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PLANT-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Disentangling herbivore impacts on *Populus tremuloides*: a comparison of native ungulates and cattle in Canada's Aspen Parkland

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Abstract Ungulates impact woody species' growth and abundance but little is understood about the comparative impacts of different ungulate species on forest expansion in savanna environments. Replacement of native herbivore guilds with livestock [i.e., beef cattle (*Bos taurus*)] has been hypothesized as a factor facilitating trembling aspen (*Populus tremuloides* Michx.) encroachment into grasslands of the Northern Great Plains. We used a controlled herbivory study in the Parklands of western Canada to compare the impact of native ungulates and cattle on aspen saplings. Native ungulate treatments included a mixed species guild and sequences of herbivory by different ungulates [bison (*Bison bison* subsp. *bison*), elk (*Cervus elaphus*) then deer (*Odocoileus hemionus*); or deer, elk, then bison]. Herbivory treatments were replicated in three pastures, within which sets of 40 marked aspen saplings (<1.8 m) were tracked along permanent transects at 2-week intervals, and compared to a non-grazed aspen stand. Stems were assessed for mortality and incremental damage (herbivory, leader breakage, stem abrasion and trampling). Final mortality was greater with exposure to any type of herbivore, but remained similar between ungulate treatments. However, among all treatments, the growth of aspen was highest with exposure only to cattle. Herbivory of aspen was attributed primarily to elk within the native ungulate treatments, with other forms of physical damage, and ultimately sapling mortality, associated with exposure to bison. Overall, these results indicate that native ungulates, specifically elk and bison, have more negative impacts on aspen saplings and provide evidence that native and domestic ungulates can have different functional effects on woody plant dynamics in savanna ecosystems.

Keywords Browsing · Damage · Herbivore guilds · Mortality · Multi-species

Introduction

Herbivores have significant impacts on vegetation, including altered growth, survival, and subsequent community dynamics. In North America, where prairies and the plants they consist of evolved with herbivory from multi-species guilds of endemic ungulates (Milchunas and Lauenroth 1989), European settlement since the early 1800s has led to the partial or complete replacement of these guilds by domestic livestock. Little information is available to understand how this change may have altered relationships between herbivory and vegetation dynamics, despite assertions that the replacement of native guilds with livestock has altered ecosystem function and may necessitate a return to evolutionary herbivory patterns to ensure conservation (Fuhlendorf and Engle 2001).

The Aspen Parkland of the Northern Plains is a savanna environment widely regarded as an ecological tension zone

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(Bird 1961), exemplified by ongoing temporal changes in the distribution and abundance of plant cover, including *Populus* species (Vance et al. 1983; Campbell and Campbell 2000). Trembling aspen (*Populus tremuloides* Michx.) is a deciduous tree that reproduces extensively via a large, creeping root system and associated suckering from underground root buds (Schier 1973). Sapling densities in young aspen stands can exceed 10 stems/m^2, and eventually decline with stand development via self-thinning (Peterson and Peterson 1992).

Recently, aspen cover has fluctuated in North America. Aspen range is determined by the net balance between moisture supply and demand (Hogg 1994) and aspen die-offs are often linked to drought (Anderegg et al. 2013; Worrall et al. 2013). In addition to being sensitive to climate, forest abundance in central Alberta reflects alterations to disturbance patterns such as fire (Vance et al. 1983; Campbell and Campbell 2000). Historically, wildfires and fires initiated by First Nations people were important mechanisms by which aspen was contained (Nelson and England 1971) although fire can also promote aspen by reducing the cover of more competitive conifers (Shepperd et al. 2000). In contrast to declines in other regions of North America, annual increases in aspen cover as great as 0.76 % have been observed in the Central Parkland of Alberta (Scheffler 1976). This expansion has been attributed to fire suppression associated with European settlement (Strong 1977) and bison extirpation (Campbell et al. 1994).

