

Aboveground and belowground mammalian herbivores regulate the demography of deciduous woody species in conifer forests

BRYAN A. ENDRESS,^{1,†} BRIDGETT J. NAYLOR,² BURAK K. PEKIN,³ AND MICHAEL J. WISDOM²

¹Eastern Oregon Agriculture and Natural Resource Program, Department of Animal and Rangeland Sciences, Oregon State University, La Grande, Oregon 98750 USA

²USDA Forest Service, Pacific Northwest Research Station, La Grande, Oregon 98750 USA

³Eurasia Institute of Earth Sciences, Istanbul Technical University, Istanbul 34469 Turkey

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Abstract. Mammalian herbivory can have profound impacts on plant population and community dynamics. However, our understanding of specific herbivore effects remains limited, even in regions with high densities of domestic and wild herbivores, such as the semiarid conifer forests of western North America. We conducted a seven-year manipulative experiment to evaluate the effects of herbivory by two common ungulates, *Cervus elaphus* (Rocky Mountain elk) and cattle *Bos taurus* (domestic cattle) on growth and survival of two woody deciduous species, *Populus trichocarpa* (cottonwood) and *Salix scouleriana* (Scouler's willow) in postfire early-successional forest stands. Additionally, we monitored belowground herbivory by *Thomomys talpoides* (pocket gopher) and explored effects of both aboveground and belowground herbivory on plant vital rates. Three, approximately 7 ha exclosures were constructed, and each was divided into 1-ha plots. Seven herbivory treatments were then randomly assigned to the plots: three levels of herbivory (low, moderate, and high) for both cattle and elk, and one complete ungulate exclusion treatment. Treatments were implemented for seven years. Results showed that cattle and elk substantially reduced height and growth of both cottonwood and willow. Elk had a larger effect on growth and subsequent plant height than cattle, especially for cottonwood, and elk effects occurred even at low herbivore densities. Pocket gophers had a strong effect on survival of both plant species while herbivory by ungulates did not. However, we documented significant interaction effects of aboveground and belowground herbivory on survival. Our study is one of the first to evaluate top-down regulation by multiple herbivore species at varying densities. Results suggest that traditional exclosure studies that treat herbivory as a binary factor (either present or absent) may not be sufficient to characterize top-down regulation on plant demography. Rather, the strength of top-down regulation varies depending on a number of factors including herbivore species, herbivore density, interactions among multiple herbivore species, and varying tolerance levels of different plant species to herbivory.

Key words: cattle; elk; grazing; North America; Oregon; plant population dynamics; plant-herbivore interactions; *Populus trichocarpa*; *Salix scouleriana*; trophic cascades; ungulate herbivory.

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† **E-mail:** bryan.endress@oregonstate.edu

INTRODUCTION

Mammalian herbivory can have profound effects on plant community structure, composition, and dynamics as well as the distribution,

abundance, and demography of individual species (Augustine and McNaughton 1998, Endress et al. 2004, Beguin et al. 2011, Sankaran et al. 2013). A diverse array of mammals have been shown to affect plant population and community

dynamics, ranging from large herbivores such as elephants, deer, and moose to small-bodied species such as hares, pocket gophers, and voles (Cantor and Whitham 1989, McInnes et al. 1992, Fritz et al. 2002, Côté et al. 2004, Howe et al. 2006, Lyly et al. 2014). While the strength of top-down regulation of vegetation by mammalian herbivores varies with environmental conditions (Oksanen et al. 1981, Gough et al. 2012, McLaughlin and Zavaleta 2013, Young et al. 2013), herbivory effects have been reported across multiple ecosystems, biomes, and continents (Gill 1992, Oksanen and Moen 1994, Asquith et al. 1997, Rooney and Waller 2003, Bakker et al. 2006).

Despite numerous studies, our understanding of specific mammalian herbivore effects on plant populations and communities remains limited for a number of reasons. First, most studies exclude herbivores from the ecosystem (often via exclosures) and then compare vegetation changes inside and outside of the exclosures (e.g., McNaughton 1985, Manson et al. 2001, Howe et al. 2006, Sankaran et al. 2013). While this approach is an important first step in documenting top-down regulation, traditional exclosure studies often report pooled effects among different herbivores (e.g., Sankaran et al. 2013, Pekin et al. 2014a). As most ecosystems contain multiple herbivores, it is difficult to separate species-specific effects or determine the relative contribution of different herbivores to the observed effects. Moreover, regardless of the number of herbivore species within the system, traditional exclosure studies treat herbivory as a binary factor (either present or absent) and compare effects of complete herbivore exclusion to an often unknown or unreported density of herbivores in the surrounding area. This makes it difficult to evaluate how results from the experiment relate to the broader landscape where herbivore densities vary in space and time. Further complicating our understanding is that herbivory often interacts with other factors such as fire, drought, insect outbreaks, and other land use activities that occur within the same ecosystem (Weisberg and Bugmann 2003, Eschtruth and Battles 2008, Endress et al. 2012, Pekin et al. 2015).

Research that explores how different herbivore species at varying densities influence the direction and strength of top-down regulation would

advance our understanding of how, when, and to what degree mammalian herbivores affect plant individuals, populations, and communities. It would also increase our ability to develop management strategies that account for herbivores role in affecting vegetation dynamics. Addressing these questions is challenging and requires long-term manipulative experiments, which have been advocated for some time (Wisdom et al. 2006, Turkington 2009), but for which only a handful have been conducted (e.g., Goheen et al. 2013, Lyly et al. 2014, Pekin et al. 2014b). Results from these studies indicate that top-down regulation on vegetation is a product of multiple herbivore species differentially affecting plant species and often interacting with other ecological factors. This highlights the need for researchers to incorporate multiple species, densities, and interactions with other ecological factors into herbivory studies to advance our understanding of top-down regulation.

