

Differential effects of cattle, mule deer, and elk herbivory on aspen forest regeneration and recruitment

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ABSTRACT

The abundance and composition of ungulate herbivore communities are changing globally, which can impact the resilience and function of Earth's ecosystems. Impacts from herbivory are compounded in areas where multiple ungulates overlap, which is common in forest ecosystems. The objective of this study was to examine the differential and combined effects of ungulate communities (deer, elk, and cattle) on aspen forest recruitment after fires that occurred in 2012. Eight sets of differential ungulate exclosures, monitored by camera traps, were established across three National Forests in Utah. We identified the differential effect of each of three ungulate species using fencing that allowed for deer-only, native ungulate only (deer and elk), all ungulates and a complete ungulate exclosure. Over a three year period (2013–2016) we quantified ungulate species impacts on aspen height, density, and browse rates using camera trap photos. Ungulate activity was nearly 10-fold higher in two National Forests compared to the third, and gradually decreased over time. Meristem removal by ungulates in unfenced plots across sites averaged 60% which we identified as a critical threshold point for aspen recruitment failure. All three ungulate species had significant and similar effects on aspen regeneration success, but when adjusted for differences in estimated forage intake (animal unit months), differential impacts became apparent (deer > elk > cattle). We estimated that 4 cattle per camera⁻¹ day⁻¹ and 2.5 deer or elk per camera⁻¹ day⁻¹ was sufficient to reach the critical recruitment threshold of 60% removal of apical meristems. We conclude that ungulates species differentially influence aspen regeneration and recruitment, and that ungulate browsing above 30% meristem removal impairs aspen recruitment with recruitment failure occurring above 60% meristem loss.

1. Introduction

Native and non-native ungulate populations can influence plant community development and reduce ecosystem stability (Côté et al., 2004, Spear and Chown, 2009). The frequency and magnitude of ungulate herbivory can define thresholds for forest regeneration and recruitment (Strand et al., 2009, Wisdom et al., 2006). Ungulate herbivory has particularly strong effects on plant recruitment in post-disturbance environments (Augustine and McNaughton, 1998). Ungulate influence on plant communities are often most intense in the early stages of forest succession following disturbance (Augustine and McNaughton, 1998, Wisdom et al., 2006). However, quantifying ungulate influence on forest regeneration and identifying forest recruitment thresholds by ungulate species are confounded by overlapping habitat and diet of multiple ungulate species.

What herbivores choose to eat is mediated by complex physiological and environmental cues (Hanley, 1982; Hoffman, 1989; Long et al., 2014). Interspecific differences in ungulate anatomy drive differences

in forage preference (Clauss et al., 2010), providing a framework for understanding ungulate forage selection and their differential impacts on forest recruitment and succession. Ungulate species are generally divided into three classes; “concentrate feeders”, “intermediate feeders”, and “grass and roughage eaters”, hereafter referred to as: browsers, mixed feeders, and grazers (*sensu lato* Hoffman, 1989). Body size, mouth anatomy, stomach type (ruminant vs. cecal), and rumino-reticular volume are among the major physiological features that influence diet strategy in ungulates (Hanley, 1982). Grazers generally have large body size and/or large rumino-reticular volume both of which favor selection of lower quality forage like grasses. Browsers generally have smaller rumino-reticular volume and must select for high-quality forage that passes relatively quickly through the digestive system. Browsers, given their smaller mouth size and need for higher quality forage, should select palatable portions of tree species such as meristems and leaf tissue. Mixed feeders fall between the two previously described types with intermediate anatomical features and diets (Hoffman, 1989). This conceptual framework predicts differential

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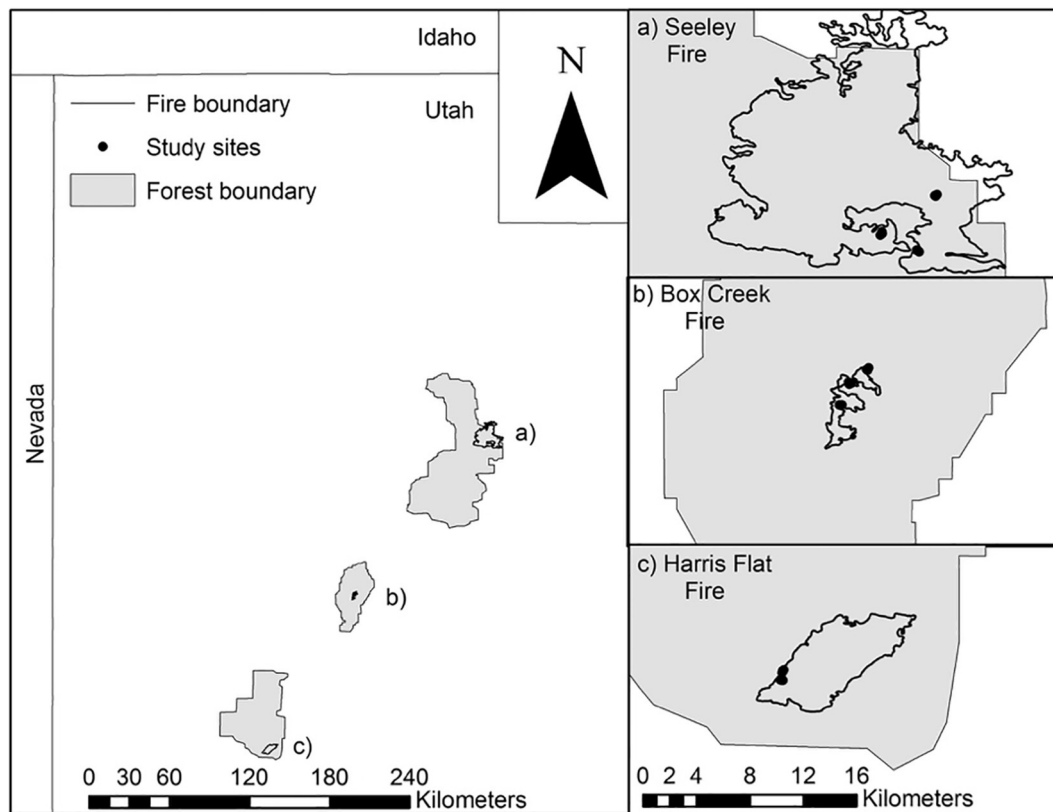