Tree abundance in savanna ecosystems is known to be influenced by large mammals. While more is understood on this ecological process in African savannas (Dublin et al. 1990; Augustine and McNaughton 1998; Goheen et al. 2004) the consequence of replacing native with domestic ungulates in North American ecosystems has not been experimentally tested. The Aspen Parkland was heavily used in the past by native ungulates, particularly Plains bison (*Bison bison* subsp. *bison*) during fall and winter (Roe 1951; Morgan 1980), but the specific impact of different herbivores on aspen dynamics in the region remains poorly understood. Contemporary herbivory in much of the Northern Great Plains is represented by widespread cattle (*Bos taurus*) grazing, which have replaced bison as the predominant herbivore. Both England and DeVos (1969) and Campbell et al. (1994) proposed that bison influenced forest cover prior to settlement through browsing, trampling, rubbing, and other direct impacts, and postulated that bison extirpation or subsequent replacement with cattle may have been an important factor aggravating recent aspen spread.

Ungulate species can have varying impacts on vegetation due to differences in morpho-physiology and associated dietary preferences (Hoffmann 1989). In comparing bison and cattle in northern temperate grasslands, Plumb and Dodd (1993) concluded that despite being similar as generalist bulk-feeding grazers, these species exhibit subtle but important differences in foraging behavior, with bison relying proportionally more on graminoids in middle to late summer than cattle. Although bison generally exhibit limited use of woodland habitats, even when grasslands are sparse, bison may increase use of woodlands (e.g., *Salix* shrublands) during winter (Reynolds et al. 1978), presumably due to the benefits of shelter from cold or the potential to access taller forage when snow is deep and other habitats are depleted of forage. In contrast, native browsing mule deer (*Odocoileus hemionus*) and mixed-feeding elk (*Cervus elaphus*) demonstrate selective foraging, and are more likely to feed on forbs and woody vegetation than cattle and bison (Didkowsky 2006). Although sustained high herbivory from a mix of native ungulates [bison, elk, moose (*Alces alces*) and deer] is known to impede forest regeneration and reduce structural diversity of aspen forest (Bork et al. 1997), the specific ungulate(s) responsible for this impact remain unclear.

Functional differences may also occur in the impact of herbivores on vegetation based on whether species graze alone or in combination (Johnson et al. 2000). Specific impacts may further depend on the sequence in which different ungulate species use vegetation, particularly if exposure to one herbivore alters the quantity and quality of remaining forage for subsequent species. “Facilitation” arises when use by one herbivore improves foraging opportunities for others that follow (McNaughton and Georgiadis 1986; Odadi et al. 2011). This may occur if bulk-feeding bison, which strive to maximize the quantity of grass intake, enhance opportunities for species such as deer and elk that select higher quality vegetation. Conversely, initial use by deer and elk may remove small amounts of high-quality forage prior to entry by bulk feeders, which in turn are relegated to using what remains, a process known as “high-grading” (Murry and Illius 2000). In contrast to sequential herbivory, simultaneous presence of multiple ungulates may lead to resource partitioning, with competitive displacement (i.e., behavioral avoidance) increasing the use of communities that would otherwise be avoided if grazed in succession (Voetin and Prins 1999).

We used a controlled herbivory study employing cattle and native ungulate species, foraging either together or in sequence, to compare their impacts on the survival of and damage to trembling aspen saplings. We focused on saplings because aspen regenerates extensively through vegetative means, and saplings, rather than trees, are susceptible to ungulates, leading to direct impacts on aspen forest dynamics in Parkland landscapes. We hypothesized that herbivore systems that include native ungulates would result in greater impact (mortality, damage and reduced size) to aspen relative to cattle. Our secondary objective was to compare the impact of bison, elk, and deer, and determine whether differences in the sequence of native ungulates altered impacts on aspen, hypothesizing that selective-feeding deer and elk would have a greater impact than bulk-feeding bison. Finally, we predict that native ungulate impacts on aspen will be greatest in a facilitation sequence led by bison compared to a high-grading sequence in which bison come last. Overall, we hypothesize that impacts on aspen will be greatest in the mixed ungulate treatment because deer and elk (i.e., selective-browsing species) will avoid grassland habitats occupied by bison.

