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Wild ungulate herbivory suppresses deciduous woody plant establishment following salmonid stream restoration

Joshua P. Averett [a,*], Bryan A. Endress [a], Mary M. Rowland [b], Bridgett J. Naylor [b], Michael J. Wisdom [b]

[a] Eastern Oregon Agriculture and Natural Resource Program, Oregon State University, Badgley Hall 205, One University Blvd., La Grande, OR 97850, USA
[b] USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Ln., La Grande, OR, 97850, USA

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A B S T R A C T

Domestic and wild ungulates can exert strong influences on riparian woody vegetation establishment, yet little is known about how wild ungulate herbivory affects riparian restoration in the absence of cattle. We evaluated elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) impacts on the establishment of deciduous woody riparian plantings along 11 km of Meadow Creek, a steelhead (*Oncorhynchus mykiss*) and Chinook (*Oncorhynchus tshawytscha*) salmon stream in northeastern Oregon, USA. We compared survival and growth between protected and unprotected plantings (from wild ungulates), and assessed the contribution of the plantings to the total deciduous woody cover after two growing seasons. Riparian use by wild ungulates was estimated by tracking a subset of the deer and elk populations using global positioning system telemetry collars. Elk riparian use was 11 times greater than deer, and in contrast to elk, deer were functionally absent from greater than 50% of the restored reach. Wild ungulate herbivory decreased planting survival by 30%, and growth by 73%, and was most detrimental to cottonwood (*Populus balsamifera*; increased likelihood of mortality by 5 times and suppressed growth by more than 90%). Herbivory impacts resulted in survival rates below regional criteria (50%) for restoration success after only two growing seasons. Naturally recovering shrubs accounted for 99% of the deciduous woody cover, and were mostly composed of the same species or genera as those planted. Our results suggest that wild ungulate herbivory can impede riparian restoration along salmonid streams by suppressing woody plant establishment and recovery.

1. Introduction

Stream and riparian habitats are among the most altered ecosystems in the western United States (Chaney, 1993; Belsky et al., 1999). Loss of native species and ecosystem function have made stream and riparian restoration a national priority (Roni et al., 2002; Bernhardt et al., 2005). According to Bernhardt et al. (2005), over $1 billion was spent each year (1990–2003) on riparian restoration in the United States. Such efforts are particularly intensive in the Pacific Northwest where recovery of endangered salmonid species directs most riparian restoration priorities (Roni et al., 2002; Bernhardt et al., 2005; Oregon Watershed Enhancement Board, 2011).

Establishment of in-stream woody debris and streamside woody vegetation are important restoration objectives in the Pacific Northwest. Widespread loss of these structural components has altered stream morphology and degraded stream habitats, resulting in channels that are often inhospitable to salmonids due to increased stream temperatures, decreased summer flows, and habitat loss (Armour et al., 1994; Reeves et al., 1995; McCullough, 1999; Obedzinski et al., 2001). Restoration of woody debris and vegetation is expected to benefit salmonids by: (1) increasing bank stability; (2) influencing stream channel development; (3) contributing organic matter (future large wood recruitment and detritus) to streams; (4) influencing trophic interactions at the aquatic-terrestrial interface; and (5) moderating the effects of future climate change to salmon through shading and increasing stream/floodplain connectivity (Kauffman and Krueger, 1984; Reeves et al., 1995; McCullough, 1999; Allan et al., 2003; Johnson, 2004). Despite huge monetary investments to implement restoration projects, effectiveness monitoring is rare (Bernhardt et al., 2005). Therefore, success rates of revegetation efforts are mostly unknown, and general factors that limit or facilitate woody species establishment are often unidentified.

* Corresponding author.
E-mail addresses: averettj@oregonstate.edu (J.P. Averett), bryan.endress@oregonstate.edu (B.A. Endress), mrowland@fs.fed.us (M.M. Rowland), bnaylor@fs.fed.us (B.J. Naylor), mwisdom@fs.fed.us (M.J. Wisdom).

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Cattle (*Bos taurus*), elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) are widespread throughout western North America, and can have profound impacts on woody plant establishment, structure, and growth (Sarr, 2002; Danell et al., 2006). High intensity browsing by livestock (Kauffman and Krueger, 1984; Belsky et al., 1999; Danell et al., 2006) and wild ungulates (Kay, 1994; Opperman and Merenlender, 2000; Schoenecker et al., 2004) can suppress woody vegetation in riparian habitats. Most restoration practitioners recognize livestock as a threat to woody riparian vegetation restoration, and livestock exclusion can result in woody riparian community recovery (Rickard and Cushing, 1982; Kaufman et al., 2002; Holland et al., 2005; Beschta et al., 2014). However, the impacts of wild ungulates on riparian restoration are often ignored and remain largely unstudied, despite examples where wild ungulates have altered riparian woody species structure and composition (Kay, 1994; Opperman and Merenlender, 2000; Peinetti et al., 2001).

Along Meadow Creek, a perennial stream in northeastern Oregon and the focus of this study (Fig. 1), 22 years of livestock exclusion along much of the stream corridor has not resulted in riparian woody vegetation recovery. Case and Kauffman (1997) reported an initial increase in deciduous woody species density and cover two years after cattle exclusion along Meadow Creek. However, two decades later, suppressed woody vegetation –particularly species preferred by elk and deer such as cottonwood and willow (See Figs. 2 and 3 in Averett et al., submitted for publication)- and low in-stream wood recruitment contributed to local land managers' decision to implement restoration including the installation of riparian plantings along Meadow Creek (USDA Forest Service, 2016). Prior restoration plantings failed to establish along Meadow Creek in the absence of livestock grazing. Bryant and Skovlin (1982) found that almost all of thousands of conifer seedlings and deciduous shrub cuttings planted in 1975 were dead by 1978. Low survival rates were observed both inside and outside of areas grazed by cattle, and were attributed to many different factors including high flow events, scouring by ice flows, wild ungulate browsing, small mammal damage, and unsuitable planting sites (Bryant and Skovlin, 1982). These findings suggest that cattle exclusion alone may not achieve desired restoration goals, and the factors limiting woody species establishment along Meadow Creek are not well understood.