Fig. 1. Map of the study area. This map shows the larger study area encompassing central and southern Utah. National forest boundaries are in gray and fire perimeters are in black. Three inset maps display black dots at the study sites. At each a four block differential fencing treatment is located. All three inset maps use the same scale.

herbivory impacts on forest regeneration as follows: browser > mixed feeder > grazer (Clauss et al., 2010; Hoffman, 1989).

Aspen is a foundation tree species (Ellison et al., 2005) that provides habitat for hundreds of plant and animal species (Peterson and Peterson, 1992). Aspen forests are preferred habitat for deer (*Odocoileus* spp.) and elk, (*Cervus canadensis*) (Beck et al., 2006) and are utilized by cattle (*Bos taurus*) due to the high productivity and forage quality in their understory (DeByle, 1985). Aspen forms the foundation of forest successional cycles in many montane and subalpine mixed conifer forests of the intermountain west of North America by regenerating through root suckering after fire (Calder and St. Clair, 2012; St. Clair et al., 2013). Regenerating aspen suckers are highly palatable and susceptible to ungulate herbivory (Seager et al., 2013) and high rates of ungulate herbivory can result in aspen regeneration and recruitment failure (Rhodes et al., 2017a). Therefore, identifying thresholds at which ungulate herbivory interferes with aspen recruitment is critical to identifying aspen regeneration success and its implication for the resilience of aspen ecosystems.

Quantifying the differential effects of multiple coexisting ungulate species is key to defining thresholds for successful aspen recruitment. Monitoring removal of apical meristems is a good indicator of ungulate effects on aspen regeneration and subsequent recruitment (Rhodes and St. Clair, 2018). Thresholds for aspen recruitment in self regenerating aspen forests not triggered by fire have been identified at or near 30% browse removal of apical meristems (Jones et al., 2005; Olmsted, 1979; Strand et al., 2009). However, there are no current estimates for browsing thresholds of aspen recruitment in post-fire conditions, and little quantification of interspecific contribution of individual ungulate species on aspen regeneration and recruitment (Bork et al., 2013). Aspen tolerance of and resistance to ungulate herbivory increases with greater burn severity (Wan et al., 2014a) and fire size (Wan et al., 2014b). Both burn severity and fire size are positively correlated with

aspen suckering density and negatively correlated with ungulate influence (Smith et al., 2011; Wan et al., 2014a, 2014b). Therefore, aspen regeneration and recruitment thresholds in response to ungulate herbivory may differ in post-fire conditions dependent on the size and severity of fires.

The effect of ungulate herbivory on forest recruitment is influenced by multiple environmental factors (Dudley et al., 2015; Rhodes et al., 2017b) and can be highly variable in space and time (Rhodes et al., 2017a; 2017b). Topography is an important determinant of ungulate-aspen interactions due to its effects on temperature, precipitation and ungulate foraging behavior (Long et al., 2014; Rhodes et al., 2017b; Smith et al., 2011). Elevation covaries with temperature and precipitation and affects subsequent snowpack persistence and hydrology (Morán-Tejeda et al., 2013; Sospedra-Alfonso et al., 2016). Snowpack depth and persistence affects ungulate herbivory of aspen by limiting the movement and access of ungulates during the winter and spring periods (Brodie et al., 2012; Martin and Maron, 2012; Rhodes et al., 2017b). Moreover, aspen at lower elevations are subjected to warmer and drier conditions (Worrall et al., 2013) which can increase susceptibility to disease and herbivory (Dudley et al., 2015; Strand et al., 2009). Therefore, incorporating a measure of elevation and relative ungulate use across space and time provides a better mechanistic understanding of how ungulate species influence aspen regeneration and forest recruitment.

The central objective of this study was to quantify the individual and combined influence of mule deer, elk, and cattle on aspen regeneration and recruitment in complex, post-fire forest environments. We hypothesized that ungulate use of aspen, as measured by removal of apical meristems, would vary across burned landscapes and years post fire due to variability in ungulate visitation over space and time. Second, we hypothesized that aspen regenerating at lower elevations would experience lower height, density, recruitment and higher browse

due to increased susceptibility to ungulates. Third, we hypothesized that mule deer, elk and cattle would influence aspen height, density, and recruitment differently according to the following theoretical framework: browsers (mule deer) > mixed feeders (elk) > grazers (cattle). Finally, we sought to identify ungulate herbivory thresholds for successful aspen recruitment in post-fire environments.