Materials and methods

Study area and treatments

We evaluated ungulate impacts on aspen saplings within a portion of the University of Alberta Kinsella Research Station, situated 140 km southeast of Edmonton, Alberta, Canada. The station is located in the Aspen Parkland Natural Subregion, on an undulating landscape of glacial moraine with approximately 5–10 m relief. This savanna consists of a mosaic of upland rough fescue (*Festuca hallii*) grasslands, trembling aspen groves, western snowberry (*Symphoricarpos occidentalis*) shrublands, and interspersed fresh and saline wetlands. Upland soils range from Dark Brown to Eluviated Black Chernozems (Wheeler 1976). The area receives a mean annual precipitation of 430 mm, usually peaking in July, with about 120 days of frost-free growing season (Environment Canada, unpublished data).

Four ungulate herbivore treatments were examined that included either: (a) beef cattle alone (cattle); (b) a simultaneous mix of bison, elk, and mule deer (mixed); (c) bison, then elk, then mule deer in successive 2-week intervals (bison-elk-deer); or (4) mule deer, then elk, then bison in successive 2-week intervals (deer-elk-bison). Treatments began in 2004, and were repeated in 2005 and summer of 2006. Each treatment was replicated using three paddocks. Animals were in each paddock for a 6-week period in summer (1 June15 July) and fall (1 September–15 October), although all measures reported here were taken during the last period in summer 2006. Paddocks were surrounded by a 2.3-m-high page-wire fence and ranged from 3.2 to 10.3 ha in size (Table 1). Each paddock contained a mixture of habitats, thereby allowing selection by ungulates under relatively free-range conditions. Aspen forest covered 7.2–8.9 % of the paddocks, while grassland (51.4–59.2 %), shrubland (30.4–32.6 %) and riparian meadows (1.5–8.8 %) covered the remaining area (Didkowsky 2006). The number of individual animals varied among paddocks to account for variation in paddock sizes, while standardizing overall stocking rates among paddocks and treatments at moderate levels for the region (Table 1). Stocking rates accounted for changes in expected forage use of animals based on body weight and number of each species. The native ungulates used in this study were all descendants of animals recently domesticated. Animals were held in separate pastures containing the same vegetation types found in the study area. Thus, all ungulates were familiar with the landscape and conditioned to using the habitat available. All animal handling was approved by the Canadian Council on Animal Care.

We established three 10-m-long and permanently marked transects in each paddock to monitor the response of aspen. Two transects were established in two randomly selected aspen stands accessible to ungulates. The third transect was within a 15 × 30-m ungulate-proof exclosure constructed around part of a randomly selected aspen stand within each paddock. In total, we monitored aspen along 24 grazed transects and 12 ungrazed transects.

Sapling assessment

During the summer 2006 study period, impacts of ungulate exposure were assessed on 20 aspen saplings systematically located along each transect ($n = 720$ saplings). The nearest sapling was selected and marked at 1-m intervals on either side of each transect in late May 2006, and permanently labeled with a metal tag to facilitate repeated sampling. All saplings were between 30 and 180 cm in height and healthy (<10 % dead branches).

Saplings were assessed in late May for maximum apical leader height, basal diameter (at 2 cm height), and the number of lateral branches, which provide measures of aspen responses to herbivory in the previous 2 years. To characterize the initial aspen understory population, the density of all stems was assessed in a 2 × 10-m belted plot overlaying each transect. Individual saplings were then repeatedly examined on 15 and 30 June, and 15 July (i.e., coincident with the end of the exposure period to each consecutive species in the rotational treatments) for evidence of recent mortality (entire sapling broken or detached), leaf and/or twig herbivory (estimated % biomass removal), apical leader breakage, trampling (i.e., stem displacement) and bark abrasion as presence/absence data. “Trampling” was defined as deviation of the primary stem from vertical in excess of 10°. “Bark abrasion” is bark stripping of some or all of the cambium, typically in response to the impacts of hooves. In the sequential assessment of damage, saplings previously damaged were considered affected for all subsequent sampling intervals, enabling tracking of incremental impacts on the aspen