A recent restoration project in Meadow Creek provided new opportunities to investigate factors influencing success of restoration plantings. This paper describes how herbivory by wild ungulates affected restoration designed as part of recovery efforts for threatened salmonids. Our objectives were to: (1) estimate wild ungulate use within the Meadow Creek study area including ~157 ha of riparian area and ~2059 ha of upland habitat along an ~11 km stream reach; (2) evaluate the effects of mule deer and elk herbivory on survival and growth of deciduous woody restoration plantings after two growing seasons; and (3) assess the contribution of plantings to the overall deciduous woody cover of the restored area after two growing seasons. Because cattle, elk, and mule deer co-occupy millions of hectares of western North America outside National Parks, and: (1) post restoration effectiveness monitoring; (2) manipulative experiments tied to restoration activities; and (3) exclusion of wild ungulates from riparian areas are rare, restoration practitioners will benefit from an increased understanding of how elk and mule deer impact stream recovery efforts in the absence of cattle.

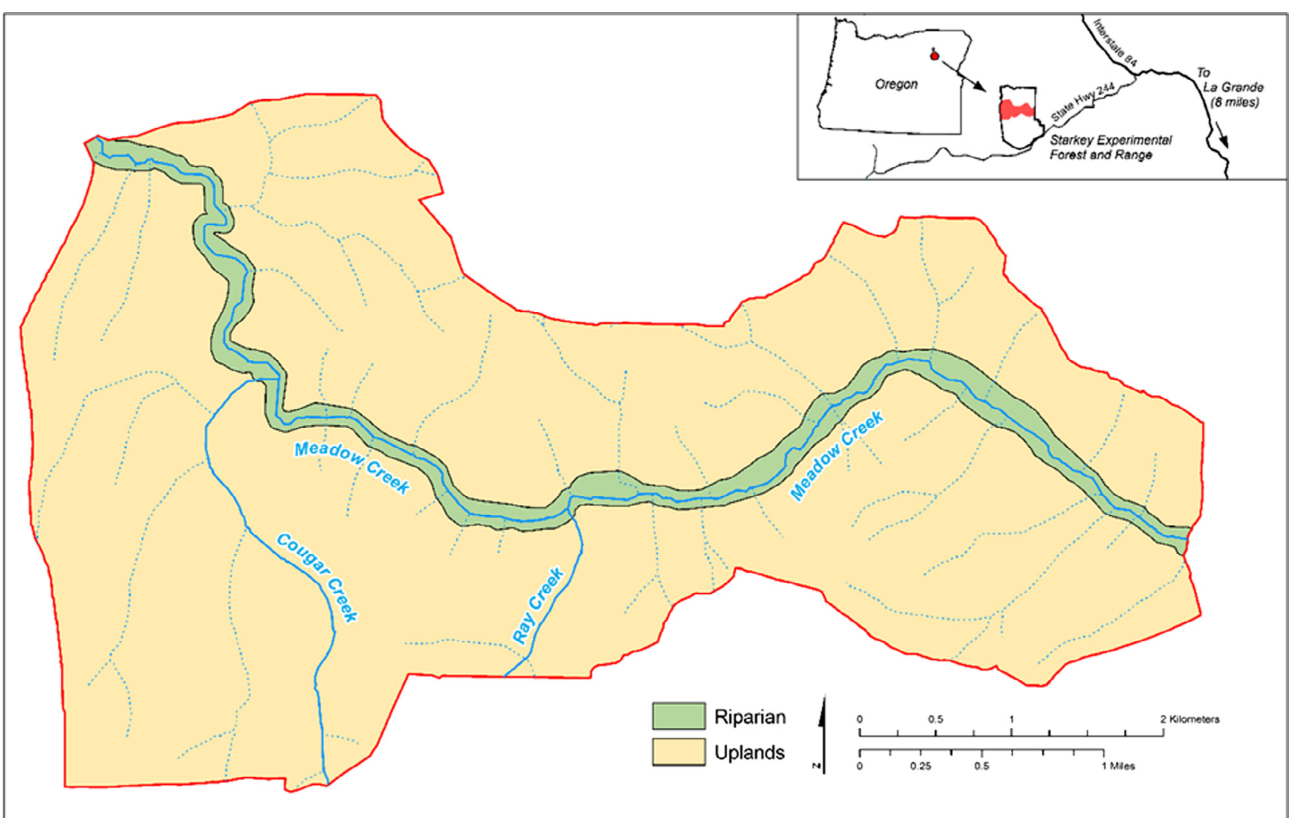

Fig. 1. The 2217-ha Meadow Creek Study Area within the Starkey Experimental Forest and Range (SEFR) in northeast Oregon, USA. The Study Area was defined by the hydrologic boundaries of Meadow Creek within the SEFR and included 157 ha of riparian area and 2059 ha of uplands.

Fig. 2. Protected (within small fenced exclosures) and unprotected woody species plantings interspersed throughout the riparian flood plain along Meadow Creek in the Starkey Experimental Forest, northeastern Oregon. Landscaping mats and shade cards mark the locations of each planting.

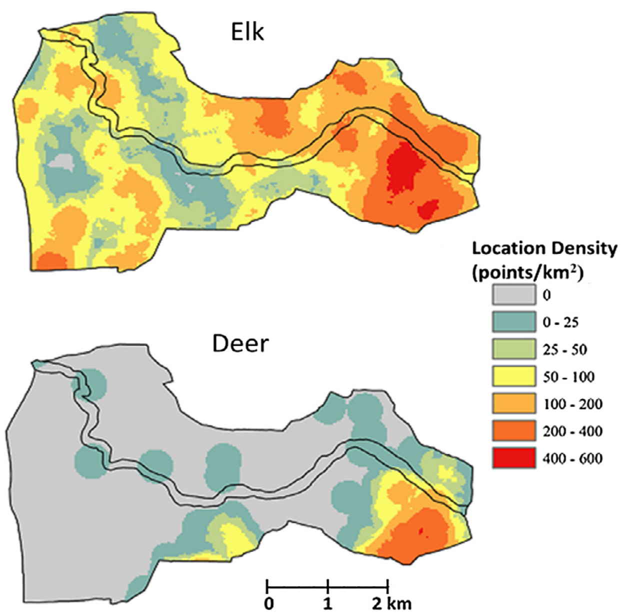

Fig. 3. Mean elk and deer location density (locations/km^2) in the riparian and upland areas of Meadow Creek during May–October of 2014.