2. Materials and methods

2.1. Study area

This study was conducted at three locations in central and southern Utah on the Manti-La Sal, Fishlake and Dixie National Forests that experienced fire in 2012 (Fig. 1). The Seeley, Box Creek, and Harris Flat fires occurred in aspen-conifer mixed forests during peak fire season (June–July 2012). Fire sizes were 19400, 900, and 3400 ha, respectively. Exclosure site elevations ranged from 2440 to 3030 m. Thirty-year annual precipitation averages ranged from 25 to 64 cm at these sites (PRISM data, Parameter-elevation Relationships on Independent Slopes Model) (Daly et al., 2009). Dominant tree species in the Seeley and Box Creek fires included; Aspen, Subalpine Fir (*Abies lasiocarpa* (Hooker) Nuttall) and White Fir (*Abies concolor* (Gordon) Lindley ex Hildebrand). While the dominant conifer component of the Harris Flat fire was Ponderosa Pine (*Pinus ponderosa* Douglas ex C. Lawson). Cattle, mule deer (*Odocoileus hemionus*), and elk were the most abundant ungulates at the study sites and only ungulates detected on remote cameras.

2.2. Study design

We selected three sites at Seeley, three at Box Creek, and two at Harris Flat. Sites were selected based on high fire severity (100% mortality of overstory), and pre-fire overstory stands having a significant aspen component (> 50% aspen stems pre-fire). At each site, three fence treatments and an unfenced plot were randomly assigned in 30 × 30 m plots. The fence treatments were: (1) mule deer access; (2) native ungulate access (mule deer and elk), (3) full exclusion (no ungulates), and (4) unfenced (cattle elk, and mule deer access). Full exclusion fencing was constructed with 3.1 m wooden posts buried 0.8 m into the ground at each corner. Fencing on each of the four sides was fixed on t-posts positioned at 3 m increments. The fencing consisted of 1.8 m of woven wire fencing and topped with a barbless wire set at 2 m. A gate was constructed in one corner of each fenced plot. Fencing that allowed access by mule deer, but not elk or cattle was constructed in similar fashion as the full ungulate exclosure except that a 0.5 m gap was created at the bottom of the fence (VerCauteren et al., 2007). Mule deer were allowed entry through the 0.5 m gap but the fence effectively excluded both elk and cattle. Fencing that allowed access by native ungulates, but not cattle consisted of 1.8 m wooden corner posts buried 0.6 m into the ground. The fencing was three barbed wires placed at heights of 0.2 m, 0.6 m, and 1.0 m. Unfenced plots were marked at the four corners with 1.8 m u-posts buried 0.6 m into the ground. We assumed that fencing might alter ungulate visitation rates when compared to an unfenced plot. Therefore, we complemented this design with wildlife camera traps to quantify ungulate visitation within each plot.

2.3. - Wildlife cameras

In each experimental plot, we placed a trail camera to determine ungulate visits by species (PC900 HyperFire Professional Covert Camera Trap) (Reconyx, Holmen, WI, USA). We used ungulate counts per camera per day (ungulate camera⁻¹ day⁻¹) as an estimate of relative ungulate use in each of the experimental plots across all sites. Cameras were placed at the corner of each plot facing inward (32 cameras), and were set at medium sensitivity to capture five photos at

three second intervals with a five-minute rest period in between triggers. Each ungulate that appeared at least once in the five-photo set with head down as evidence of browsing were counted and these counts were summed and divided by the number of active camera days for each plot. Ungulate counts were summed from the growing season (May through August period) preceding each aspen survey in order to characterize the relationship between relative ungulate use and aspen recruitment. Overwinter browse (Nov–April) was not observed on the cameras. While, ungulates were occasionally photographed, they did not stop to forage at any of the sites. September browse rates were also low. We anticipated that each yearly evaluation during the growing season would adequately reflect the ungulate impact on aspen sucker height, density, browse rates, as well as longterm recruitment.

2.4. Elevation

We associated GPS locations of each study plot with elevation taken from 30 × 30 m digital elevation models (DEM). The DEM used was a United States Geological Survey product using the UTM Zone 12 projection and NAD83 geodetic network (Universal Transverse Mercator, North American Datum, respectively). We used ArcMap 10.3 (ESRI, 2016, Redlands California, USA) to associate our GPS locations with their respective elevation from the DEM.

2.5. Characterization of aspen regeneration and recruitment

Within each 30 m × 30 m plot, 25 1 m² subplots for surveys of aspen were established in a 5 by 5 grid with a 5 m boundary layer from the fence edge. Aspen suckering density, height, and meristem removal were characterized at the end of August from 2013 to 2016. We counted aspen suckers as individuals if they had emerged independently from the ground. Removal of apical meristems was characterized by examining the percent of apical meristems removed by herbivory from the leading branch and the sub-leading branches in the top 15 cm of an aspen sucker (Jones et al., 2005; Rhodes et al., 2017a; Strand et al., 2009; Wan et al., 2014a). Removal of apical meristems is reported as the sum of browsed meristems divided by the sum of all stems witacross subplots. In 2016, the fourth year of the study, we evaluated aspen recruitment by counting aspen stems ≥ 150 cm in height that likely represented successful escape from ungulate herbivory (Seager et al., 2013).

2.6. Statistical analysis

In order to characterize differences in aspen regeneration across fence types we used linear mixed-effects models with aspen sucker height, density, and percent browse of apical meristems as response variables. We evaluated fence type as a categorical explanatory variable and ungulate camera counts as a continuous explanatory variable that predicted our response variables in two different sets of models. Photo counts allowed us to evaluate ungulate herbivory as a measure of relative use in a controlled framework provided by the fencing design. We modeled fence, year, and fence by year interaction along with elevation as fixed effects and site location as a random effect. In analysis of photo counts, data from the full exclosure plots was removed given that there was no incidence of browse in these plots resulting in $\mu = 0$ and $\sigma^2 = 0$ for this group, which made modeling problematic.