Table 1 Summary of paddock sizes, animal numbers and associated stocking rates [animal-unit-months of forage demand (*AUM*)] used during the 1 June–15 July 2006 study period

Treatment	Paddock area (ha)	Number of animals				Stocking rate (AUM ha^{-1})
		Cattle	Bison	Elk	Deer	
Cattle	7.64	8	–	–	–	1.82
	12.98	12	–	–	–	1.60
	7.90	8	–	–	–	1.76
Mixed	6.62	–	3	3	2	1.47
	7.27	–	3	3	2	1.34
	6.16	–	3	3	2	1.58
Bison-elk-deer	3.27	–	6	2	2	1.61
	3.99	–	8	2	2	1.67
	5.20	–	11	2	2	1.67
Deer-elk-bison	3.53	–	6	4	2	1.77
	3.93	–	8	4	2	1.60
	5.48	–	11	4	2	1.63

cohort along each transect over time, including the response to different ungulate species in the bison-elk-deer and deer-elk-bison treatments.

Analysis

Cumulative effects of herbivory among treatments were assessed at the end of the aggregate herbivory period on 15 July, and enabled comparison among all treatments, including testing the impact of replacing an historical native ungulate guild (either together or in sequence) with contemporary herbivory by cattle, or no herbivory. In addition, repeated measures were used to assess the incremental effects of ungulates during each 2-week period from the start of the herbivory period. Successive assessments in the bison-elk-deer and deer-elk-bison treatments coincided with bison, elk and deer, and deer, elk and bison, respectively. As the individual stocking rates of bison, elk, and deer were not equivalent over the 6-week period in the sequential native treatments, emphasis in the temporal analysis was placed on the detection of changes in aspen responses through successive sampling intervals rather than on direct comparisons among treatments. Because it is likely that the saplings in this study were suckers off the root system of clonal aspen, we analyzed data at the transect level and individual stems were not treated as replicates. Significant ANOVA results on main effects ($P < 0.05$) were followed with a Tukey mean comparison test to examine differences among treatments, using a significance of $P < 0.05$. All analyses were done in R (R Core Team 2012).

Aspen stem mortality from May to July of 2006 on each transect was assessed over time within treatments using a repeated measure ANOVA in which sampling date was fixed, transect was the repeated measure and paddock random. Aspen survival over the 2006 season was assessed between treatments with an ANOVA in which herbivory treatment was fixed and paddock random. We further examined the specific relationship between bison densities in each paddock and the number of stems that died using a Poisson general linear model (GLM). The extent of herbivory (% leaf and twig removal) on aspen stems was compared over time among treatments with a repeated measure ANOVA in which sampling date was fixed, stem was the repeated measure and paddock random. Final accumulated herbivory on 15 July was compared among treatments using ANOVA in which herbivory treatment was the fixed effect and paddock random.

The number of aspen stems on each transect with damage (leader breaks, trampling and stem abrasion) was compared over time within each treatment using a GLM ANOVA against a Poisson distribution. Observation date was fixed, transects were the repeated measure and paddocks random. Final damage counts were compared between ungulate herbivory treatments using an ANOVA in which herbivory treatment was the fixed effect and paddock random.

Finally, the response of aspen basal diameter, height and number of lateral branches to the ongoing ungulate treatments, were tested with an analysis of covariance (ANCOVA). Ungulate herbivory treatment was a fixed effect, aspen stand density was included as a covariate, and paddock was a random effect. Basal diameter and height were log($x + 1$) transformed, while the count of lateral branches was square root transformed.