In the semiarid coniferous forests of western North America, ungulates are important regulators of plant population and community dynamics (Riggs et al. 2000, Wisdom et al. 2006, Endress et al. 2012). Yet, despite high densities of wild and domestic ungulates throughout ecosystems of the region, few studies have examined the role of mammals in influencing conifer forest dynamics (Wisdom et al. 2006). It has been hypothesized that ungulate herbivory coupled with episodic disturbances such as fire, insect outbreaks, or timber harvest is a key driver influencing trajectories of forest succession (Wisdom et al. 2006, Vavra et al. 2007). Endress et al. (2012) found when ungulates were excluded from early-successional postfire stands, recruitment of deciduous woody species including black cottonwood (*Populus trichocarpa* Torr. and A. Gray ex Hook), willow (*Salix* spp.) and aspen (*Populus tremuloides* Michx.) was four times greater than in adjacent areas that were exposed to herbivory by *Bos taurus* (domestic cattle), *Odocoileus hemionus* (mule deer), and *Cervus elephus* (Rocky Mountain elk). Additionally, ungulates suppressed plant growth as individuals that established in ungulate-excluded areas were significantly taller, with some species more than three times greater in height than individuals in areas exposed to herbivores. These findings further suggest strong herbivore effects on

certain deciduous woody species by ungulates following disturbance events. However, results were pooled effects from multiple ungulates and compared complete herbivore exclusion to background herbivore density levels. We still know little about the relative importance of the different herbivores species and how the strength of top-down regulation varies with herbivore density. Additionally, ungulates are not the only mammalian herbivores in these landscapes, and previous research suggests that root herbivory by pocket gophers (*Thomomys talpoides*) may also affect deciduous woody species establishment and survival (Bryant and Skovlin 1982, Cantor and Whitham 1989). Belowground herbivory is an overlooked aspect of mammalian herbivore studies despite their presence in many ecosystems and the recognition that root herbivory can result in large impacts on plant demographic performance (Zvereva and Kozlov 2012, Stephens et al. 2013).

Here, we report on a large-scale, seven-year experiment in the semiarid coniferous forests of western North America that examines the effects of different ungulate herbivore species (elk, cattle) at varying densities on the growth and survival of two deciduous woody species. To compare the relative importance of different ungulate herbivores, we experimentally manipulated densities of cattle and elk in early succession postfire forest stands following fuel reduction treatments (stand thinning followed by prescribed fire) and evaluated the growth and survival of cottonwood and Scouler's willow (*Salix scouleriana* Barratt ex. Hook.), two deciduous woody species that recruit prolifically following fire and whose abundance and size appears to be strongly regulated by ungulate herbivores (Endress et al. 2012). Demographic performance of individuals was then used to evaluate how different herbivore species and densities influenced the strength of top-down regulation. We also monitored belowground herbivory by pocket gophers during the study to explore the effects of both aboveground and belowground herbivory on plant vital rates. We hypothesized that elk, considered "mixed feeders" that both graze herbaceous species and browse woody species (Hobbs et al. 1981, Cook 2002), would exert more pressure on cottonwood and willow than cattle, which are primarily grazers who prefer herbaceous species

(Clark et al. 2013), resulting in greater effects by elk on the survival and growth of the two plant species. Moreover, we hypothesized that for both ungulates, increasing herbivore density would increase pressure on plant populations and have greater impacts on individual plant demographic performance.

METHODS

Study area and species description

Research was conducted in mixed conifer forest stands dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) and *Abies grandis* (Douglas ex D. Don) Lindl. (grand fir) within the Starkey Experimental Forest and Range (hereafter "Starkey") in the Blue Mountains Ecological Province of northeast Oregon. Elevations range from 1200 to 1500 m above sea level with approximately 400 mm annual precipitation, most of which occurs as winter snow or spring rain, with a predictable drought from late summer to early fall (Rowland et al. 1997). Forests are typical of those found throughout interior western North America (Wisdom 2005). Understories were a diverse mix of grass and grass-like species, forbs, and deciduous woody shrubs (Pekin et al. 2014a, b, 2015).

During the past 25 years, approximately 500 cow-calf pairs of cattle have grazed Starkey from mid-June through mid-October. During this same period, approximately 200 mule deer and 350 elk have grazed/browsed during spring, summer, and fall (April through November) of each year (Rowland et al. 1997, Wisdom 2005). Population densities of cattle (7.15/km²), elk (4.55/km²), and mule deer (1.95/km²) at Starkey are typical of densities on summer ranges in western North America (Wisdom and Thomas 1996).

Both Scouler's willow and cottonwood are solitary, non-clonal species with the ability to stump sprout from the root crown following disturbance. Scouler's willow is a common understory shrub in conifer forest throughout western North America and recruits readily following fire (Anderson 2001). Cottonwood is often associated with floodplains and riparian areas (Steinberg 2001); however, it can frequently occur at low abundances in early-successional conifer forest stands (Moeur 1992, Endress et al. 2012). Within Starkey, high abundances of both species were reported

following stand thinning and prescribed fire when cattle, elk, and deer were excluded from the sites (Endress et al. 2012). Additionally, in post-fire stands exposed to ungulates, cottonwood and Scouler's willow individuals were significantly less abundant and heavily browsed, resulting in suppressed plant heights.

Silvicultural treatments and enclosure design

Three large ungulate enclosures, Half Moon (7.3 ha), Bally Camp (6.8 ha), and Louis Spring (7.3 ha), were constructed following fuel reduction treatments across Starkey as part of a comprehensive research effort to examine forest management—ungulate herbivory interactions (Endress et al. 2012, Clark et al. 2013, Pekin et al. 2014a, b, 2015). Fuel reduction treatments were designed to reduce extremely high fuel loads (>150 tons/ha) that developed from an outbreak of western spruce budworm (*Choristoneura occidentalis*) that killed the majority of grand fir and Douglas fir trees in the overstory in the 1980s–1990s (Vavra et al. 2004a, b, Bull et al. 2005). Stands were mechanically thinned to reduced fuel loads to <35 tons/ha, and following thinning, sites were broadcast burned. Treatments were designed and implemented in a manner typical of fuel reduction activities across coniferous forests in the western United States (Agee and Skinner 2005). Stand thinning for the three sites occurred during summer 2001, and both Bally Camp and Louis Spring were broadcast burned in the fall of the same year (2001). Half Moon was not burned until the summer 2002 to meet desired conditions for prescribed burning compatible with burn conditions at the other enclosures.