We present results in two separate groups of models: first, we used fence as a categorical variable and, second, we used camera counts as a continuous variable. Our experimental design allowed for both types of analyses where we have fencing that controls access, but are able to account for relative ungulate use. Accounting for site-to-site variation in ungulate abundance through camera traps is key to improving our knowledge of the influence of ungulates on their environment (Wisdom et al., 2006). In order to quantify the differential influence of ungulate species on aspen recruitment, we created a separate model for each

ungulate species. We modeled mule deer effects using camera counts from mule deer only plots and subtracted their estimated effect from native ungulate plots to estimate elk effects. We then subtracted mule deer and elk estimated effects from unfenced plots in order to model cattle effects. Therefore, we were able to produce beta estimates for each ungulate species' effect on the response variables. We model each species at 1 ungulate camera⁻¹ day⁻¹ and evaluate the results in terms of animal unit months (AUM) (NRCS, 2003). Here, our modeling assumed that only additive and no interactive ungulate effects were present.

In order to evaluate recruitment, we averaged browse across all years for each 30 m × 30 m plot and split browsing into high and low categories. High was defined as ≥30% and low was defined as < 30%. This browse limit was consistent with other studies that defined 30% percent removal of apical meristems as a critical threshold for aspen recruitment into the overstory (Jones et al., 2005; Rhodes et al., 2017a; Strand et al., 2009; Wan et al., 2014a). For all statistical models mentioned above, we included a heterogeneity of variance identity structure across fence types. We checked assumptions of normality by visually inspecting a histogram of model residuals. We checked assumptions of homogeneity of variance by visually inspecting fitted residuals versus predicted residuals. While elevation does not distinguish between winter and growing season precipitation, both winter and growing season precipitation are highly correlated with elevation. We found precipitation measures from PRISM to be collinear with elevation and, therefore, used elevation as an explanatory variable. All analyses were generated using R statistical software (R Core Team, 2016) with the MuMIn, (Barton, 2015) and nlme (Pinheiro et al., 2015) packages. Conditional and marginal r^2 values were computed for mixed effects analyses (Nakagawa and Schielzeth, 2013).

3. Results

3.1. Hypothesis 1: Relative ungulate use patterns across years and site

Removal of apical meristems was highly variable across the three fires and generally decreased over time (Fig. 2). Removal of apical meristems was influenced by fence type, year and elevation ($p < 0.05$) but not the fence by year interactions (Table 1). Removal of apical meristems in unfenced plots was nearly 10 times greater in the Box Creek and Harris Flat fires compared to the Seeley Fire (Fig. 2). Removal of apical meristems trended downward throughout the four-year

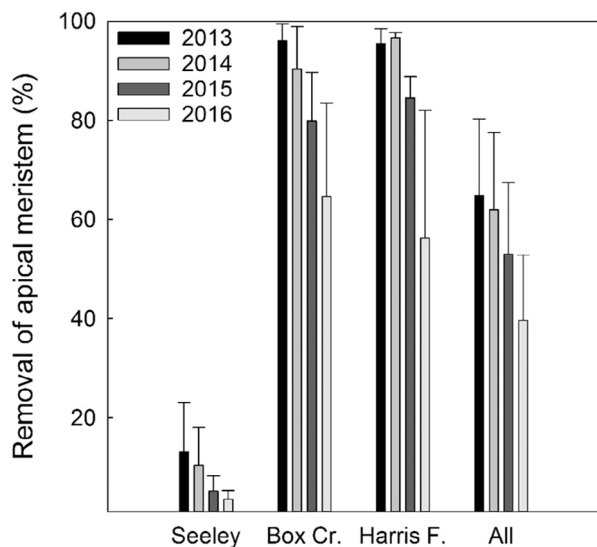


Fig. 2. Browse of apical meristems vary across time and space. This figure presents the mean browse of apical meristems $\pm$ 1 SE in unfenced plots at each fire.

Table 1

Results from analysis of suckers in fenced treatments from 2013 to 2016. F-statistic, p-value, degrees of freedom (df) and marginal model goodness of fit (r_m^2) are presented for the three response variables and the fence by year interaction. Browse refers to percent removal of apical meristems (%), height is mean height (cm), and density is aspen ha⁻¹.

Parameter	df	Browse		Height		Density	
		F	p	F	P	F	p
Fence	3,81	17	< 0.001	10	< 0.001	7.3	< 0.001
Year	3,81	2.6	0.06	37	< 0.001	8.2	< 0.001
Fence x Year	6,81	28	0.58	0.6	0.77	0.3	0.58
Elevation	1,81	27	< 0.001	19	< 0.001	0.3	0.97
Full model r^2		$r_m^2 = 0.12$		$r_m^2 = 0.54$		$r_m^2 = 0.35$	

study period across all fencing types. Removal of apical meristems dropped from 64% to 51% in unfenced plots from 2014 to 2015. A similar trend was observed in native ungulate and mule deer only plots where estimates decreased from 44% to 26% and 33% to 16% respectively. (Fig. 4a). There was 0% removal of apical meristems in full enclosures and no evidence of trespass (no photos or feces) throughout the four-year study period.

