [1], increasing root density for erosion prevention [2], and establishing channel vegetation structure for faunal habitats [3]. Woody riparian species provide valuable ecosystem services by increasing retention of flood water, reducing sedimentation, regulating temperature by providing shade, and improving water quality [4,5]. Willows (*Salix* spp.) are commonly utilized for revegetation of riparian ecosystems due to their simple propagation, demonstrated high survivorship, and rapid growth rate. Willows can reach heights of over 10 meters (m) and may grow approximately 2 to 3 m after a single growing season, thereby rendering most branches inaccessible for browsing by herbivores [6]. While their rapid growth makes willows resistant to browsing, cuttings are highly susceptible to intense browsing during the first few years after being planted [6]. Excessive grazing has been shown to negatively affect plant growth and reproduction [7-9], completely eradicate populations of woody plants [10], and has contributed to the worldwide degradation of riparian ecosystems [11,12]. Over time, frequent removal of woody stems and foliage by herbivores can result in a reduction in the carbon reserves below ground surface, thereby preventing natural defense mechanisms, including chemical resistance and rapid vertical growth, rendering the plants more susceptible to browsing [13].

Disturbed soil conditions can also adversely affect willow growth and overall survivorship. Construction activities commonly required for riparian restoration projects include: channel realignment; bank stabilization; reconstruction of geomorphic features such as floodplain benches, riffle pools, and depositional basins; placement of streambed material and large woody debris; and grade control structures. The use of heavy machinery and intensive ground disturbance required for these restoration activities can result in heavily compacted soils and reduced quantities of topsoil and organic material. Although increased soil compaction reduces the potential for soil erosion, it can also reduce the total porosity of the soil [14], effectively decreasing the potential for water to infiltrate the soil. Soil compaction may also reduce carbon and nitrogen cycling, soil microbial biomass [15,16], or impede plant growth, specifically root length, depth, and penetration through the soil [17]. Stunted willow growth may be indicative of an ecological stress which could negatively influence the overall success of a restoration project if not resolved. Due to the dynamic complexity of ecosystems, any number of ecological factors (e.g., excessive grazing by livestock, natural predation, poor soils, or low water availability) could detrimentally affect vegetation health [18].

Based on existing site conditions observed in the restored riparian ecosystem, we hypothesized that the leading ecological constraint contributing to stunted willow growth was either browsing by large herbivores or decreased soil moisture due to increased soil compaction resulting from ground-disturbing restoration activities. The objectives of our study were to 1) evaluate the effects of browsing by large herbivores on willow cuttings through the use of exclusionary fencing and 2) evaluate the effects of soil characteristics on willow growth through the collection of soil compaction, moisture, and composition data and comparison with data from a healthy riparian reference ecosystem.

Methods

Study location

Our study site was located along a restored reach of Redwood Creek in Marin County, California, within a 46-acre restoration project completed in 2014 by the National Park Service. The main objective of restoration activities at Redwood Creek was to create habitat for Coho salmon by utilizing common bioengineering approaches for restoring the stream channels. Bioengineering approaches included installing a combination of large woody debris, fiber matting, straw ground cover, and live staking of arroyo willow (*Salix lasiolepis*) cuttings.

Experimental design

We established eight fenced and unfenced study plots that contained 20 cuttings each, with four plots on each side of Redwood Creek (Figure 1, Table 1). The plots were equally divided among willows in their second or third year of growth. Fenced and unfenced study plots were located adjacent to one another to ensure all other conditions were similar. Plots of 3-m-tall exclusionary fencing were installed in April, remained in place for the duration of the growing season, and were removed in October before the rainy season.

Willow growth and herbivory

To evaluate the effects of herbivory, we measured growth metrics for all willow cuttings immediately following installation of exclusionary fencing in May and at the end of the growing season prior to fence removal in September. For each cutting, we took measurements for height (cm); canopy diameter (cm); and aerial percent cover (%). We used mean volume (cm^3) of willow cuttings as a nondestructive estimate of above ground biomass. To document deer browsing of willows, a Bushnell Nature View remote, motion and heat sensor camera trap was deployed from May through December (Figure 1).

Soil characteristics

We collected soil compaction, moisture, and composition data within the same eight study plots to evaluate the effects of soil characteristics on willow growth. We measured soil compaction and moisture monthly, from April through September, within 10 cm of the base of each unfenced willow cutting. We used a time domain reflectometer (TDR) to sample soil moisture and recorded measurements in volumetric water content (VWC), accurate to ± 3.0% VWC.