The enclosures were established following fuel treatments by constructing an eight-foot high fence that excluded all ungulates (cattle, elk, and mule deer), but allowed for other wildlife to pass under, over, or through. The enclosures were constructed in the year following the fuel treatments: 2002 for Bally Camp and Louis Spring, and 2003 for Half Moon. The size and shape of each enclosure varied depending on site conditions (topography, slope, forest structure, and the shape of the forest patch) to minimize variation within enclosures. Each enclosure was then divided into seven, roughly equal-sized and shaped plots (ranging from 0.95 to 1.02 ha/plot), and seven levels of cattle and elk herbivory were randomly

assigned to the plots. The levels included low, moderate, and high late summer browsing by elk or by cattle and one level of total ungulate exclusion.

Ungulate herbivory treatments

Herbivory treatments began three years following enclosure construction (Bally Camp and Louis Spring: 2005, Half Moon: 2006) and were conducted annually for seven years. Herbivory levels for each treatment level (low, moderate, and high) were defined in terms of the number of days per ha, or stocking density, that elk and cattle use Douglas fir and grand fir forests in the interior northwestern United States, broken down into three levels of forage utilization: high—45% utilization; moderate—30% utilization; and low—15% utilization. These levels typify the range of use established for cattle on summer ranges in Douglas fir and grand fir habitat types on public lands like those at Starkey (Holechek et al. 1998). Public land grazing policies typically do not allow a level of forage utilization by cattle that exceed the high treatment level, nor is it common that utilization levels by cattle on public lands occur below our established low treatment level (Holechek et al. 1998). Consequently, our levels of forage utilization encompass the broad range of levels that typically occur on public grazing allotments in the western United States.

Stocking density (SD) for cattle and elk was then calculated using standard forage allocation procedures based on the specified level of forage utilization (FU, expressed as a proportion), the available forage for each ungulate (AF, kg/ha), and the average daily forage intake of each ungulate (DFI, $\text{kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$) as $\text{SD} = (\text{FU} \times \text{AF}) / \text{DFI}$. Using this formula, stocking densities were determined as follows: for elk (low, moderate, and high): 8, 16, and 32 d/ha respectively; for cattle (low, moderate, and high): 10, 20, and 30 d/ha, respectively. Use of this algorithm to establish stocking densities of domestic ungulates, and wild ungulate equivalencies, is a conventional method based on standard forage allocation procedures used on public grazing allotments throughout the western United States (Holechek et al. 1998) and encompass the range of cattle and elk densities that typically occur on public ranges during summer in the western United States.

The calculated stocking densities were then refined so that the final number of cattle days per ha and elk days per ha for each treatment level corresponded to what was logistically feasible to implement with the tractable animals. Moreover, the number of animals must be compatible with each ungulate's group behavior for foraging and the need to complete the trials in as few days as possible to minimize changes in forage availability and phenology. As a result, we used four elk and six to eight cattle per trial to most efficiently approximate the calculated stocking densities. The diets of elk and cattle tend to converge during late summer in grand fir and Douglas fir forests (Findholt et al. 2004) when both ungulates typically increase selection for nutritious deciduous shrubs because grasses and forbs senesce and are of low quality following the onset of summer drought (Cook et al. 2004). We thus carried out the browsing treatments each year during August because we hypothesized that browsing would have the greatest effect on deciduous woody species during this time (Vavra et al. 2004a).

Demography of cottonwood and willow

We conducted a census to identify, count, and permanently tag cottonwood and willow individuals within the exclosures before implementing the herbivory treatments. Plots were systematically searched on three separate occasions between May and July 2005 (Louis Spring, Bally Camp) and 2006 (Half Moon). When encountered, all individuals were given a unique ID number and tag, and their location georeferenced with a Global Positioning System (GPS) unit (Trimble Pathfinder ProXRS; Trimble, Austin, Texas, USA). In July, before initiating the herbivory trials, we revisited all individuals and measured their heights. We remeasured tagged individuals annually each summer over the seven years of the study. During each sampling event, we recorded plant survival and height. When we encountered newly recruited plants during sampling, they were tagged, measured, and growth and survival tracked throughout the duration of the study.

At the beginning of our study, we observed considerable pocket gopher activity at the base of willow and cottonwood individuals, often killing individuals by chewing through the entire stem just below the soil surface (Fig. 1a, b). To incorporate pocket gopher effects into our study,

we recording the presence of recently created soil mounds directly at the base of individuals (1 = yes; 0 = no) during our measurements. Additionally, we verified the cause of plant mortality by excavating individuals that died during the study and examining for gopher damage near the root crown (Fig. 1b). Monitoring and measuring subterranean herbivore effects on plants using mounds presence and density is a frequent and standard approach when destructive or more formal experimental measurements are not possible (e.g., Cantor and Whitham 1989, Cox and Hunt 1994, Campos et al. 2001, Lara et al. 2007).

For individuals exposed to ungulate herbivory treatments (all individuals except those in the complete ungulate exclusion treatment), we also resampled individuals immediately following implementation of herbivory treatments (late August or early September of each year) and recorded if the plant had been browsed in the most recent herbivory trial (1 = yes, 0 = no), and their height remeasured. Over the course of the study, we tracked the fate of 946 cottonwood individuals and 1290 willow individuals. This resulted in the following sample sizes: for cottonwood—low elk ($n = 113$), moderate elk ($n = 51$), high elk ($n = 130$), low cattle ($n = 186$), moderate cattle ($n = 109$), high cattle ($n = 87$), and ungulates excluded ($n = 270$) and for willow—low elk ($n = 163$), moderate elk ($n = 109$), high elk ($n = 243$), low cattle ($n = 127$), moderate cattle ($n = 145$), high cattle ($n = 252$), and ungulates excluded ($n = 251$).

Data analyses

To evaluate herbivory intensity on willow and cottonwood populations exposed to the herbivory treatment levels, we calculated “browse pressure” for each species for each year of the experiment. This was calculated as the proportion of individual plants in the population that were browsed. We used logistic regression within a mixed modeling framework (Schall 1991) to test whether the proportion of plants browsed (browse pressure) differed among ungulates (cattle, elk) and densities (low, moderate, and high). We used the function `glmmPQL` of the MASS package (Venables and Ripley 2002) in R (R Core Team 2012). Because the proportion of browsed plants was calculated annually over seven years,



Fig. 1. (a) Pocket gopher mound at the base of a wilting cottonwood (*Populus trichocarpa*) seedling; (b) evidence of pocket gopher herbivory near root crown of a Scouler's willow (*Salix scouleriana*); (c) cattle grazing one of the experimental plots; and (d) an elk browsing *S. scouleriana* during the experiment.

we included sampling year as a random effect along with study site. Ungulate density (low, moderate, or high) and type (cattle or elk) were included as fixed effects. We ran three separate analyses. The first analysis included a fixed variable indicating the species (willow or cottonwood) to test for differences in browse pressure among the two plant species. We then ran the

model separately for cottonwood and willow species to specifically evaluate effects of stocking densities and ungulate type by plant species. Interactions between effects were initially tested and left in the models if significant ($P < 0.05$).