2. Materials and methods

2.1. Study area

The 2217-ha Meadow Creek Study Area (Fig. 1) encompassed 11 km of the Meadow Creek drainage within the Starkey Experimental Forest and Range (SEFR) in northeastern Oregon, and included 157 ha of riparian area (7.1%) and 2059 ha (92.9%) of adjacent uplands (Fig. 1). Elevations in the SEFR range between 1120 m and 1500 m, and annual precipitation averages 51 cm occurring primarily in the winter as snow (Rowland et al., 1997; Kie et al., 2013). Average temperatures range from −4 °C in January to 18 °C in July (Kie et al., 2013).

The Meadow Creek Study Area is used extensively by elk and mule deer from spring through fall. Pre-parturition densities of elk (5.6–6.8 elk/km^2) and mule deer (2.8–3.6/km^2) in the SEFR are typical of those in western North America (Wisdom and Thomas, 1996; Ager et al., 2003). Elk and deer are functionally absent from Meadow Creek during winter, because they migrate to the SEFR winter area (Rowland et al., 1997). Cattle grazing did not occur along Meadow Creek during this study, and most of the study area had not been grazed by cattle for approximately 20 years prior to this research project.

A stream restoration project was implemented along Meadow Creek in 2012 and 2013 to improve habitat for federally threatened populations of steelhead (*O. mykiss*) and chinook (*O. tshawytscha*) salmon. Restoration activities included the addition of large in-stream structures (woody debris and boulders), and the installation of more than 50,000 woody plant bare-root seedlings and cuttings. All woody plantings used for restoration were native to and common in low-browse riparian areas in the region.

The Meadow Creek riparian area (Fig. 1) consisted of three major vegetation types—dry meadow, wet meadow, and open forest. Common dry meadow species included meadow foxtail (*Alopecurus pratensis*), Idaho fescue (*Festuca idahoensis*), and Canada goldenrod (*Solidago canadensis*). Northwest Territory sedge (*Carex utriculata*), panicled bulrush (*Scirpus microcarpus*), and California false hellebore (*Veratrum californicum*) were common in wet meadows. Black hawthorn (*Crataegus douglasii*) and gray alder (*Alnus incana*) were the most abundant deciduous woody species in both meadow types. Dominant species in open forests included ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) in the over-story and snowberry (*Symphoricarpos albus*) and Woods' rose (*Rosa woodsii*) in the understory.

2.2. Experimental design

Approximately equal numbers of deciduous woody plantings were exposed to two different herbivory treatments: (1) protected from large ungulate herbivory using small circular fenced exclosures (diameter ∼2 m; exclosure height ∼1.2 m; 12.5 gauge wire with hinge-lock knot design); and (2) unprotected from browsing by free-ranging elk and mule deer. The protective exclosures used in this study were consistent with those used to protect plantings from wild ungulate damage on Forest Service land in the region. Protected and unprotected plantings were interspersed relatively evenly along the 11-km Meadow Creek riparian reach (within the toe-slopes of either side of the stream channel; Fig. 2 and see Fig. 1 in Averett et al., submitted for publication). Species chosen for analyses included: black hawthorn, cottonwood (*Populus balsamifera*), golden currant (*Ribes aureum*) and willow (*Salix* spp; combined group of *S. exigua* and *S. geyeriana*). We chose these species because they had adequate sample sizes (Averett et al., submitted for publication) for meaningful analyses.

A total of 154 belt-transects (width = 4 m) extending toe-slope to toe-slope were established perpendicular to the stream channel for vegetation sampling, following the methods of Winward (2000). We sampled within transects to track survival and growth of a subset of restoration plantings as well as measure woody species cover. Transects were spaced at 100-m intervals along the entire restoration reach with higher density sampling (15-m interval spacing between transects) at three sites which are part of a future, long-term manipulative experiment.

2.3. Sampling

2.3.1. Wild ungulate use

Sixteen adult female mule deer (deer) and 31 adult female elk (elk) were captured at Starkey during the winter of 2013–14, and fitted with global positioning system (GPS) telemetry collars for monitoring (Rowland et al., 1997) spring-fall use in the Meadow Creek Study Area. GPS-collared ungulates represented approximately 16% of deer and 10% of elk within the SEFR.

Location densities were calculated for both the riparian and upland areas. We evaluated use of these areas separately to determine if deer and elk use of the riparian area was disproportionate to the availability of riparian habitat. To estimate location densities (Kenward et al., 2001) for elk and deer, we sampled the telemetry data at two locations per day (locations nearest 0500 and 2000 h daily) for each collared animal. Next, a moving window average with a 300-m radius circle centered at each 30-m pixel was used to estimate locations per km^2 across the study area. Lastly, mean location densities (use) for each species in the riparian and adjacent upland areas, and selection ratios (SR; proportion use/proportion available) for the riparian area by species were calculated. We assumed that mean location density in the riparian area directly indexed time spent there by each species and thus provided a measure of herbivory pressure on the plantings.

2.3.2. Shrub growth and survival

Sampling occurred at the beginning of growing season one (May), at the end (September) of growing season one, and at the end (September) of growing season two. We identified plantings within transects to species, recorded planting height, survival status, habitat type (dry meadow or wet meadow) and noted whether or not there was evidence of browsing. When an exclosure was encountered, if at least one planting in the exclosure was rooted within the belt transect, all plantings within that exclosure were sampled. We recorded several spatial metrics (to identify individual plantings) including distance along each transect, side of transect center line, and distance perpendicular to the transect center line for each planting so that growth and survival of individuals could be tracked. Because each planting site was prepared by the localized removal of vegetation down to bare soil and installation of a shade card and landscape mat, each plant was very conspicuous (Fig. 2). Therefore, all planting sites (protected and not protected from herbivory) were easily found during all three sampling periods, and we were able to use the spatial locations of plantings along transects to track individual plant survival and growth over time.