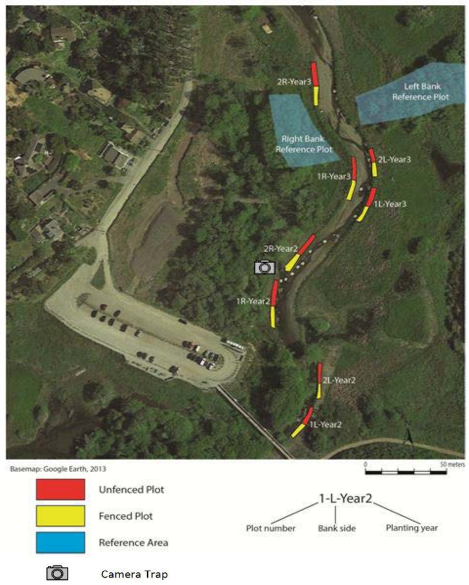

Figure 1: Location of restoration and reference plots along Redwood Creek at Muir Beach, California.

Table 1: Study design for willow cutting growth measurements along the restored banks of Redwood Creek.

Willow Age (Growing Season)	Bank	Plot Number	Total Number of Unfenced Replicates per Plot	Total Number of Fenced Replicates per Plot
Second Season	Right	1	10	10
Second Season	Right	2	10	10
Second Season	Left	1	10	10
Second Season	Left	2	10	10
Third Season	Right	1	10	10
Third Season	Right	2	10	10
Third Season	Left	1	10	10
Third Season	Left	2	10	10
	Total number of cuttings		80	80

Although many natural processes contribute to compacted soils [19], natural causes typically only affect the top 5 cm of soil, whereas anthropogenic influences may affect soil 20 to 60 cm below ground surface (bgs) [17]. We sampled soil compaction using a soil compaction meter at approximate depths of 15, 30, 45, and 60 cm bgs, recording measurements in pounds per square inch (psi). Due to the variability between soil horizons, study site conditions, and the accuracy of the instrument, we categorized soil compaction readings as: 1) 0-200 psi; 2) 200-250 psi; 3) 250-300 psi; 4) 300-450 psi; and, 5) greater than 450 psi. A larger range was assigned to soil compaction 'Category 1' due to the relative ease at which the compaction meter penetrated soft soils and the inability to record static values in soil horizons that lacked significant resistance. We were unable to quantify soil compaction greater than 450 psi due to extreme compaction and instrument limitations.

We also measured soil texture and organic matter within the study plots. For each study plot, we collected and analyzed eight composite soil samples composed of seven subsamples consisting of cores collected at a depth of 45 cm bgs. Following thorough mixing of the subsamples, a single composite sample was extracted for each of the eight study plots. Soil samples were dried and total organic content (TOC) was calculated following the Environmental Protection Agency's protocol for loss-of-ignition [20]. We determined grain size and soil texture using a hydrometer.

Reference plots

We selected two reference plots, one on each bank of Redwood Creek approximately 35 feet from the stream channel, to compare soil characteristics between our restoration plots and adjacent, undisturbed riparian conditions dominated by mature arroyo willows. We collected soil compaction, moisture, and grain size data from the reference plots with the same methods used on our restoration plots.

Statistical analysis

To evaluate the effectiveness of the exclusionary fencing, our statistical analysis was a full factorial design for the factors of bankside (left and right), age of willows (second and third year), and exclusionary fencing (fenced and unfenced). We conducted a three-way Analysis of Variance (ANOVA) to analyze the interactions between three factors (bankside, age of willows, and exclusionary fencing) and four growth metrics (mean height, mean canopy diameter, mean aerial percent cover, and 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, we conducted pairwise comparison of means using Tukey's Honestly Significant Difference test to analyze differences between group means.

Since we collected willow growth data at the beginning and end of the growing season, we averaged the monthly soil moisture and soil compaction data at each of the 80 cuttings to illustrate the representative soil characteristics over the course of the growing season. We converted the categorical data to continuous data by using the average of the categorical ranges. We conducted two-way ANOVA for soil moisture and soil compaction to determine if seasonal averages of each study plot were related (Systat Software, Version 13). We also compared the monthly average soil moisture and soil compaction of the study plots to the monthly averages of the reference plots. We then paired the monthly averages of soil moisture and compaction data with the growth differences in height and canopy cover for each cutting. Using pairwise Pearson r-correlation analysis, we analyzed each soil characteristic against each growth metric, investigating for any potential correlations, isolating cutting age and bankside for each pairwise analysis.