3.2. Hypothesis 2: Elevation mediates ungulate:aspen interactions

When using fence type as a categorical variable, estimated percent removal of apical meristems decreased by 3.5% for every 100 m increase in elevation ($t = 5.9$, $p < 0.01$). Mean height increased 5 cm for every 100 m increase in elevation ($t = 4.5$, $p < 0.01$). When using camera counts as a continuous explanatory variable, elevation was a significant indicator for browse of apical meristems in the cattle model but not the mule deer and elk models (Table 2). Removal of apical meristems was estimated to be 4% lower for every increase in 100 m of elevation in the cattle model. Elevation was a significant predictor of aspen density in the elk and cattle model (Table 2), but not in the mule deer model. Elevation was not significant for height across any ungulate model (Table 2). Elevation was not significant in models for aspen recruitment in 2016.

Table 2

Effects of each ungulate species using camera counts was modeled through their individual effect on three response variables and the ungulate camera count by year interaction. F-statistic, p-value, degrees of freedom (df) and marginal model goodness of fit (r_m^2) are presented for each of three response variables. Browse is removal of apical meristems (%), height is mean height (cm), and density is aspen suckers ha⁻¹. Response variables with $p < 0.05$ are presented in bold font.

Model	df	Browse		Height		Density	
		F	p	F	P	F	p
Cattle	1,24	20	< 0.001	19	< 0.001	3.9	0.06
Year	3,24	1.4	0.26	3.1	0.05	1.4	0.27
Cattle x Year	3,24	0.16	0.92	1.6	0.23	1.2	0.35
Elevation	1,24	11	0.003	2.5	0.13	18	< 0.001
Full model r^2		$r_m^2 = 0.67$		$r_m^2 = 0.54$		$r_m^2 = 0.09$	
Mule Deer	1,24	119	< 0.001	60	< 0.001	5.5	0.03
Year	3,24	1.7	0.21	14	< 0.001	4.8	0.01
Deer x Year	3,24	1.1	0.02	5.3	0.007	0.11	0.29
Elevation	1,24	6.4	0.36	0.2	0.67	1.1	0.95
Full model r^2		$r_m^2 = 0.81$		$r_m^2 = 0.87$		$r_m^2 = 0.24$	
A. Elk	1,24	28	< 0.001	8.7	0.007	5.6	0.03
Year	3,24	1.6	0.21	19	< 0.001	2.6	0.07
Elk x Year	3,24	2.2	0.12	3.9	0.02	0.18	0.91
Elevation	1,24	0.61	0.44	0.01	0.91	4.2	0.05
Full model r^2		$r_m^2 = 0.56$		$r_m^2 = 0.67$		$r_m^2 = 0.36$	

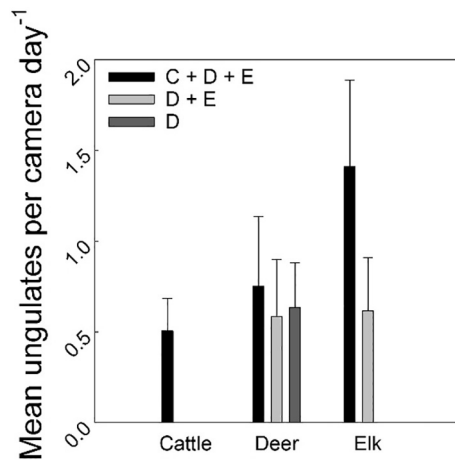


Fig. 3. Camera counts per ungulate per day at each fence type. This Figure presents the mean camera counts of each ungulates species as ungulates per camera day $\pm$ SE. Colored bars represent the mean camera count for that species. The legend shows letters for ungulates that are allowed into the plot: “D” for deer-only plots, “D + E” for native ungulate plots, and “C + D + E” for unfenced plots allowing access to all ungulates.

3.3. Hypothesis 3: Differential ungulate effects

Our fences differentially excluded ungulate species as designed. We found no evidence of any ungulate entrance into full enclosure plots, and no cattle in native ungulate plots. Mule deer entered the deer-only plots at similar rates as unfenced and native ungulate plots, but there were only one third as many elk in cattle excluded plots compared to unfenced plots (Fig. 3).

3.3.1. Fence models

Removal of apical meristems varied significantly depending on fence type, an effect that was consistent across all four years (Table 1). There was no evidence of browsing in full enclosure plots. Unfenced, native ungulate plots, and mule deer access plots averaged 64%, 44%, 40%, and 33% meristem removal, respectively, over the four year period, an effect that diminished over time (Fig. 4a). Averaged across all fencing types, removal of apical meristems was highest in 2013 and was reduced by 3.5% in 2014, 4.5% in 2015, and 11% in 2016 (Fig. 4a).

Mean aspen height was significantly influenced by all main effects (fence type, year, and elevation) but not the fence type by year interaction (Table 1). Fence type had modest but statistically significant effects on mean aspen height over the four-year study period. Over the four-year study period, mean aspen height was reduced by 13 cm in mule deer access plots, 17 cm in native ungulate access plots, and by 37 cm in unfenced plots when compared to full enclosure plots (Fig. 4b). Mean aspen height averaged across all plots had yearly growth of 25 cm in 2014, 26 cm in 2015, and 16 cm in 2016 (Fig. 4b).

Aspen regeneration density was impacted by fence type and year (Table 1), but elevation and the fence by year interaction were not significant. Aspen sucker density was highest in 2013, and followed a downward trend across the four-year period dropping by as much as 50% by 2016 (Fig. 4c). Aspen densities were lowest in the full exclusion and mule deer access plots, and were significantly higher in unfenced and native ungulate access plots (Fig. 4c).