Results

Mortality in 2006

Final aspen mortality was influenced by herbivory treatment (Fig. 1; $F_{4,20} = 4.61$, $P = 0.008$). No stems died in the exclosures, while 14.2 % died under cattle exposure, 12.5 % in the bison-elk-deer, and 8.3 % in each of the deer-elk-bison and mixed treatments; aspen stands in the bison-elk-deer and cattle treatments had greater mortality than the exclosures ($P < 0.05$). Biweekly mortality differed over time in the deer-elk-bison ($F_{2,13} = 5.60$, $P = 0.018$), bison-elk-deer ($F_{2,13} = 6.71$, $P = 0.01$), and mixed ($F_{2,13} = 4.91$, $P = 0.026$) treatments, but the pattern was not significant for cattle ($F_{2,13} = 1.34$, $P = 0.295$) (Fig. 1). In both the deer-elk-bison and bison-elk-deer treatments, mortality was observed in the survey immediately after bison had been in the paddock, while mortality within the mixed treatment was observed after the first 2 weeks. Subsequent correlation of mortality rates with bison densities across the native ungulate treatments indicated aspen mortality increased with bison density (Fig. 2; Poisson GLM $P < 0.001$, pseudo $R^2 = 0.53$).

2006 Herbivory

Final leaf ($F_{3,438} = 73.5$; $P < 0.001$) and twig defoliation ($F_{3,436} = 23.1$; $P < 0.001$) at the end of the trial varied among herbivory treatments. Almost no herbivory occurred on aspen saplings by cattle throughout the trial (<0.3 %), regardless of sampling date (Fig. 3). In contrast, treatments consisting of native ungulates led to 28–38 % leaf defoliation, and 12–15 % twig defoliation. Although final twig defoliation levels were similar among all treatments containing native ungulates, leaf defoliation remained greatest under mixed herbivory (Fig. 3).

Leaf defoliation also changed over time within those treatments containing native ungulates (deer-elk-bison, $F_{2,228} = 118.1$; bison-elk-deer, $F_{2,220} = 70.76$; mixed, $F_{2,232} = 47.65$; all P-values <0.001) but not cattle ($F_{2,223} = 1.01$; $P = 0.365$) (Fig. 4). The same pattern was observed for twig defoliation by native ungulates (deer-elk-bison, $F_{2,228} = 43.5$; bison-elk-deer, $F_{2,220} = 16.6$; mixed, $F_{2,232} = 38.74$; all P-values <0.001) and cattle ($F_{2,223} = 0.06$; $P = 0.946$). Defoliation on aspen saplings progressively increased through subsequent sampling times within the mixed treatment, but in the rotational treatments largely coincided with the period when only elk were present (Fig. 2). Low levels of defoliation were detected on aspen leaves and twigs by bison within the bison-elk-deer, but no defoliation was detected by deer within the deer-elk-bison treatment.

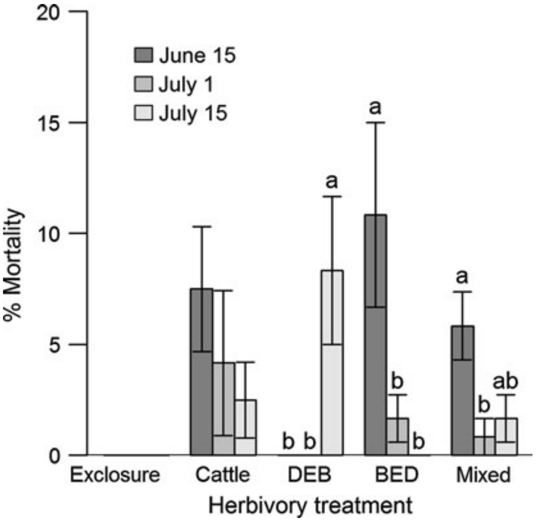

Fig. 1 Aspen mortality in four herbivory treatments sampled over time (mean ± SE). Herbivory treatments were: not grazed (*Exclosure*), continuous herbivory by cattle (*Cattle*), grazed sequentially by deer-elk-bison (*DEB*), grazed sequentially by bison-elk-deer (*BED*); deer, elk and bison all present simultaneously (*Mixed*). Within each treatment, *lower-case letters* indicate significance based on a post hoc Tukey test ($P < 0.05$). Some data points have been jittered to show overlapping data