Two habitat types were differentiated by functional traits of the dominant species including: (1) dry meadow (grasses and forbs dominant); and (2) wet meadow (sedges, rushes, and or bulrushes dominant). Wet meadows are typically flooded for several weeks each spring, whereas dry meadows in this system rarely experience overland flooding. These habitat types correspond to steep environmental gradients in hydrology and soil redox status and thus serve as important indicators of underlying environmental gradients that may affect shrub growth, survival, and response to herbivory (Dwire et al., 2006).

2.3.3. Planting cover

Cover of deciduous woody species ($\leq$2 m) was measured in September 2015 along each transect using the line-intercept method (Canfield, 1941). We differentiated cover between existing shrubs and plantings as well as by species so that the relative contribution of planted versus natural deciduous woody cover and composition could be distinguished. The conspicuous nature of the planting sites, including shade cards, landscaping mats, and removed vegetation, made it easy to distinguish between plantings and naturally existing woody species over the study period (two growing seasons).

2.4. Statistical analysis

Survival data were analyzed with multiple logistic regression models (R V 3. 2. 0; R Core Team, 2015). Survival (0/1) after two growing seasons was the response variable. The categorical predictors were exclosure use (Yes/No), plant species, and habitat type. All major effects and two-way interactions were included in the model. Significance of each effect was assessed by comparing the full model (including all major effects and two-way interactions) to a reduced model (full model minus the effect of interest) using likelihood ratio tests. Significance of effects was evaluated based on Chi-squared values with $p \leq 0.05$. Post-hoc analyses including generalized linear hypotheses tests ('multcomp' package V 1. 4. 4; Hothorn et al., 2008a) were used to perform pairwise contrasts between species, and separate logistic regression models were run for each species to contrast species specific survival between herbivory treatment and habitat levels. Survival was the response variable, and exclosure use and habitat type were the predictors. Probabilities of survival were calculated by back transformation of the coefficient estimates from species specific logistic models ($e^{coef}/1 + e^{coef}$), and survival ratios (% survival of protected plantings/% survival of unprotected plantings) were calculated from the back transformed model estimates. We initially included "site" (groupings of transects for each 1-km increment along the restoration reach) as a random effect in our survival model (mixed effect logistic regression); however, we chose to use the simpler multiple logistic regression model because: (1) the interpretation of results including significance of fixed effects and effect size estimates were comparable between the two different models (see Table 2 in Averett et al., submitted for publication), suggesting that site was not an important source of variation in survival across our study area; and (2) to reduce noise for post-hoc species specific pairwise comparisons across habitat types, i.e., rarer species, did not have adequate sample sizes for mixed effects regression analyses when modeled independently because multiple observations for both herbivory treatments and habitat types were not available for all sites.

Growth data were analyzed using a linear mixed effects regression model with a random intercept for transect site ('lme4' Package V 1.1.7; Bates et al., 2015). We grouped transects for each 1-km increment (site) along the restoration reach to ensure multiple observations for each unit of the random effect. Growth, (cm; final height – initial height) after two growing seasons, was the response variable. Exclosure use, plant species, habitat type, and initial height (cm) of plantings were predictors. Only major effects were included in the model because a likelihood ratio test gave little evidence ($p = 0.12$) to include the two-way interaction terms. Significance of each effect was assessed by comparing the full model (including all major effects) to a reduced model (full model minus the effect of interest) using a likelihood ratio test. Predictors with Chi-squared $p \leq 0.05$ were considered significant. We used permutation tests with 10,000 randomizations of group assignments (coin package V 1. 0. 24; Hothorn et al., 2008b) to test for differences in mean growth between groups (significant categorical predictors) identified in the mixed model analysis. The 'boot' package V 1. 3. 17 (Canty and Ripley, 2015) was used to bootstrap 95% confidence intervals for mean growth based on 1000 replications. Growth ratios (growth of protected plantings/growth of unprotected plantings) were also calculated. Height distributions of plantings were plotted and visually compared to the exclosure height and to the browse line, defined as the height above which the ungulates in this system can no longer reach plants to browse.

That height was 2.5 m for elk, and 1.5–2.0 m for deer (Keigley et al., 2002).

3. Results

3.1. Wild ungulate use

Mean location density of elk (117.1 locations/km^2) was 10.5 times greater than that of deer (11.2) in the riparian area (Fig 3). Location densities in the uplands were similar, with elk mean location density (112.9) 5.8 times that of deer (19.5; Fig. 3). Elk were distributed throughout the riparian area, with positive location densities for every cell. In contrast, location density was zero for deer in more than half of the riparian area (57%; Fig. 3). Use by both species was concentrated in the eastern half of Meadow Creek, and deer were virtually absent from large portions of the western half of the study area (Fig. 3). Elk used the riparian area slightly more than expected (SR = 1.22), whereas deer used the riparian area less than expected (SR = 0.34).

3.2. Shrub survival

Significant main effects included exclosure use and species, and there was weak evidence that survival differed between habitat types (See Table 1 in Averett et al., submitted for publication). Protected plantings (survival = 78.8%) were 1.7 times as likely to survive compared to unprotected plantings (survival = 47.2%; Fig 4, Table 1). The interaction term exclosure by species was significant (See Table 1 in Averett et al., submitted for publication), indicating that the effects of herbivory on survival varied by species. Protection from herbivory increased survival for all species (Figs 4 and 5). Increased likelihood of survival ranged from 1.4 times for willows and golden currants to 2.5 times for cottonwoods (Fig 4 and Table 1). Survival of golden currants (93%) and black hawthorns (90%) was greater than that of cottonwoods (68%) and willows (68%) when protected (Fig 4 and Table 1). This pattern was consistent for unprotected plantings with the exception of survival of black hawthorns (53%) vs. willows (47%), which was not significant (Fig 4 and Table 1). Habitat type influenced survival, for willows only, which were about 1.4 times as likely to survive in wet meadows compared to dry meadows regardless of exclosure use (Fig 4 and Table 1). The significance of the habitat by species interaction was demonstrated by the differential survival of willow in response to habitat type (Fig 4 and Table 1).