3.3.2. Camera count models

When ungulate effects on aspen suckers were modeled using camera counts: cattle, mule deer, and elk each reduced aspen sucker height, and density, while increasing removal of apical meristems, when compared to a model of 0 ungulates per camera per day (Fig. 4). Cattle, elk, and mule deer increased removal of apical meristems by $16\% \pm 9\%$, $24\% \pm 4\%$, and $24\% \pm 4\%$ for each 1 ungulate

camera⁻¹ day⁻¹, across the entire 4 year study period (Table 2). Cattle, mule deer, and elk had each reduced mean aspen height by the end of the study. In 2016, full exclusion plots had a predicted height of 151 cm, while 1 ungulate camera⁻¹ day⁻¹ of each species (elk, cattle, and mule deer) led to a predicted height of 105 cm, 88 cm, and 77 cm, respectively, (Fig. 4e). Our models predicted that, over the entire four year period, elk and mule deer reduced aspen sucker density by $26,800 \pm 10,400$ ha⁻¹ and $23,200 \pm 6000$ ha⁻¹ per ungulate camera⁻¹ day⁻¹, respectively while cattle had no significant influence on aspen sucker density (Table 2). Therefore, while cattle, elk, and mule deer had similar predicted effects on aspen suckering based on camera counts, the relative daily estimated intake of dry forage per AUM (≈ 12 kg dry forage/day), differentiates the impact across the three ungulate species where: mule deer > elk > cattle.

3.4. Aspen recruitment thresholds

Aspen in plots subjected to $\geq 30\%$ removal of apical meristems had minimal recruitment success 5 years post-fire while $\geq 57\%$ removal of apical meristems showed complete recruitment failure (Fig. 5b). In contrast, most plots with meristem removal below 30% showed recruitment at densities which make stand replacement likely (Fig. 5a). Aspen recruitment densities in plots with less than 30% meristem removal were 18-fold higher than plots with $> 30\%$ meristem removal ($15,000 \pm 880$ aspen recruiting ha⁻¹ vs 880 ± 400 aspen recruiting ha⁻¹) ($F = 17$, $p < 0.01$, $r^2 = 0.38$).

4. Discussion

4.1. Changes in relative use across space and time

Ungulates demonstrate complex behavior and forage patterns across space and time that are influenced by a myriad of factors (Long et al., 2014). At regional scales, ungulate use can vary greatly across space, making it difficult to extrapolate total and interspecific effects on aspen regeneration (Rhodes et al., 2017b). Our first hypothesis that ungulate use would vary across the three fires and across years was well supported. Relative ungulate use, as measured by percent removal of apical meristems, was nearly 10 times greater in Box Creek and Harris Flat fires when compared to the Seeley Fire and decreased rapidly across years (Fig. 2). Large fire size and high fire severity improve aspen regeneration by increasing tolerance and chemical resistance to ungulate herbivores (Wan et al., 2014a, 2014b). The large size of the Seeley fire relative to Box Creek and Harris Flat (Fig. 1), may have contributed to the reduced use of aspen by ungulates (Fig. 2) and its overall successful regeneration.

4.2. Elevation

Elevation mediates the influence of ungulate herbivory in forest systems (Rhodes et al., 2017b) through effects on snow pack, and water availability (Martin and Maron, 2012). Increasing elevation was associated with taller aspen and less browse of apical meristems when using fence as a categorical variable. When modeled by camera counts, elevation was associated with reduced browse of apical meristems and increased density. Similarly, a regional study across Utah found improved aspen regeneration and recruitment at higher elevations in undisturbed stands (Rhodes et al., 2017b). Elevation is also likely associated with differences in snow persistence that can influence the timing of ungulate access to regenerating aspen suckers (Brodie et al., 2012; Martin and Maron, 2012; Rhodes et al., 2017b). This relationship suggests that aspen at lower elevation are more susceptible to ungulate herbivory. If predicted changes, in our study area, of temperature and precipitation occur aspen at lower elevation may be more affected by ungulate herbivory (Strand et al., 2009; Worrall et al., 2013).