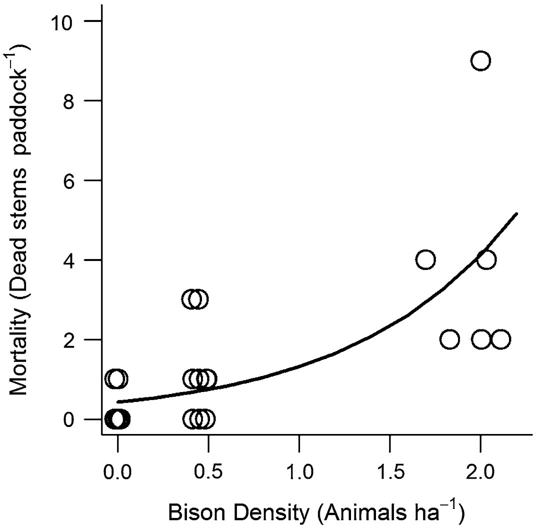

Fig. 2 Mortality of aspen in response to bison density within each of the native ungulate treatments. On the *x*-axis, zero corresponds to the elk and deer sequences in the rotational herbivory sequences. The *line* is the fitted Poisson general linear model ($P < 0.001$, pseudo $R^2 = 0.53$)

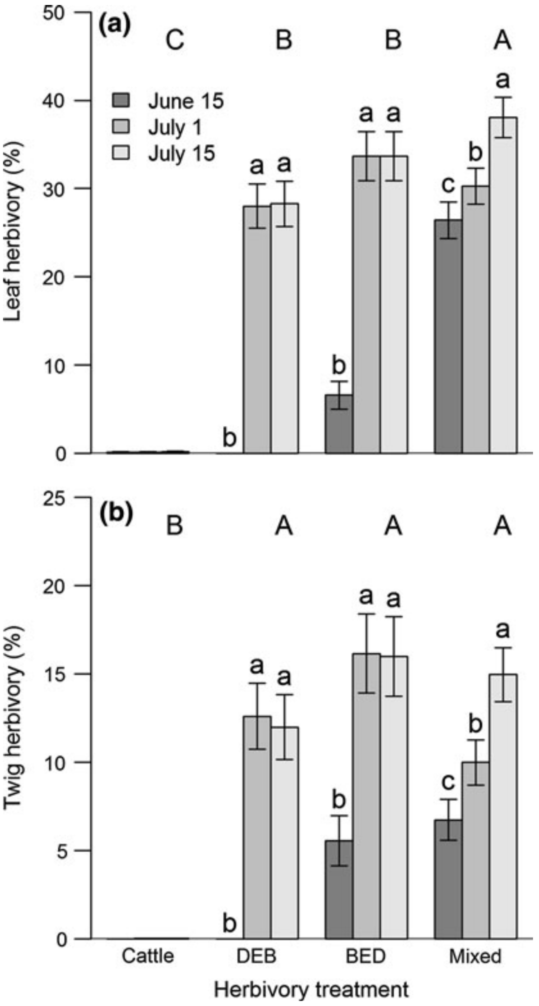

Fig. 3 Herbivory on aspen **a** leaves and **b** twigs in each of four ungulate herbivory treatments. *Bars* are mean (±SE) herbivory per tree ($n = 6$). *Lower-case letters* indicate significant differences within treatments over time based on a post hoc Tukey test ($P < 0.05$). *Upper-case letters* indicate significant differences among treatment groups on 15 July at the end of the experiment. See Fig. 1 for treatments and abbreviations

Aspen sapling damage in 2006

Mortality withstanding, damage to remaining aspen saplings was in the form of leader breaks, trampling, and bark abrasion, affecting 7.3, 7.9 and 8.3 % of all initially marked stems, respectively, across treatments. Damage to saplings generally increased over time within the cattle and mixed treatments (Fig. 3). Although final damage levels within the rotational treatments were similar to all other herbivory treatments ($P > 0.05$), the timing of damage (of all forms) to aspen saplings within the rotational treatments clearly coincided with periods of bison use: early on in the bison-elk-deer and later in the rotation of the deer-elk-bison (Fig. 4).