Results

We observed highly ($0.01 \geq P > 0.001$) and very highly significant ($P \leq 0.001$) trends in the second-year willow cuttings growth between fenced and unfenced treatments. For each metric, willow cuttings were larger when they were inside exclusionary fencing. Results of the three-way ANOVA resulted in significant interactions between all factors, as described below (Table 2).

Willow height

Fenced second-year willow cuttings on the right bank had a significantly greater mean height at the end of the growing season and were more than four times taller compared to unfenced second-year willow cuttings (Table 2, Figure 2). We also found a significantly greater mean height among unfenced third-year cuttings compared to unfenced second-year cuttings (Table 2, Figures 2, 3).

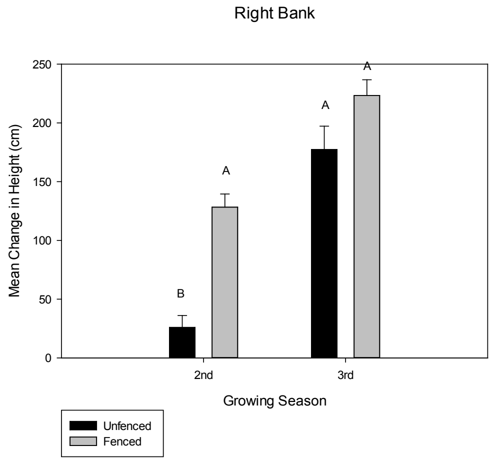

Figure 2: Mean change in height over the growing season between fenced and unfenced and second-year versus third-year willow cuttings on the right bank.

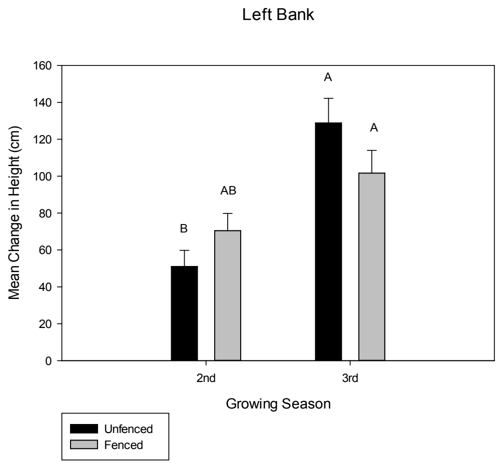

Figure 3: Mean change in height over the growing season between fenced and unfenced and second-year versus third-year willow cuttings on the left bank.

Willow canopy diameter

We found that fenced second-year willow cuttings had a significantly greater mean canopy diameter (four times greater) compared to unfenced second-year cuttings on the right bank (Table 2, Figure 4). Fenced third-year willow cuttings also had significantly larger mean canopy diameter than unfenced cuttings (Table 2, Figure 4). Fenced third-year cuttings resulted in a greater mean canopy diameter at the end of the growing season than unfenced third-year cuttings for both banks (Table 2, Figure 5).

Table 2: Results of 3-Way ANOVA for factors of bank (left or right), age of the willow cuttings (second or third growing season), and exclusionary fencing (fenced or unfenced) and growth metrics including height, canopy diameter, aerial percent cover, and mean volume (cm^3) collected for willow cuttings along the restored banks of Redwood Creek over the course of one growing season.

	Factors of Interest						
Growth Metrics	**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 based on a 95% confidence level.

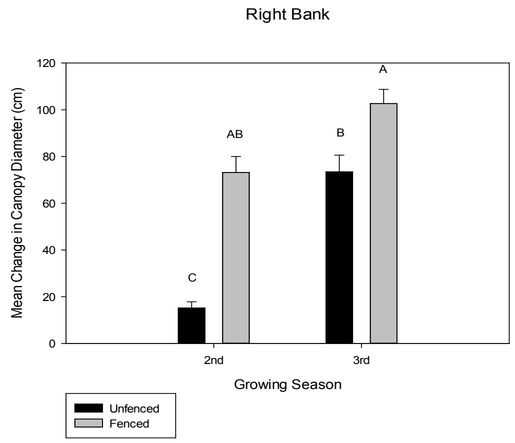

Figure 4: Mean change in canopy diameter (cm) over the growing season between fenced and unfenced and second-year versus third-year willow cuttings on the right bank.