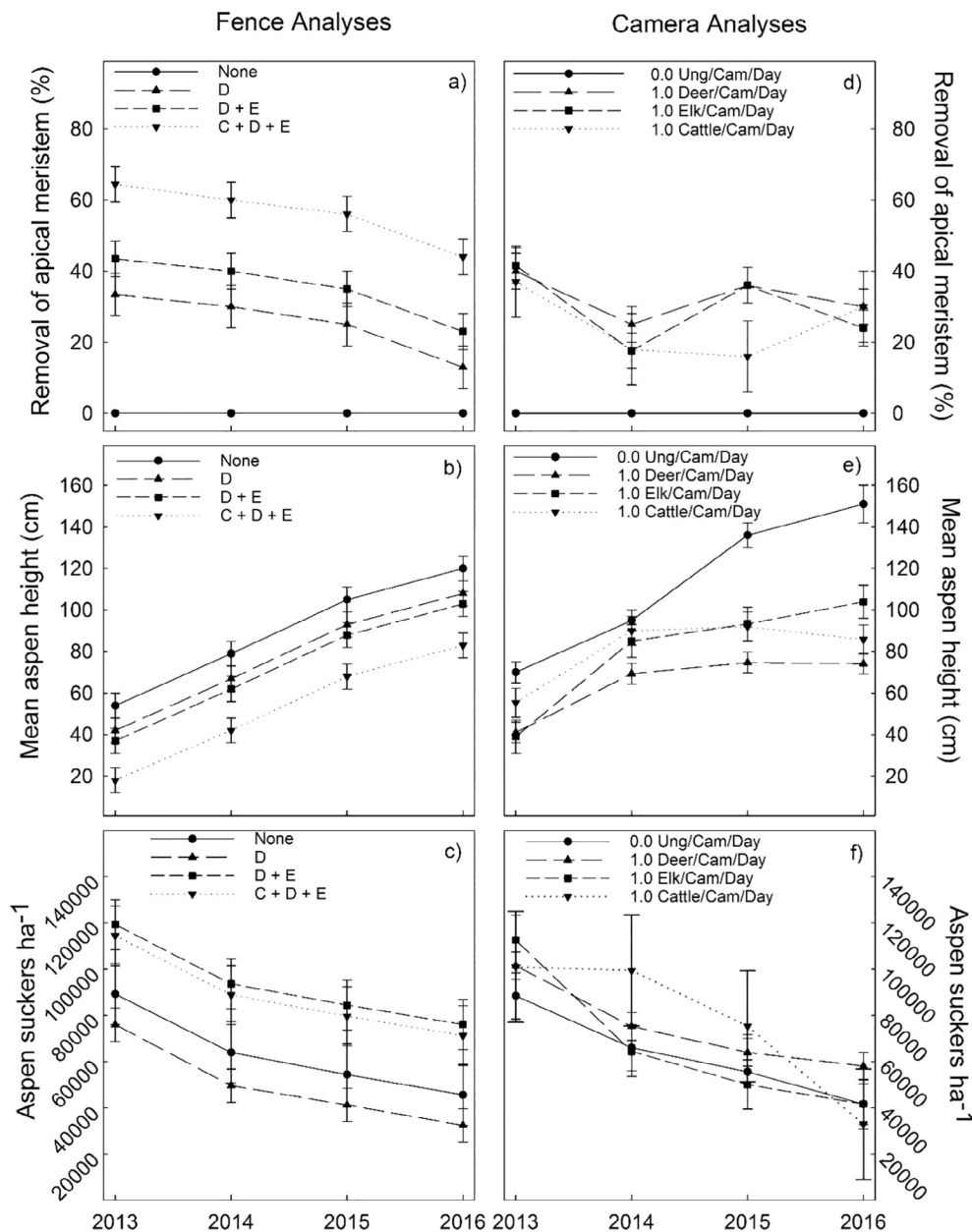


Fig. 4. Plotted results from the analyses involving fences are plotted on the left column for (a) removal of apical meristems, (b) mean aspen height (cm), (c) aspen suckering density (ha^{-1}). The legend for the left column includes: “None” for no ungulates allowed, “D” for deer-only plots, “D + E” for native ungulate plots, and “C + D + E” for unfenced plots allowing access to all ungulates. The models involving camera counts are plotted on the right using model predictions for 1 ungulate per camera day and the standard error associated with that ungulate species’ impact. Each of the response variable is the same order as the fenced analyses: (d) removal of apical meristems, (e) mean aspen height (cm), and (f) aspen suckering density (ha^{-1}).

4.3. Differential species impacts

At landscape scales, wild and domestic ungulate habitat often overlaps (Wisdom and Thomas, 1996) and understanding their differential effects has been difficult to estimate in natural environments (Wisdom et al., 2006). Our second hypothesis that there are fundamental differences in use of aspen between the ungulate species studied was also supported. However, a caveat with our study design is the assumption that there were no significant interactive effects between ungulate species. Competition is stronger between elk and cattle than between cattle and mule deer, likely due to similar diets of mixed feeders with grazer (Coe et al., 2001). Further, cattle can displace elk spatially across gradients of elevation (Stewart et al., 2002) and cattle, elk, and mule deer avoid foraging in the same habitat over short time scales (within 6 h of visitation) (Stewart et al., 2002). There is evidence that cattle can remove preferred plant species and change native ungulate habitat use patterns (Madhusudan, 2004). However, using cameras to model visitation rates and evaluate them in an additive fashion captured the main effects of each ungulate species and were

consistent with results from similar studies (Bork et al., 2013; Walker et al., 2015).

We found that 1 ungulate per camera day^{-1} of any species had similar effects on aspen height and browse of apical meristems (Fig. 4). However, when adjusted to differences in animal diet requirements and comparable AUMs (cattle 1.0 AUM, elk 0.6 AUM, mule deer 0.2 AUM) (NRCS, 2003), differences in ungulate species impacts were identified (mule deer > elk > cattle). In other words, the estimated effect of mule deer was greatest, and cattle the least. Therefore, we estimate that while the total forage intake of mule deer is one fifth that of cattle, the total intake of aspen in mule deer diet is higher than cattle based on visitation estimates via camera counts.