We evaluated treatment effects on survival rates of plants over the seven-year study using Cox proportional hazards regression analyses

(Andersen and Gill 1982) with the R function `coxph` in the survival package (Therneau and Grambsch 2000). Independent variables included in the models were ungulate type (elk and cattle), ungulate density (none, low, moderate, and high), and the intensity of belowground herbivory (none, low, moderate, and high). Levels of belowground herbivory were determined by calculating the percentage of years that we observed active pocket gopher activity directly at the base of each individual. We grouped percentages into four intensity levels: low (0–24%), moderate (25–49%), high (50–74%), and very high ($\geq 75\%$). Interaction effects among independent variables were initially tested, and both independent variables and interaction effects were dropped from the final model if not significant ($P > 0.05$).

We evaluated the effect of ungulate browsing on plant height using Poisson regression within a mixed modeling framework using the MASS function `glmmpQL`. Fixed independent variables included ungulate type and density, initial plant height, and belowground herbivory. Sampling year and site were included as random factors in

the models. Models for willow and cottonwood were run separately.

RESULTS

Browse pressure

When the experiment began, densities of cottonwood and willow were similar. Cottonwood densities averaged 34 individuals per hectare ($SE = 4.9$), while willow densities averaged 31 individuals per hectare ($SE = 6.2$). Over time, willow densities remained fairly constant while cottonwood densities declined rapidly, resulting in a mean cottonwood density of 13.4 individuals per hectare ($SE = 2.8$) at the end of the study (Fig. 2). The proportion of plants browsed during the study differed significantly depending on plant species (cottonwood vs. willow), ungulate type (elk vs. cattle), and ungulate density (low, moderate, and high). Browse pressure was significantly greater for willow than cottonwood ($t = 5.049$, $P < 0.001$), and elk browsed a significantly greater proportion of plants (cottonwood and willow combined) than cattle ($t = 5.003$,

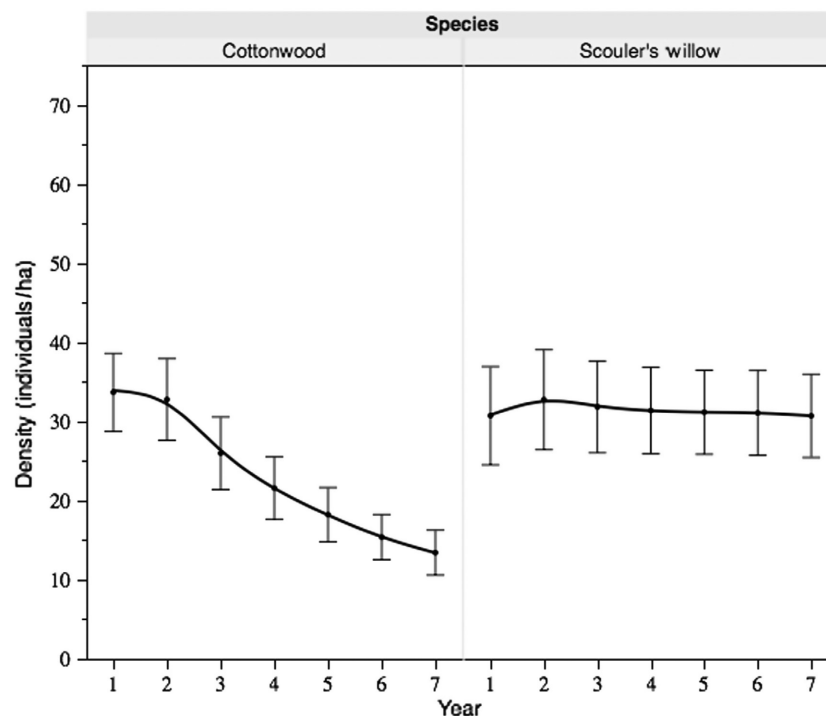


Fig. 2. Mean density ($\pm SE$) of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) across the herbivory treatments over the seven-year experiment.

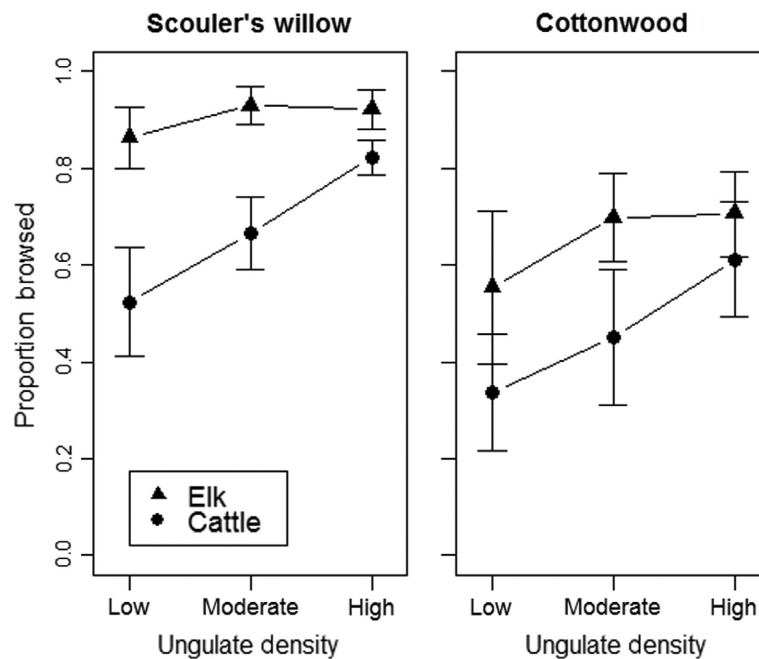


Fig. 3. The average proportion ($\pm 95\%$ confidence intervals) of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals browsed per year by cattle (*Bos taurus*) and Rocky Mountain elk (*Cervus elephus*) over a seven-year period.