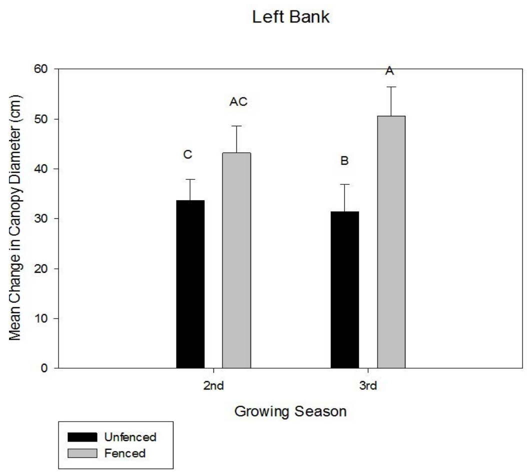

Figure 5: Mean change in canopy diameter (cm) over the growing season between fenced and unfenced and second-year versus third-year willow cuttings on the left bank.

Willow aerial percent cover

Mean aerial percent cover was more than five times greater in fenced compared to unfenced second-year willow cuttings on the right bank (Figure 6). Fenced second- and third-year cuttings had greater mean aerial percent cover than unfenced cuttings on the left bank (Table 2, Figure 7).

Willow volume

Fenced second-year willow cuttings were more than eight times greater in mean volume than unfenced second-year cuttings on the right bank and two times greater in mean volume on the left bank (Figure 8). Unfenced third-year cuttings exhibited a higher mean volume than unfenced second-year cuttings on the right bank (Table 2, Figure 8). Unfenced third-year cuttings showed a greater mean volume than unfenced second-year cuttings on both banks (Table 2, Figures 8, 9).

Deer herbivory

Camera trap photo-documentation confirmed that mule deer were browsing on newly planted willows within the study site. Analysis of camera trap photos showed that deer were successfully restricted from browsing on fenced willow cuttings but continued browsing on unfenced willow cuttings. The camera data revealed that deer consistently browsed on unfenced willows from May through December, with a mean of two and six visits per day (Figure 10). Frequency of deer browsing was highest in May, July and December.

Soil characteristics

We found soil moisture to be significantly lower within the study plots than the adjacent reference plots in all months studied. Mean soil moisture throughout the third-year study plots was 23.93 ± 5.68 VWC compared to the reference mean of 37.73 ± 6.89 VWC. Significant differences in soil moisture existed between plots of second- and third-year willows and within the plots of second-year willows. Variances in soil moisture over time were greater within the study plots compared to the reference plots.

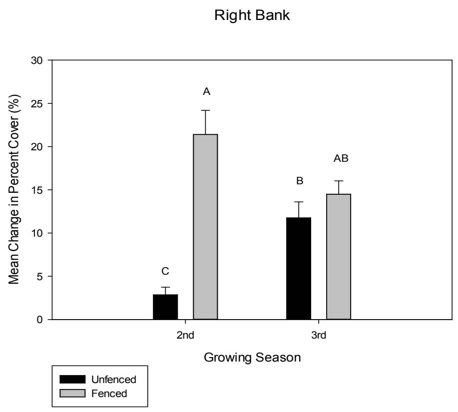

Figure 6: Mean change in percent aerial cover over the growing season between fenced and unfenced and second-year versus third-year willow cuttings on the right bank.

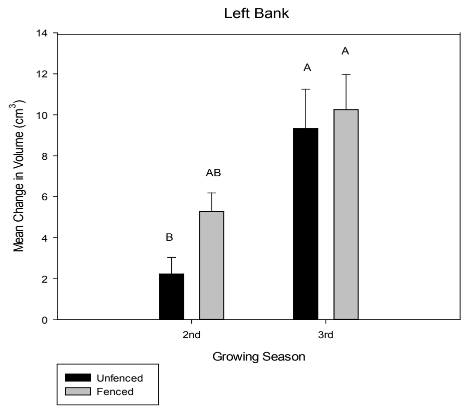

Figure 9: Mean change in volume (cm^3) over the growing season between fenced and unfenced and second-year versus third-year willow cuttings on the left bank.