This gradient of use of aspen supports the conceptual framework based on ungulate functional groups (browser > mixed feeder > grazer) (Hoffman, 1989). The only difference between our models of ungulate preference was that cattle did not significantly reduce aspen density (Fig. 4). This is consistent with an earlier study in Alberta, Canada which found that cattle have less of an effect on aspen browse, defoliation and mortality rate than browsers or mixed feeders at similar

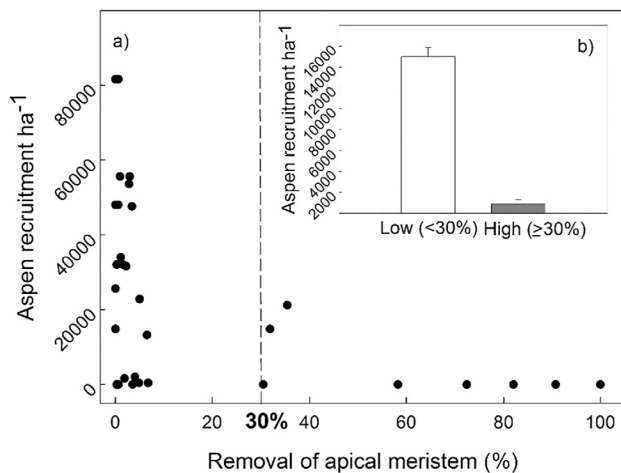


Fig. 5. The large panel (a) shows the raw recruitment data (aspen stems $> 1.5 \text{ m ha}^{-1}$) plotted against the removal of apical meristems (%). The inset panel (b) shows the modeled recruitment data using 30% removal of apical meristems as the browse threshold. The error bar is one standard error.

stocking rates (Bork et al., 2013).

Fencing is often used to differentiate individual species effects within ungulate communities (Faison et al., 2016; Goheen et al., 2013; Walker et al., 2015), but fencing cannot always control for natural variability in ungulate visitation and use (Wisdom et al., 2006) (Fig. 2). Therefore, some measure of ungulate use is critical to evaluating their effect (Wisdom et al., 2006). Due to variability in removal of aspen meristems across species in both space and time (Fig. 2), camera counts may be a more accurate estimator for parsing out interspecific impacts of different ungulate species than using fencing treatments alone. When cameras are unavailable, monitoring of removal of apical meristem and pellet counts can help to identify important thresholds for aspen recruitment (Fig. 5) (Rhodes and St. Clair, 2018).

4.4. Removal of apical meristem thresholds for aspen recruitment

Ungulates have the capacity to act as keystone species, exerting disproportionate effects on ecosystem processes (Côté et al., 2004; Wisdom et al., 2006). Our study suggests that ungulates at sufficiently high rates of use can impair aspen suckering density and aspen recruitment after fire (Fig. 5). We estimated that 2 cattle per camera $^{-1} \text{ day}^{-1}$ and 1.25 mule deer or elk per camera $^{-1} \text{ day}^{-1}$ was sufficient to suppress aspen recruitment at 30% removal of apical meristem (Figs. 4b and 5). We identified a conservative threshold at 30% removal of apical meristem for recruitment of aspen (Fig. 5b), that was similar to predicted thresholds of 27% in intact stands (Strand et al., 2009). This finding is consistent with several other studies that found reduced recruitment when removal of meristems was greater than 30% in stands in later stages of forest succession (Jones et al., 2005; Olmsted, 1979). However, our results had variability around the 30% threshold (Fig. 5a), with two sites recruiting well ($\approx 20,000$ stems ha^{-1}). Therefore, we define $> 30\%$ removal of apical meristems as a conservative threshold while $\geq 57\%$ showed complete recruitment failure (Fig. 5). Thresholds in post-burn environments may be higher due to higher growth rates and higher production of defense chemicals in aspen foliar tissue (Wan et al., 2014a).

5. Management and ecological implications

Cattle, mule deer, and elk differ in their preference for aspen. After, adjusting for body size using AUM equivalents (NRCS, 2003), we found that differential use of aspen was consistent with the browser-mixed-grazer continuum predicted by ungulate physiology (Hanley and

Hanley, 1982; Hoffman, 1989). Monitoring removal of apical meristems can help managers define ungulate use thresholds for aspen recruitment potential. This study found a conservative threshold at 30% removal of apical meristems and a strict threshold at $> 57\%$ removal of apical meristems for recruitment densities needed for aspen stand replacement (Fig. 5). We estimated that 2 cattle per camera $^{-1} \text{ day}^{-1}$ and 1.25 mule deer or elk per camera $^{-1} \text{ day}^{-1}$ coincided with sufficient relative use to reach 30% browse of apical meristems (Fig. 4d). Managers should also recognize site and annual differences in ungulate relative use and monitor removal of apical meristems to quantify ungulate impact across space and time (Fig. 2). The influence of ungulates on aspen suckers after fire are more pronounced in the first two years (Fig. 2) and can lead to long-term reductions in recruitment potential (Rhodes et al., 2017a). Our estimates provide clarity to managers in terms of differential effects between ungulate species, but also cautions that ungulate population size of any species or combination of species at sufficient density can cause aspen regeneration failure (Rhodes et al., 2017b).

Global changes in ungulate communities create novel pressures that disrupt plant communities and ecosystem processes (Asner et al., 2004; Spear and Chown, 2009). Land use change to pasture lands, spread of invasive ungulates, and extinction or extirpation of native ungulates pose threats to ecosystem stability across Earth's forested rangelands (Bevins et al., 2014; Echeverria et al., 2012; Lopez-Sanchez et al., 2016; Spear and Chown, 2009). Human driven increases in ungulate population size, particularly livestock, is closely linked with human population trends (MeyFroidt et al., 2010; Reid, 2012). Therefore, improving our ability to identify individual ungulate species impacts on important plant species is imperative for mitigating future trends in global change across grazed lands (Asner et al., 2004; Wisdom et al., 2006). Our data show that theoretical frameworks using both animal species and plant response data can aid in understanding how complex interactions between ungulates and plant communities may unfold in a changing world.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.04.013>.

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