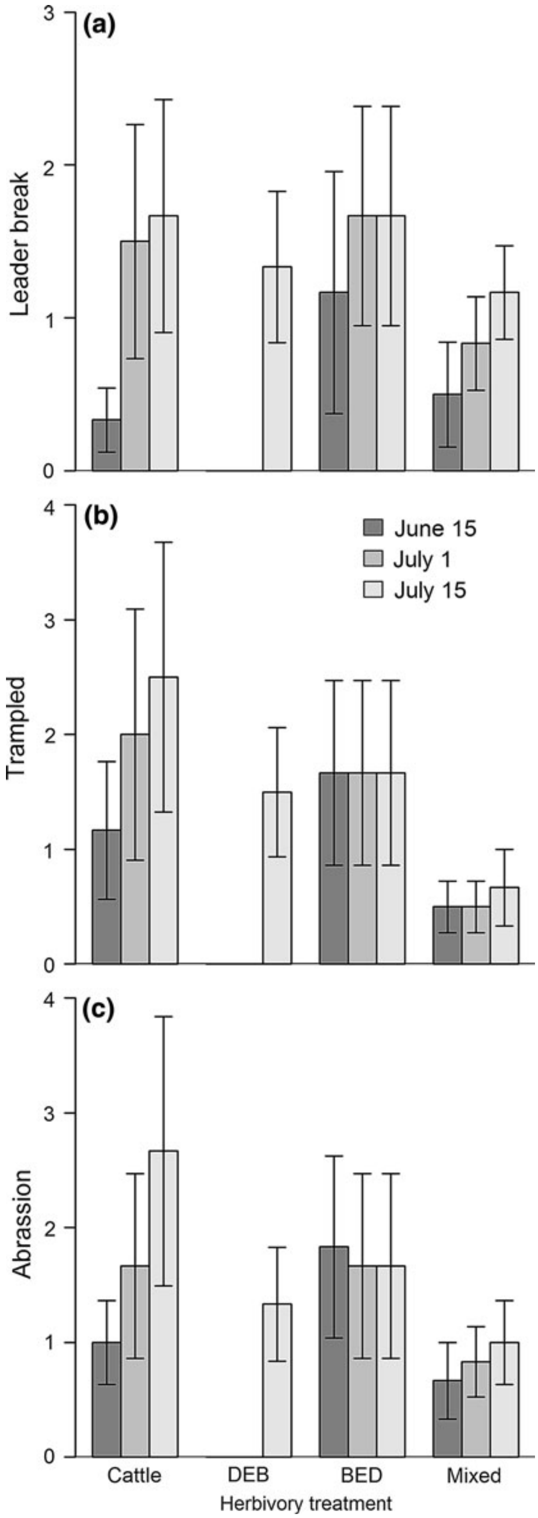

Fig. 4 Damage to aspen (number of trees per transect) in the form of **a** leader breakage, **b** trampling, and **c** stem abrasion, in each of four ungulate herbivory treatments. No damage was observed in the DEB treatment on 15 or 30 June. See Fig. 1 for treatments and abbreviations

Sapling size

After more than 2 years herbivory treatments had an effect on aspen sapling basal diameter, height, and the number of lateral branches per stem (Table 2). Aspen diameter, height, and branch counts were consistently greatest in the absence of herbivory (i.e., in exclosures), and decreased through the cattle, deer-elk-bison, bison-elk-deer and mixed herbivory treatments (Fig. 5). Treatments in which aspen were exposed to bison in early summer (i.e., either exclusively in early June, or throughout the herbivory period within the mixed) had lower aspen heights and branch counts (Fig. 5b, c). Similarly, the mixed treatment led to smaller basal diameters and shorter aspen stems compared to all other treatments (Fig. 5a, b).