$P < 0.001$). Additionally, regardless of the ungulate species, increasing stocking density resulted in a greater proportion of browsed plants ($t = 6.311$, $P < 0.001$).

For cottonwood, regardless of the ungulate species (cattle or elk), as herbivore density increased, so did browse pressure (Fig. 3, Table 1). However, elk browsed a greater proportion of individuals than cattle (Fig. 3, Table 1). Mean percentage of individuals browsed per year for the cattle treatment ranged from 34% (SE = 5.8) in the low-density treatment to 61% (SE = 5.7) in the high-density treatment. For elk, browse pressure ranged from 55% (SE = 7.4) in

the low-density treatment to 71% (SE = 4.2) in the high-density treatment.

Similar results were found for willow (Fig. 3, Table 1). Browse pressure by elk was high ranging from 86% (SE = 3.0) at the low stocking density to 92% (SE = 2.0) in the high-density treatment. Browse pressure by cattle was lower and increased as density increased, ranging from 34% (SE = 5.8; low treatment) to 61% (SE = 4.2; high treatment).

Effects on survival

Survival rates differed considerably between the two plant species: 87.7% of willow individuals survived over the seven-year experiment, while cottonwood survival was 22.6%. This resulted in significant differences in survival probabilities between cottonwood and willow ($z = -11.410$, $P < 0.001$). Despite considerable browse pressure by both cattle and elk across stocking densities, we found no significant effect of ungulate herbivory on survival of either plant species. However, we found a significant effect of belowground herbivory on survival probabilities ($z = 10.185$, $P < 0.001$), with increased mortality

Table 1. The effect of ungulate species (elk or cattle) and density on the proportion of browsed willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) based on logistic regression.

Parameters	Effect	Estimate	SE	P
Scouler's willow	Density	0.603	0.109	<0.001
	Species	1.593	0.192	<0.001
Cottonwood	Density	0.506	0.108	<0.001
	Species	0.835	0.173	<0.001

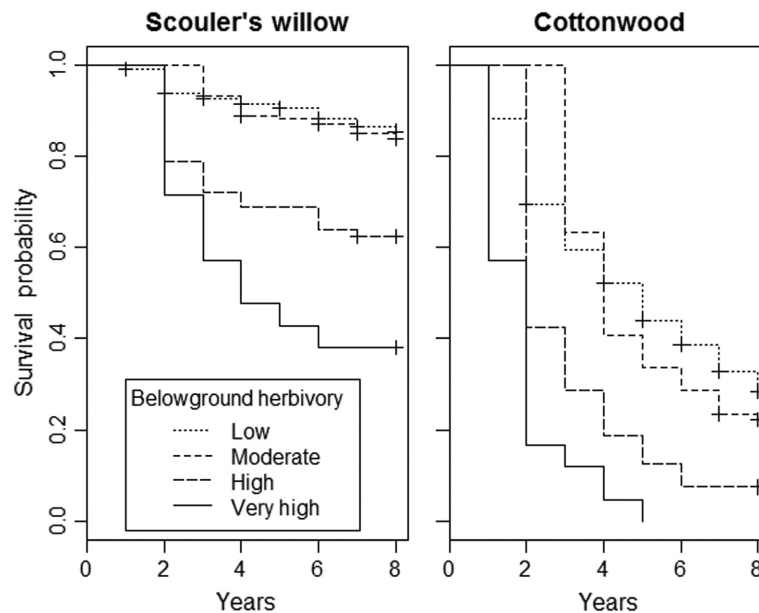


Fig. 4. Survival probability of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals over a seven-year period under variable belowground herbivory intensities by *Thomomys talpoides* (pocket gopher).

associated with increased belowground herbivory. A significant plant species by belowground herbivory interaction was found ($z = 1.8461$, $P = 0.065$) as survival decreased more rapidly for cottonwood than willow (Fig. 4).

For willow, survival probabilities and 95% CI were quite high at low (0.86, CI: 0.83–0.89) and moderate (0.84, CI: 0.79–0.89) levels of belowground herbivory and then dropped under high (0.62, CI: 0.51–0.77) and very high (0.38, CI: 0.22–0.66) intensity levels (Fig. 4, Table 2). Cottonwood showed a similar pattern, but survival rates were much more affected by belowground herbivory (Fig. 4, Table 2). At low belowground herbivory

intensities, the probability of survival was 0.30 (CI: 0.25–0.34) and declined rapidly thereafter; no cottonwood individuals exposed to very high levels of belowground herbivory were alive after four years (Fig. 4).

Effects on height

Both aboveground and belowground herbivory affected the growth and size of cottonwood and willow (Figs. 5 and 6, Table 3). For willow, individuals in the complete ungulate exclusion treatment grew nearly 80 cm during the study from 72 cm (SE = 3) to 151 cm (SE = 7) and were significantly taller than willows in any of the

Table 2. The effect of belowground herbivory on Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) survival probability based on Cox proportional hazards regression.

Parameters	Belowground herbivory	Coef	Exp(coef)	SE(coef)	z	$P(> z)$
Scouler's willow	Moderate	0.1478	1.1593	0.2343	0.6309	0.528
	High	1.0908	2.9767	0.2601	4.1938	<0.001
	Very high	1.8988	6.6779	0.3043	6.2389	<0.001
Cottonwood	Moderate	0.1236	1.1316	0.1083	1.1412	0.254
	High	0.8510	2.3420	0.1080	7.8760	<0.001
	Very high	1.4345	4.1975	0.1492	9.6125	<0.001

Note: Model tests whether effects of shown herbivory groups (moderate, high, and very high) differ from the low belowground herbivory group.