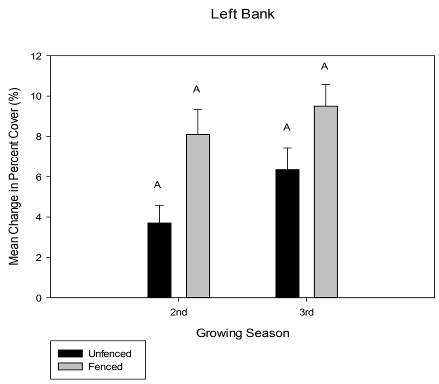

Figure 7: Mean change in percent aerial cover over the growing season between fenced and unfenced and second-year versus third-year willow cuttings on the left bank.

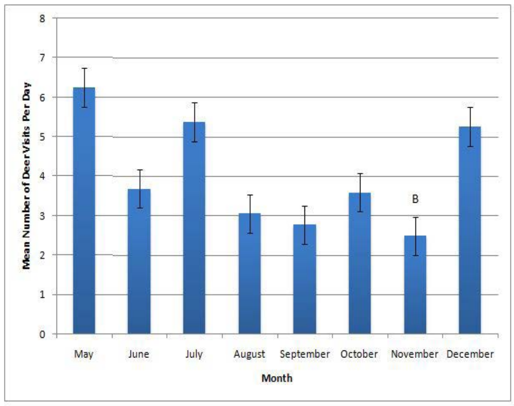

Figure 10: Mean number of deer visits per day for unfenced willows in their second growing season.

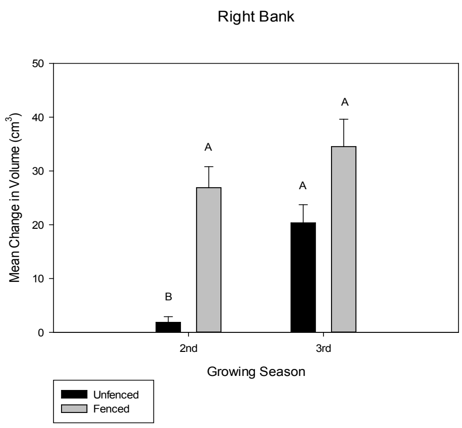

Figure 8: Mean change in volume (cm^3) over the growing season between fenced and unfenced and second-year versus third-year willow cuttings on the right bank.

Soil moisture varied significantly between months, plots, and cuttings in restoration and reference sites. Soil compaction levels remained relatively consistent throughout the study period. Soil probes were capable of penetrating the ground surface with minimal effort within the reference plots. However, soils within the study plots were so heavily compacted that the soil compaction meter was not capable of penetrating to the first sample depth of 15 cm. Soil moisture and compaction for the reference plots indicated very strong inverse correlations at all depths (r-values ranging from -0.764 to -0.963), with increased soil moisture in less compact soils. Similarly, we observed many strong correlations between soil moisture and compaction within the study plots (Table 3). Analysis of the six composite samples identified similar soil characteristics within the study and reference plots; however, the study plot samples contained approximately half of the quantity of TOC (4.1 to 5.0 percent by volume) compared to the reference plot samples (7.6 and 10.9 percent).

Table 3: Composite sample analysis results for soil grain size, texture, and organic content of the study and reference plots at the NPS Redwood Creek Restoration Project site at Muir Beach.

Study Plot Type	Bank	Grain Size			Texture	Organic Matter (% by volume)
		Sand (%)	Silt (%)	Clay (%)		
Third Season	Right	31.75	47.00	21.25	Loam	4.6
Third Season	Left	34.5	44.25	21.25	Loam	4.1
Second Season	Right	45.00	41.25	18.75	Loam	4.9
Second Season	Left	60.75	25.50	13.75	Sandy Loam	5.0
Reference	Right	30.5	48.25	21.75	Loam	10.9
Reference	Left	55.5	30.75	13.75	Sandy Loam	7.6

Soil characteristics vs willow growth

The difference in cutting height and canopy were highly correlated in three of the four study plots (r-values of 0.787, 0.540 and 0.693). The second-year cuttings on the left bank (r-value of -0.363) differed from the other three study plots where the cuttings grew in height but had limited canopy expansion. We observed no strong correlations between willow growth and soil moisture with any combination of correlation analysis (r-values ranged from -0.367 to 0.215) (Table 3).

Discussion

Our analysis of soil characteristics concluded that restoration activities created significantly different soil conditions within the restored portions of the study area compared to undisturbed reference site conditions. Significant differences in soil moisture and compaction were observed between the study and reference plots, with mean soil moisture within the study plots measured at nearly half that of the soil within the reference plots and mean soil compaction measured at more than double that of the soil within the reference plots. These variations could be attributed to the difference in distance from the stream or the difference in soil texture between our study and reference plots [21].