3.3. Shrub growth

Exclosure use, species, and initial height influenced plant growth (see Table 3 in Averett et al., submitted for publication). Mean growth of protected plantings (39.4 cm) was about four times greater than that of unprotected plantings (10.6 cm; Figs 5 and 6 and Table 1). The overall effect size of protection from herbivory on growth was relatively consistent for golden currants (Growth ratio = 3.8), black hawthorns (3.2), and willows (3.5), and greatest for cottonwoods (>10; Fig 6, Table 1). Initial height of plantings had a negative relationship with growth (see Table 4 in Averett et al., submitted for publication). For every 1 cm decrease in initial height, growth after two years increased by approximately 0.39 cm (see Table 4 in Averett et al., submitted for publication). The exclosure effect was strengthened slightly when initial height was included in the regression model (see Table 4 in Averett et al., submitted for publication). The average height of protected species after two growing seasons was 80 cm compared to 40 cm for unprotected plantings (Fig 6). The tallest plantings after two growing seasons were approaching the height

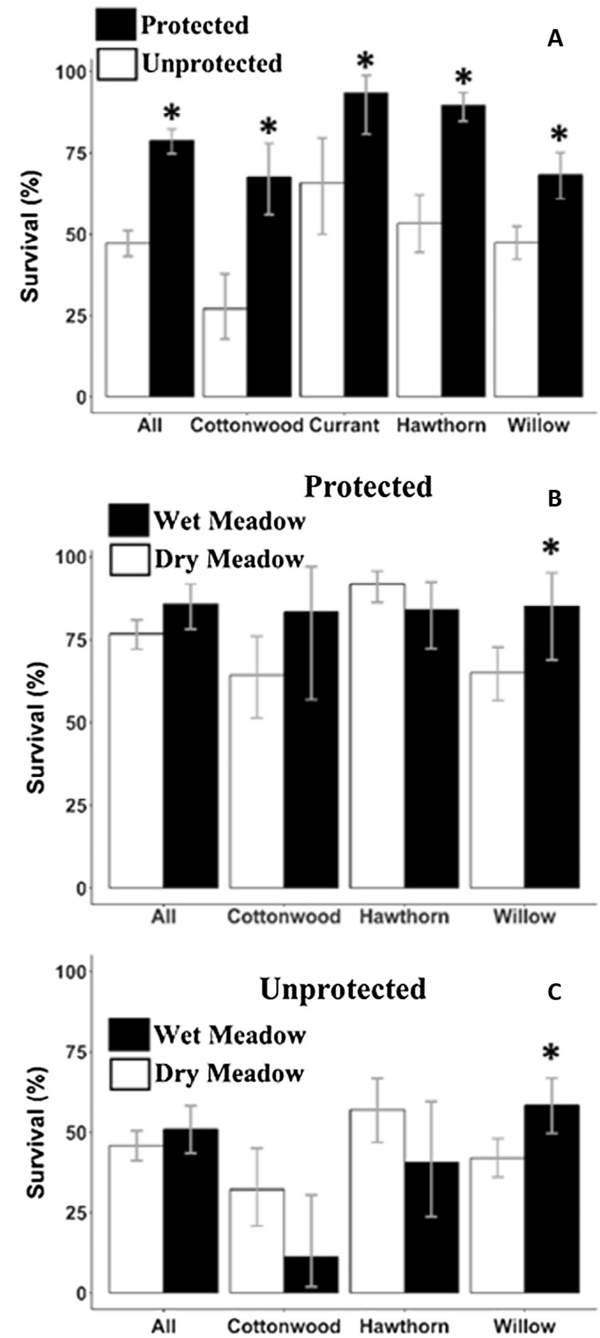

Fig. 4. Mean survival of deciduous woody riparian plantings. Error bars depict 95% confidence intervals. Asterisks indicate significant differences between mean survival for (A) protected vs. unprotected (from elk and deer herbivory) plantings stratified by species, and (B and (C) plantings in wet meadows vs. dry meadows stratified by species for both protected and unprotected plants respectively.

of the exclosures (1.2 m), but were still well below the browse line for elk (2.5 m; Fig 6). Exclosures decreased but did not eliminate browsing events on plantings (Fig 6). Browsing frequency of unprotected plantings was 48% at the end of growing season one, and 91% after growing season two compared to 6% and 29% for protected plantings after growing seasons one and two respectively (Fig 6).

3.4. Planting cover

Total deciduous woody cover, which included existing woody species and planted individuals, averaged 6.1% (range = 0.2–25%;

Table 1
Survival (%) and growth (cm) of riparian plantings after two growing seasons along Meadow Creek in northeastern Oregon for main effects included in multiple regression models. 95% confidence intervals around the mean are depicted parenthetically. Mean values followed by different upper case letters are significantly different between columns (protected/unprotected from ungulate herbivory). Mean values followed by different lower case letters are significantly different between rows (predictors). When no difference was found, groups were denoted with the same letter. Survival ratios (survival of protected plantings/survival of unprotected plantings), and growth ratios (growth of protected plantings/growth of unprotected plantings) are shown.

Predictor	Survival			Growth		
	Protected	Unprotected	Survival Ratio	Protected	Unprotected	Growth Ratio
Exclosure	78.8A (74.8,82.4)	47.2B (43.4,51.2)	1.7	39.4A (36.8,41.9)	10.6B (8.0,12.8)	3.7
Species						
Cottonwood	67.6Aa (56.0,77.9)	27Ba (17.8,37.8)	2.5	32.7Aa (23.2,41.4)	−0.8Ba (−6.6,5.7)	>10
Currant	93.3Ab (80.8,98.9)	65.8Bb (50.0,79.5)	1.4	36.0Aa (30.1,41.9)	9.4Ba (4.1,14.8)	3.8
Hawthorn	89.7Ab (84.7,93.5)	53.3Bb (44.4,62.1)	1.7	42.4Aa (39.3,45.8)	13.1Ba (9.0,17.1)	3.2
Willow	68.3Aa (60.9,75.2)	47.4Bb (42.4,52.4)	1.4	38.7Aa (33.2,43.9)	11.1Ba (7.6,14.4)	3.5
Habitat						
Dry Meadow	76.7Aa (72.1,81.0)	45.8Ba (41.2,50.5)	1.7	38.4Aa (35.4,41.3)	11.1Ba (8.3,13.9)	3.5
Wet Meadow	85.9Ab (78.1,91.8)	50.9Ba (43.4,58.3)	1.7	44.0Aa (39.1,48.4)	8.9Ba (3.0,14.3)	4.9