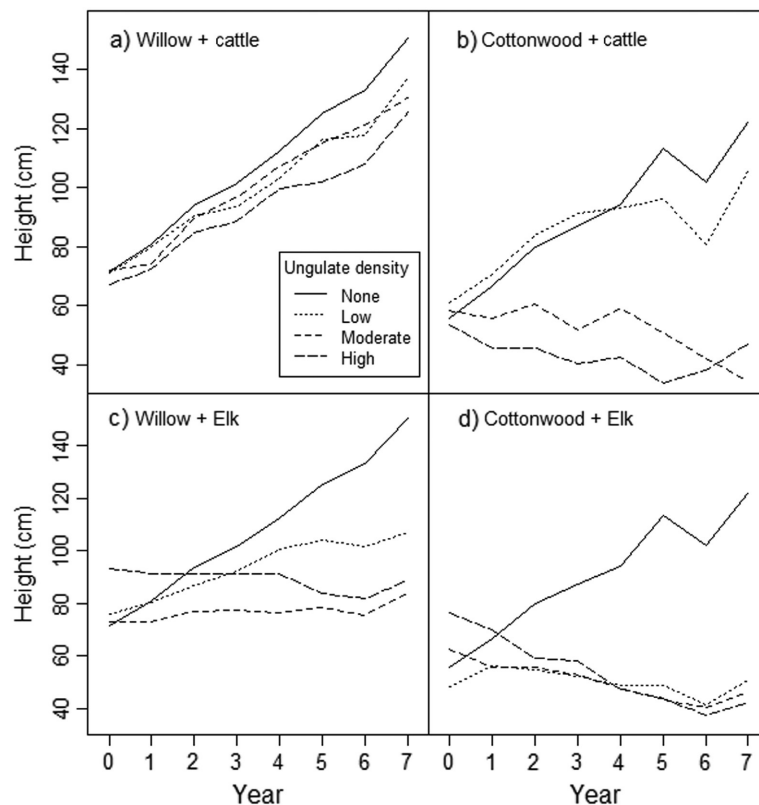


Fig. 5. Mean height of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals within different cattle (*Bos taurus*) and Rocky Mountain elk (*Cervus elephus*) browsing treatment plots over seven years. Year 0 represents the pretreatment height for individuals within browsing treatment plots.

ungulate herbivory treatments. Herbivory by elk had a greater impact on height than cattle and as stocking density increased, effects on height were more pronounced. While willow individuals in the cattle treatments were significantly smaller than those in the ungulate exclusion treatment, willows in all cattle treatments grew over the seven years, with mean height increases ranging from 59 to 66 cm. This was not the case for the elk treatments; not only were growth rates much lower, but also the mean height of individuals in the high elk treatment at the end of the study (mean = 90 cm; SE = 8.7) was shorter than the initial mean height prior to the herbivory treatment of 93 cm (SE = 5.4). Belowground herbivory by pocket gophers also had a significant negative effect on willow height (Fig. 6), and a significant interaction between cattle and belowground herbivory was found (Table 3).

The effect of herbivory (above and below) on cottonwood height was even more pronounced

(Figs. 5 and 6). On average, individuals in the ungulate exclusion treatment grew 66 cm over the seven years. This was not the case in any of the herbivory treatments. In fact, only the low cattle treatment showed any meaningful increase in height during the study; cottonwood in all other cattle and elk treatments were either similar or shorter at the end of the study than at the beginning, regardless of stocking density (changes in height ranging -34 to 3 cm). Cottonwood was also highly sensitive to belowground herbivory by pocket gophers, with large declines in plant height accompanying very high level of gopher herbivory.

DISCUSSION

Our study is one of the first to evaluate top-down regulation of plant species by multiple herbivore species across a range of herbivore densities. We found that herbivore species,

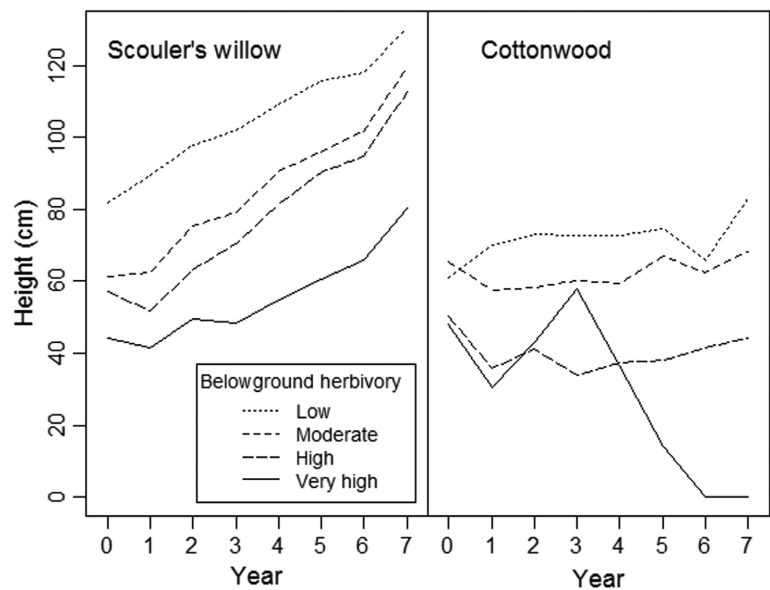


Fig. 6. Mean height of Scouler’s willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals under different levels of pocket gopher (*Thomomys talpoides*) pressure over a seven-year period. Year 0 represents the pretreatment height for individuals within browsing treatment plots. No cottonwoods were alive in years 6 and 7, and mean heights are shown as zero values.

herbivore density, and plant species all influenced the strength of top-down regulation and that the effect of herbivore abundance on plant demographic performance and populations depended on the herbivore species, differential herbivore preference for specific plant species, and the ability of plant species to tolerate herbivory. We also found that top-down regulation of cottonwood and willow was not driven solely by large ungulates; belowground was also a strong

driver of demographic performance, and significant aboveground–belowground herbivory effects were found.

Ungulate species

Results showed that herbivory by cattle and elk significantly reduced growth of the two plant species, with elk having a larger effect than cattle. This result supported our hypothesis regarding differences in foraging ecology between the two

Table 3. The effect of aboveground and belowground herbivory on height of Scouler’s willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals after 84 months based on Poisson regression.