Evette et al. [22] found that all growth metrics of willow cuttings are significantly related to available soil moisture and drought conditions generally increase willow growth stress compared to moist, well-drained conditions [23,24]. Highly-compacted soils may result in increased soil strength, reduced bulk density, and a reduction in water-holding capacity, all of which can restrict root growth and hinder plant health [25]. Furthermore, natural recovery of compacted soils may require many years depending on the regional climate, soil texture, and the level of compaction. Contrary to findings of similar studies, we only found weak correlations between soil characteristics and willow growth.

Our study identified a clear effect of willow growth within the exclusionary fencing along the banks of Redwood Creek. This effect was especially well pronounced in the second growing season. Fenced willow cuttings generally exhibited increased growth and increased biomass compared to cuttings located outside of fenced plots during the growing season. These results indicate that grazing contributed to stunted growth of planted willow cuttings. Although many studies have found a correlation between unrestricted browsing by herbivores and adverse effects to vegetation growth, the findings of our study were unique in that the effect of fencing was different between second- and third-year cuttings and the sides of the bank.

Overall, most fenced second-year cuttings demonstrated an increased change in growth for all metrics compared to unfenced cuttings. However, fenced third-year cuttings demonstrated no significant difference in growth metrics compared to unfenced third-year cuttings. These results suggest that the effects of browsing have a greater detrimental effect on second-year willows compared to third-year willows in the same habitat. Other studies have also found the effects of herbivory to depend on the age of the willows [26-29]. Several studies have shown that the nutritional value of willow leaves and shoots in their first two years of growth is valuable to large herbivores [29,30]. Additionally, juvenile willows are likely to be more accessible to herbivores due to their smaller stature and may have reduced chemical defenses as they prioritize early rapid growth [27]. 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 value if they continued to prioritize the production of photosynthetic material over chemical defenses.

The effectiveness of exclusionary fencing between second- and third-year willows suggests resilience to the effects of herbivory was different between the two age groups. These results differ from studies which conclude that younger willows may demonstrate increased compensatory responses to herbivory than older willows due to greater accumulation of stored reserves. However, Hanley and Fegan [31] found that younger willows were more susceptible to the detrimental effects of herbivory since biomass removal can greatly reduce the reserves necessary for compensatory responses. Therefore, younger willows with less biomass may have a reduced ability to recover under conditions of unrestricted browsing. Our results indicate that willow cuttings at this site become more resistant to the effects of herbivory by the third growing season following initial planting; however, the mechanism (chemical or reserves) for resistance remains unknown.

Willows are a common preferred food source for herbivores in riparian ecosystems [32]. Observations of increased growth among willows protected from browsing in this study were consistent with many studies, including De Jager et al. [33], who demonstrated improved survivorship and growth among willow communities following the removal of large herbivores. However, several studies used fencing to restrict access by livestock, not wild herbivores [34,35]. Our study corroborates findings from other studies that the use of exclusionary fencing can be a successful tool for protecting restored vegetation from wild herbivores as well as livestock [28,36].

Our study suggests that the use of exclusionary fencing may be an effective method for facilitating recovery of riparian vegetation at riparian restoration sites where herbivory is prevalent. Understanding the timing and frequency of browsing is particularly valuable information for installing exclusionary fencing treatment [37]. Fencing has a greater impact if implemented during the first two years following initial planting when willows are most accessible by herbivores, or until willows demonstrate sufficient tolerance to effects of herbivory. High levels of browsing found in our study may be more detrimental during the growing season because the tearing of leaves directly affects the ability of the plant to photosynthesize; whereas during the winter, browsed willows have demonstrated increased shoot growth, branch frequency, and bud formation [38].

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 restoration projects. Depending on site conditions, fencing could result in additional adverse effects such as inadvertent entrapment of wildlife or obstruction of wildlife corridors.

In this study, fenced plots were originally intended to remain in place for at least two consecutive years; however, during the winter season, water levels rose substantially in Redwood Creek. Due to concerns that fencing could inadvertently trap fish utilizing the riparian corridor, fencing was removed before final measurements were taken for the remainder of the wet season and re-installed in April. This is why we did not show results for first year willow cuttings. 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. Therefore, while the use of exclusionary fencing can be an effective, low-cost, low-maintenance method for restricting browsing by large herbivores; it is important to consider the potential indirect effects of implementing this method.

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