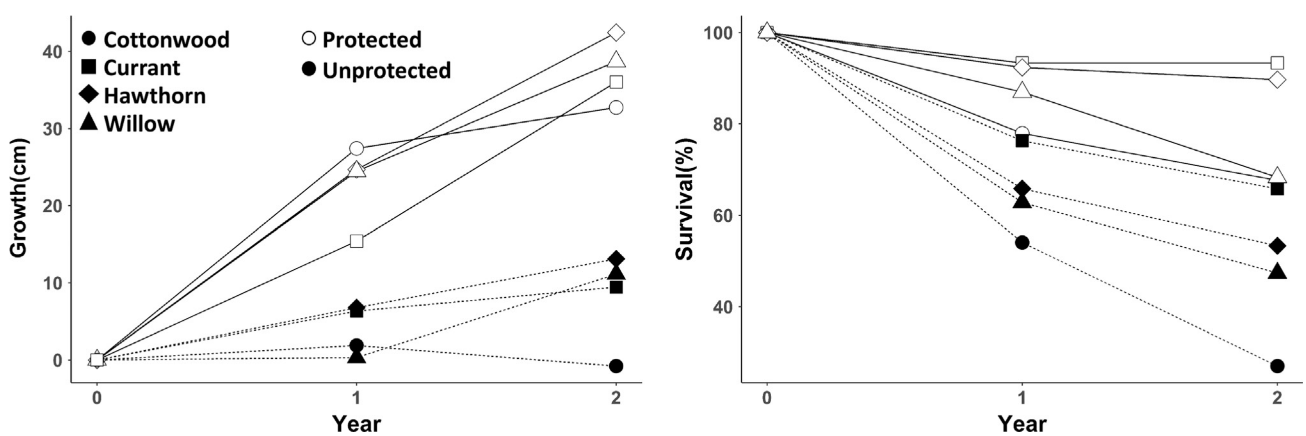

Fig. 5. Mean growth and mean percent survival of protected and unprotected (from wild ungulate browsing) plantings stratified by species over two growing seasons.

Fig 7). Plantings accounted for less than 1% of this cover across the entire restoration area (Fig 7); the remaining 99% came from woody vegetation already present. The contribution of planting cover to overall deciduous woody cover ranged from 0% to 33% along the restored reach (Fig 7). More than 50% of the existing deciduous woody cover was composed of either the same species or species from the same genera as the plantings installed in the Meadow Creek restoration site, and most of those species were widely distributed along the restoration reach (Fig 7).

4. Discussion

Our results demonstrate that wild ungulate herbivory can have measurable and immediate impacts on riparian planting establishment. Herbivory by mule deer and elk decreased survival of deciduous woody plantings by 30% and suppressed planting growth by about 73% after two growing seasons. Reduced survival of this magnitude is not inconsequential. The total cost of deciduous woody riparian plantings - excluding protective fencing along Meadow Creek - was $127,224. A decrease of 30% in planting survival would cost $38,167. Perhaps more importantly, exposure to wild ungulate herbivory resulted in overall planting survival of less than 50%, which is below the acceptable survival criteria for riparian plantings in the region (Crawford, 2011; Smith, 2013; Salmon Recovery Funding Board, 2014). When monitoring occurs, follow up actions including re-planting are often triggered when planting survival falls below 50%. Thus wild ungulate herbivory would be implicated in not only the costs associated with browsing-related mortality, but also with additional maintenance costs to compensate for low planting survival. However, if the underlying problem of high browsing pressure is not alleviated, then damage to subsequent planting efforts is likely to recur. In contrast to the unprotected plantings, almost 80% of the protected plantings survived, a level that meets current regional restoration objectives (Crawford, 2011; Smith, 2013; Salmon Recovery Funding Board, 2014).

Elk location densities were 11 times greater than those of mule deer in the riparian area, mule deer were absent in more than 50% of the Meadow Creek riparian area, whereas elk were well-distributed across the entire riparian area, and a larger percentage (81%) of collared elk used the riparian area compared to mule deer (9%). These results suggest that browsing by elk probably led to most of the herbivory-related impacts on riparian plantings in our study area. Multiple lines of evidence support this finding: (1) the population of elk at the SEFR is at least two times greater than that of mule deer (Ager et al., 2003); (2) a strong herbivory effect by elk on willow and cottonwood species has been previously documented at the SEFR (Endress et al., 2016); (3) mule deer