Parameters	Herbivory	Estimate	SE	P
Scouler’s willow	Cattle	−0.13	0.033	<0.001
	Elk	−0.301	0.041	<0.001
	Gopher	−0.123	0.021	<0.001
	Initial plant height	0.009	0	<0.001
	Cattle × gopher	0.09	0.023	<0.001
	Elk × gopher	0.028	0.031	0.38
Cottonwood	Cattle	−0.183	0.065	0.005
	Elk	−0.452	0.078	<0.001
	Gopher	−0.08	0.037	0.033
	Initial plant height	0.008	0	<0.001
	Cattle × gopher	−0.024	0.047	0.61
	Elk × gopher	−0.043	0.061	0.485

ungulate species. Cattle are “bulk grazers,” with a diet composed largely of fibrous grasses and grass-like species even during late summer as grasses senesce with summer drought in dry forests (Clark et al. 2013). By contrast, elk are “intermediate grazers,” with a broader diet of grasses, forbs, and shrubs in these same dry forests, and more pronounced switch to a shrub diet in late summer with senescence of grasses and forbs (Findholt et al. 2004). These differences in diet selection and foraging ecology between cattle and elk likely explain differences in browse pressure between the two herbivores and the subsequent effects on plant growth documented in our experiment. Elk had much greater impact on plant growth than cattle, suppressing growth of both willow and cottonwood across herbivore density treatments. Cattle also reduced plant growth, but effects were not as strong or as consistent.

We found no cattle or elk herbivory effect on plant survival rates or probabilities. However, this result must be interpreted with caution, as our experiment likely underestimated ungulate effects on survival. Due to the logistics of implementing the experiment, cottonwood and willow populations were not exposed to herbivory for three years after completion of the ungulate exclosures, providing time for plants to establish and grow in the absence of ungulate herbivory. This likely allowed willow and cottonwood to tolerate higher levels of herbivory than if they had been exposed to herbivores immediately after stand thinning and prescribed fire. Thus, it would be inappropriate to conclude that cattle and elk have no effect on survival rates based solely on this experiment given the time lag between the construction of the exclosures and the initiation of the herbivory treatments.

We hypothesized that elk would exert more pressure on deciduous woody plant species than cattle given that *Salix* spp. and *Populus* spp. are preferred forage species for elk (Cook 2002). Pekin et al. (2015) recently showed that elk reduced woody plant cover in the forest understory significantly more than cattle. Despite cattle's preference for herbaceous forage, browse pressure on cottonwood and willow by cattle was still moderate, ranging from 34% to 61%, which resulted in modest impacts on plant growth. Direct impacts of cattle on upland woody plant demography in the region have not received

much attention, likely because cattle are primarily grazers of herbaceous species and deciduous woody species represent a very small proportion of their diet (Clark et al. 2013). Our study indicates that in addition to wild ungulates, cattle can also regulate woody species growth and size, despite their strong preference and selection for herbaceous vegetation. Thus, predicting herbivore impacts on plant population and community dynamics based on herbivore diet composition may miss important herbivore effects.

Role of ungulate abundance

One novel aspect of our research was the evaluation of herbivore impacts along an ungulate density gradient. Results showed that the importance of herbivore abundance on top-down regulation varied by ungulate and plant species. Herbivore pressure and effects by cattle on both willow and cottonwood increased as cattle densities increased. This was not the case for elk, where the effect of ungulate density depended on the plant species. Increasing elk density increased browse pressure on cottonwood populations. However, effects on growth of cottonwood were similar regardless of elk density, and any level of elk herbivory resulted in suppressing the species' growth.

Elk effects on willow showed a different pattern. In this case, browse pressure was similar regardless of elk density (ranging from 86% to 92%), with effects on growth increasing slightly with elk density. These results suggest that for elk, willow is a highly preferred browse species, with high levels of browse pressure even at low elk abundances, yet willow appears much more tolerant of herbivory than cottonwood, the latter exhibiting larger suppression effects on growth at lower browse pressures. Thus, when evaluating herbivore effects on plant populations, it is important to consider not only herbivore species and density, but also herbivore forage preference and each plant species' tolerance to herbivory. These issues have been largely ignored in studies evaluating the importance of top-down regulation by mammalian herbivores. Our results highlight the challenges in identifying and interpreting the strength and direction of top-down regulation of vegetation by herbivores when using traditional ungulate exclusion approaches that evaluate herbivory solely as a binary factor

or when studies ignore factors such as foraging behavior and preference.

Evaluating herbivore effects across a range of herbivore densities provides opportunities to identify herbivory thresholds where top-down effects are expressed. For example, cottonwood appears tolerant of cattle herbivory at low cattle densities, with minimal impacts on growth; increasing cattle abundances results in large effects. On the other hand, any level of elk herbivory suppressed cottonwood growth, indicating a much lower herbivore threshold density for top-down regulation of plant demography. These findings indicate the need for a more thorough understanding of the role of herbivore abundance in regulating individual plant performance, plant population, and plant community dynamics.

The heavy browse pressure by elk and corresponding impacts to growth, even at lower densities, suggests that in the case of upland coniferous forests, increasing the abundance of top predators (e.g., wolves, cougars) may not result in large increases in the recruitment and abundance deciduous woody species that have been reported in some riparian ecosystems of western North America (e.g., Ripple and Larsen 2000, Ripple and Beschta 2004, 2007, Beschta 2005). Several reasons may explain the difference. First, our results showed that even in the low-density elk treatment, elk were able to suppress plant growth, particularly for cottonwood, where effects were nearly identical to the moderate- and high-density elk treatments. Additionally, the slow growth rates of cottonwood and willow measured in our study may weaken the importance of trophic cascades in this instance. Annual growth rates of cottonwood in the complete ungulate exclusion treatment averaged 9 cm/yr, which is half the growth rate reported in an adjacent riparian area by J. P. Averett (*unpublished data*). Assuming constant growth rates through time, it will take twice as long for cottonwoods in upland forests to grow above the browse line than in riparian zones, substantially increasing the probability of being browsed and suppressed by herbivores. Thus, it remains unclear what level of predator pressure would be required to reduce elk pressure on plant populations, either through altering elk distribution patterns, reducing densities, or both, to such a degree that cottonwood

and willow would be able to escape herbivory and grow above the browse line (~2.5 m), particularly given the slow growth rates of willow and cottonwood in the uplands and high browse pressure. Finally, and perhaps most importantly, results indicate that pocket gophers, not ungulates, are a major regulator of cottonwood and willow abundance and size. Given that gophers are not a key prey species for large predators, the role of other smaller predators may be more important for deciduous woody plant dynamics in upland forests than large predators.