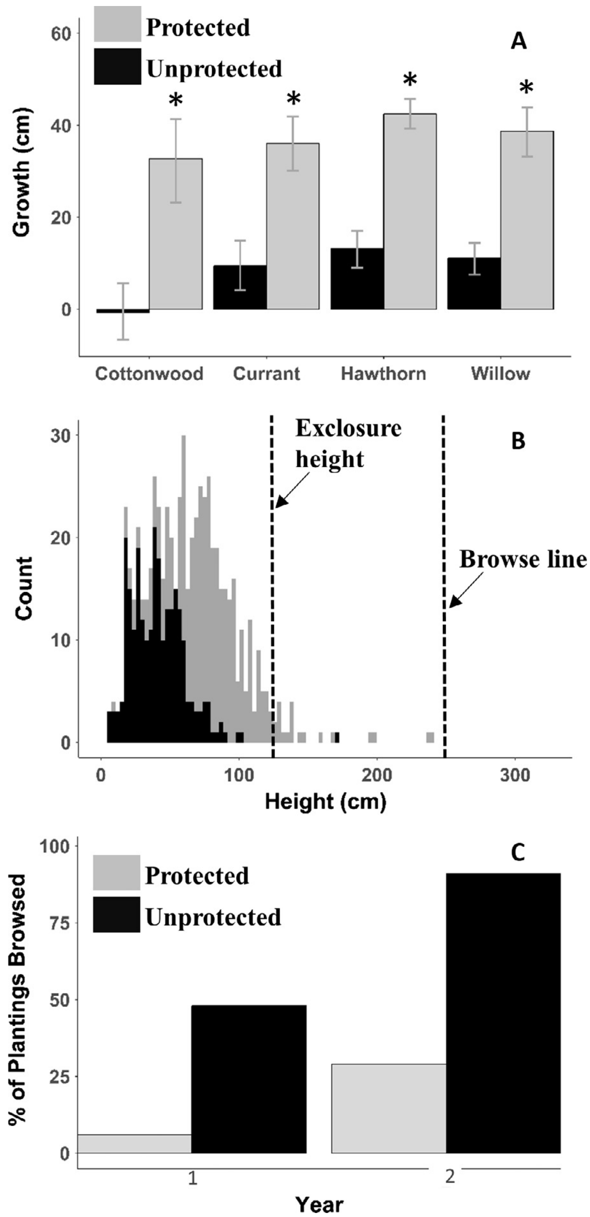

Fig. 6. (A) Mean growth, (B) height distributions, and (C) frequency of browsing for riparian woody plantings (protected vs. unprotected from deer and elk browsing) after two growing seasons. Asterisks indicate significant differences between mean growth of protected vs. unprotected plantings. Error bars depict 95% confidence intervals.

consistently avoid habitats occupied by elk at the SEFR, resulting in widespread distribution of elk but compressed distribution of mule deer (Johnson et al., 2000; Wisdom et al., 2005); (4) the daily forage intake of one elk greatly exceeds that of one deer (Cooperrider and Bailey, 1984). Thus, our use of location density to evaluate browsing impacts of elk versus deer likely underestimates the herbivory effect of elk; and (5) the percentage of GPS-collared deer (16%) was higher than that of elk (10%), further underestimating the potential herbivory effect of elk.

When protected from herbivory, survival for golden currants (93%) and black hawthorns (90%) was much higher than cottonwoods (68%) and willows (68%), and their survivorship was not influenced by habitat type. In contrast, willows, regardless of herbivory treatment, were 1.4 times as likely to survive when planted in wet meadows compared to dry meadows. These results likely reflect differences in drought tolerance between these species. Black hawthorns and golden currants are generally more tolerant of drought compared to riparian willows and cottonwoods. Numerous studies have linked favorable willow and cottonwood establishment with increased access to water resources (Bilyeu et al., 2008; Hall et al., 2011; Marshall et al., 2014). With high water availability willows can compensate for browsing pressure with increased growth (Bilyeu et al., 2008; Marshall et al., 2014). While we detected an overall increase in willow survival in wet meadows compared to dry meadows, habitat type was not a significant effect for growth, indicating that with greater access to water, plantings did not compensate for browsing by increasing growth over the duration of our study.

The effects of herbivory on survival and growth were consistent for golden currants, black hawthorns, and willows. When these species were protected from herbivory, survival increases ranged from 140% to 170% and growth increases ranged from 320% to 380%. We found that protection from herbivory not only facilitated the early establishment of cottonwoods and willows, species known to be sensitive to wild ungulate browsing (Kay, 1994; Beschta, 2003), but also black hawthorn, a species generally considered resistant to browsing. Researchers have reported that because black hawthorn is not preferred by elk and deer (primarily due to protective thorns), it can invade into areas where wild ungulates select more palatable shrubs (Bartuszevige et al., 2012). Our detection of comparable herbivory effects on the survival of willow and black hawthorn are likely explained by the lack of protective thorns on young hawthorns and current year's growth (Danell et al., 2006). Seedlings and annual suckers of hawthorns are thorn-less, and the thorns of new leaders do not harden until the end of the growing season. Thus, recruitment of new hawthorns into riparian areas with high browsing pressure occurs primarily beneath the canopy of mature hawthorns, where they are protected from herbivory (Danell et al., 2006). Isolated and unarmed hawthorn seedlings/saplings, like those installed as restoration plantings, may succumb to browsing pressure where wild ungulates concentrate if not protected.

Wild ungulate herbivory had the greatest impacts on cottonwood establishment compared with other planted species. We found that exposure to herbivory resulted in a fivefold increase in likelihood of mortality and greater than 90% suppression of growth for cottonwoods. Additionally, cottonwood was one of the rarest of the naturally existing woody species in our study area (see Fig. 2 in Averett et al., submitted for publication). This does not necessarily mean that the potential for cottonwood recruitment is inherently low in our study area. Previous research suggests that cottonwood recovery can be vigorous with large ungulate exclusion along Meadow Creek (Case and Kauffman, 1997). Alternatively, our results likely reflect the high palatability of cottonwoods, and thus strong selection by wild ungulates for cottonwoods over other deciduous woody species. Our findings are consistent with others who have reported considerable wild ungulate suppression of cottonwood recruitment and disproportionate wild ungulate use of cottonwood compared to less palatable deciduous woody species in riparian areas (Kay, 1994; Case and Kauffman, 1997; Beschta, 2005). Failure to establish cottonwood communities along Meadow Creek may have important implications for salmonid recovery. Because cottonwoods grow faster and taller than most other deciduous woody species in the interior Pacific Northwest, cottonwood communities may provide key and unique ecosystem services to salmonid streams including: (1) extensive shading and subsequent stream temperature moderation, a major limiting factor for salmonid populations in the Pacific Northwest (McCullough, 1999); (2) large wood addition to streams; and (3) support of unique species assemblages that pro-

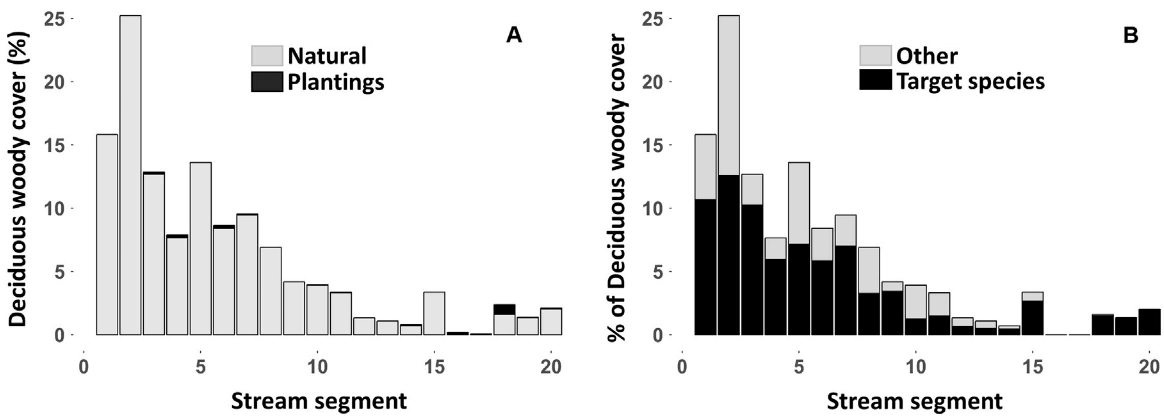

Fig. 7. Canopy cover of deciduous woody species (≤2 m) along the Meadow Creek restoration area in northeastern Oregon. (A) Total deciduous woody cover stratified by stream segment (0.5-km stream sections) for both naturally existing woody species and plantings; and B) percentage of total natural deciduous woody cover, by site, composed of the same species or genera planted (Target species) during the Meadow Creek restoration project. Stream segments progress from east to west with increasing site number.

vide allocthonous resources, e.g., detritus and insects, to streams (Braatne et al., 1996; Beschta, 2005).

Protected plantings grew about 40 cm over two growing seasons compared to 10 cm for unprotected plantings. If plantings continue to grow at our observed rates of 20 cm per year for protected plantings and 5 cm per year for unprotected plantings, protected plantings will reach the browse line (i.e., 2.5 m) in eight additional years, but unprotected plantings will require more than 40 years. Importantly, plants taller than the browse line would remain susceptible to heavy browsing pressure for some time because all but the uppermost portion of any plant would be accessible for browsing. Moreover, saplings - particularly willows and cottonwoods - at such heights are thin-stemmed, and thus easily bent over by large ungulates while browsing. Therefore, additional time may be needed to allow plantings to escape heavy browsing pressure. Realistically, growth rates will vary somewhat by year and by species; however, given the growth rates observed in our study, it is probably safe to state that several years (5–10) for protected plantings, and several decades for unprotected plantings, may be necessary from the time of planting to escape heavy browsing by ungulates in similar systems. It is common practice on federal land in the Pacific Northwest to rest riparian areas from cattle grazing for a minimum of two years, but up to five years post-restoration to allow for woody vegetation recovery. After two growing seasons, heights for both protected (80 cm) and unprotected plantings (40 cm) were well below the browse line for elk (2.5 m), and cattle (1.5–2.0 m), which suggests that a two-year minimum rest period is inadequate to allow plantings to escape heavy browsing pressure in this system.

Our results indicate that the exclosures reduced, but did not eliminate, browsing. Browsing of protected plantings was possible because the exclosures were too short to provide long-term protection from elk herbivory. As planting heights approached the tops of the exclosures, our observations indicate that elk were able to lean in and browse the tops of the plantings. In other areas without ungulate protection, high concentrations of elk have restricted the height growth of woody vegetation below the browse line (Kay, 1994; Schoenecker et al., 2004). Our detection of suppressed growth of unprotected plantings suggests that a similar pattern may be occurring along Meadow Creek (Also see Fig. 3 in Averett et al., submitted for publication). Therefore, the reduced efficacy of the exclosures used in our study once plantings have reached the top (~1 m) may result in elk limiting planting growth to the exclosure height. A similar effect was documented where white-tailed deer (*Odocoileus virginianus*) browsing suppressed riparian tree growth within protected shelters in New England (Keeton, 2008). Keeton (2008) concluded that shelters would need to be taller (≥1 m) to exclude deer browsing for successful seedling establishment. Fenced exclosures 2.4 m high have been effective for elk exclusion, and may be necessary to provide long-term protection for plantings from elk (Walter et al., 2010). Because hawthorns develop protective thorns with age, exclosures may provide more long-term growth benefits to black hawthorns compared to unarmed plantings by allowing hawthorns to survive long enough to produce anti-herbivory protection.

Riparian plantings contributed an almost negligible percentage (about 1%) to the total cover of deciduous woody species after two growing seasons. Our results indicate that the existing deciduous woody cover, while low (averaging about 6%), was distributed across most of the restoration area. Additionally, more than half of the existing shrub cover was composed of either the same species or genera as those planted along Meadow Creek. These data suggest that the existing woody vegetation in our study area has much greater potential to contribute to the overall regeneration of the deciduous woody community compared to the plantings, if not suppressed by wild ungulate herbivory. Although planting of seedlings is one of the most common restoration tools used when recovery of woody species is desired (Palmer et al., 2007), there is evidence in some areas that if barriers to recovery, e.g., heavy browsing pressure, are removed, then natural recovery may be more successful and cost-effective than revegetation efforts (Pollock et al., 2005). Because several of the planted species, e.g. cottonwoods, were rare throughout our study area, the planting effort may contribute to increased compositional and functional diversity if those species survive long-term.

4.1. Implications

Our findings suggest that exclusion of livestock alone may not result in riparian vegetation recovery, and that reduction of wild ungulate browsing should be a management goal for riparian woody species recovery in this and similar systems. We detected clear survival advantages to planting black hawthorn and golden currants over willows and cottonwoods. Practitioners may consider planting these species where they can meet restoration goals. If willow-dominated communities are desired, then focusing planting efforts in areas with abundant water resources should increase survivorship. The growth rates for plantings in our study did not align with common management practices, e.g., a two-year rest period minimum for livestock following restoration, on federal land in the interior Pacific Northwest. Widespread survival and growth rate monitoring of woody species post restoration may be necessary to develop realistic time frames and appropriate exclosure designs for exclusion of problematic ungulates, whether domestic or wild. Lastly, our results provide an example where the natural release of deciduous woody species had, by far, the greatest potential for recovery along Meadow Creek. We recommend that practitioners (1) evaluate the potential for natural recovery of existing deciduous woody species prior to restoration, (2) protect natural recruitment from browse pressure where practical, and (3) supplement natural recruitment with plantings to meet restoration goals, e.g. planting species that are not well represented in the naturally recruiting species composition or are functionally important.

Author contributions

BE, MR and MW conceived and designed the research; JA, BE, MR, BN and MW performed the experiment, analyzed the data, and wrote the edited manuscript.

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