Belowground herbivory

The role of gophers in affecting vital rates of willow and cottonwood was an unexpected finding. Thus, more research should focus on the role of belowground herbivores in regulating willow and cottonwood. Cantor and Whitham (1989) reported that pocket gophers significantly reduced growth and survival in a related species, quaking aspen (*P. tremuloides*). Our approach was sufficient to identify pocket gopher-caused mortality, but our estimates of belowground herbivory intensity were imprecise and likely an underestimate. While gopher mounds directly at the base of individual plants are indicative of belowground herbivory (Fig. 1a), we could not account for root herbivory away from the stem or in instances where a mound did not form. However, the clear trends in increased mortality and decreased growth along our belowground herbivory intensity gradient suggest that our approach and interpretation were appropriate. Cantor and Whitham (1989) suggested that belowground herbivores feeding on roots are likely more important than aboveground herbivores that consume leaves and branches because of the effects of root herbivory on a plant's water balance. Results from the growing body of research on belowground invertebrate herbivory also indicate that plants respond to root herbivory much differently than to aboveground herbivory and that plants have a lower tolerance to root herbivory than aboveground defoliation (Zvereva and Kozlov 2012, Stephens et al. 2013, Johnson et al. 2016). Our results appear to support these findings and show that small mammal herbivory on root systems may be a primary force regulating the abundance and population dynamics of these two plant species. Manipulative

experiments that control for both aboveground and belowground herbivores are needed to better understand herbivore impacts alone and in concert on plant demography.

Our results are similar to Lyly et al. (2014) in boreal forests, who found that while deer reduced growth of deciduous woody species, small mammals (voles and hares) had the largest effect on their survival. Herbivory by small mammals has been recognized as an important ecological process regulating plant populations and communities (Van der Wal et al. 2000, Howe et al. 2006, Smit et al. 2010, Gough et al. 2012, Goheen et al. 2013, McLaughlin and Zavaleta 2013, Rebollo and García-Salgado 2013), although most mammalian-focused herbivory research has focused on large-bodied species with some suggesting that larger mammalian herbivores are stronger regulators than smaller species (Bakker et al. 2006). Our findings and those by others (e.g., Goheen et al. 2013, McLaughlin and Zavaleta 2013, Rueda et al. 2013, Lyly et al. 2014) suggest that the strength of effect of mammalian herbivores in regulating vegetation is not related to body size. Rather, the entire herbivore community must be considered when evaluating herbivore impacts.

Plant species

Our experiment to evaluate effects of herbivores on two plant species provided insight on how differential herbivore preference, combined with differential tolerance levels to herbivory between plant species, affected the strength of top-down regulation. Both willow and cottonwood were browsed by the two ungulates but pressure on willow was considerably greater. However, herbivore effects were stronger on cottonwood, indicating this willow species is more resilient to ungulate herbivory than cottonwood. Responses to belowground herbivory were similar, with willow having higher survival and growth rates than cottonwood. These findings may help explain why Scouler's willow is common and widely distributed in upland conifer forests in the interior Pacific Northwest (Johnson 1998). By contrast, cottonwood is associated with more mesic forests or riparian ecosystems (Burns and Honkala 1990) and not as common in upland forests as willow. It is possible that our upland sites were near soil moisture tolerance limits of

cottonwood given the 20% survival rate of cottonwoods in the ungulate exclusion treatment and the lower growth rates of cottonwoods relative to those found in nearby riparian areas (J. P. Averett, *unpublished data*).

Our results further suggest that willow and cottonwood may respond to herbivore density levels in different ways, likely along environmental and productivity gradients as shown for other plant species (Gough et al. 2012, Goheen et al. 2013, McLaughlin and Zavaleta 2013, Young et al. 2013). Thus, plant responses to herbivory that we documented may vary more widely across the landscape not only in response to herbivore species and abundance, but also with environmental gradients. This underscores the complexity of predicting the strength and direction of top-down regulation of vegetation by herbivores.

Implications for forest dynamics

The implications of top-down regulation of deciduous woody species by herbivores for long-term forest dynamics remain unclear. Based on our findings, in cases where ungulate herbivores are absent or exert very low browse pressure on deciduous woody species, low densities of cottonwood and willow will likely recruit to the canopy and change the overstory from one dominated exclusively by conifers to one that also includes a deciduous tree component. Densities of conifer seedlings in these postfire stands reach >1500 seedlings per hectare (B. A. Endress, *unpublished data*), much greater than densities of cottonwood and willow (Fig. 2). However, these two species are not the only deciduous woody species present with the potential to grow above the browse line and potentially influence forest structure, composition, and dynamics. A number of additional deciduous woody species including *Acer glabrum*, *Amelanchier alnifolia*, *P. tremuloides*, *Prunus virginiana*, *Sambucus* spp., and *Sorbus scopulina* are found in these forests, many of which are also browsed by ungulates (Dayton 1931, Johnson 1988, Riggs et al. 2000, Endress et al. 2012). If these species respond similarly to herbivory as cottonwood and willow in our study, under low ungulate browse pressure scenarios, a deciduous woody layer 3–10 m in height may develop and increase the structural complexity and diversity of these conifer dominated forest stands. Long-term

monitoring is required to better understand whether and to what degree this occurs.

CONCLUSION

Our research identified four key factors that influence the strength of herbivory as a top-down regulator of plant structure and demographic performance: (1) herbivore species, (2) herbivore abundance, (3) herbivore diet selection, and (4) the ability of plant species to tolerate herbivory. Our research further demonstrated the importance of moving beyond traditional herbivory research that (1) only evaluates pooled herbivore effects and (2) considers herbivory solely as a binary variable (i.e., ungulate presences versus absence). Our results demonstrate the need for increased understanding of the importance and strength of herbivore effects both theoretically and in practice by incorporating multiple species across a range of herbivore densities. This would be particularly helpful to inform effective management of ecosystems that contain multiple herbivores that vary in abundance. This would substantially advance our knowledge of herbivory effects and mechanistic processes of regulation, particularly if new research evaluates responses along a wide spectrum of environmental gradients. Unfortunately, such research designs are both expensive and logistically challenging, particularly related to varying ungulate species and densities in a controlled manner across environmental conditions over long periods. These challenges largely explain the large knowledge gaps regarding herbivores as top-down regulators of plant dynamics, and why mammal herbivory research continues to focus on binary exclusion experiments.

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as required by the United States Animal Welfare Act of 1985 and its regulations. We followed protocols established specifically by the IACUC for conducting cattle and elk research in our study area (Wisdom et al. 1993).

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