Discussion

Comparative impacts of native herbivores and cattle

Removal of bison and their replacement with cattle has been proposed as a factor contributing to increases in aspen across western Canada (Campbell et al. 1994). We found mixed evidence to support our hypothesis that replacement of native ungulate guilds with cattle has reduced aspen mortality (Fig. 1) and growth (Fig. 5). For example, native ungulates were found to impart greater herbivory and damage to aspen, as well as reduce sapling growth relative to cattle, thereby supporting the notion that native ungulates were more detrimental to aspen. However, similar levels of overall mortality by cattle and native ungulates do not support our hypothesis, and suggest that the impacts of ungulates in regulating forest dynamics are complex within this ecosystem. These results contrast with those of Goheen et al. (2010) where tree establishment in an African savanna was favored by cattle due to the suppression of competitive understory grasses, while wild herbivores had a negligible direct effect on tree establishment. Woody species dynamics in the latter study were also mediated by the impact of small herbivores (rodents) (Maclean et al. 2011), a factor not addressed in the present study.

Table 2 Results from analysis of covariance for within-subject test of the response of aspen sapling size parameters to different ungulate herbivory treatments, with aspen stand density as a covariate (26 residual *df*)

	df	Basal diameter		Height		Lateral branches	
		F-value	*P*	*F*-value	*P*	*F*-value	*P*
Ungulate (U)	4	10.37	<0.001	32.79	<0.001	41.09	<0.001
Density (D)	1	3.50	0.06	29.18	<0.001	1.41	0.24
U × D	4	1.02	0.40	1.11	0.35	2.13	0.08

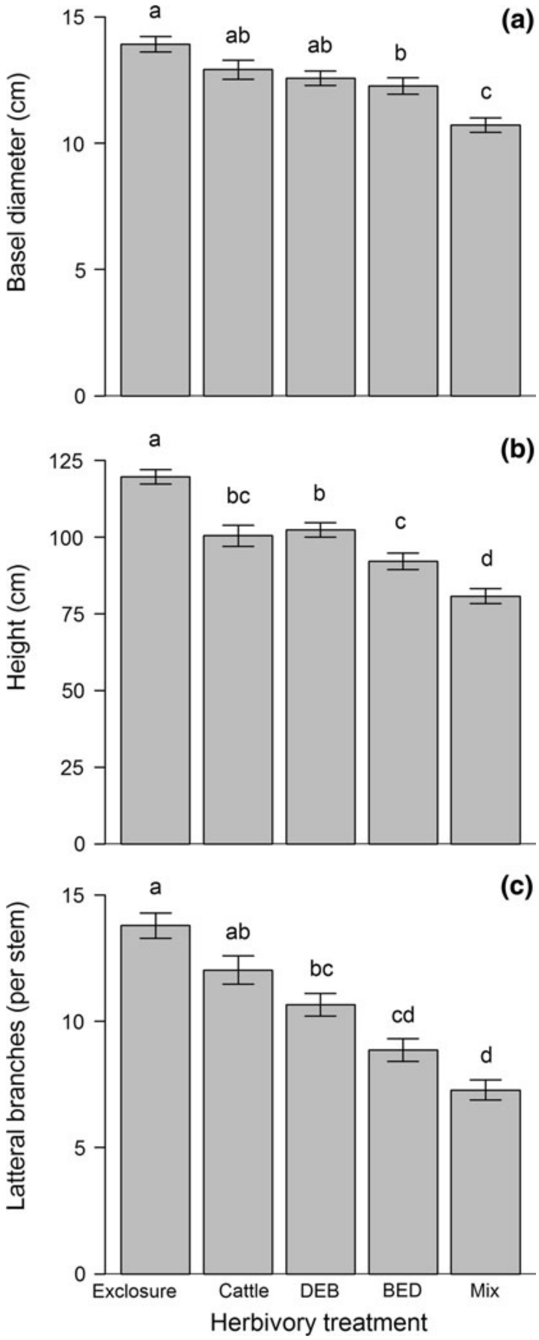

Fig. 5 Effect of different ungulate herbivory treatments on **a** basal diameter, **b** height, and **c** number of lateral branches of aspen (mean ± SE) after 3 years. *Lower-case letters* indicate significant differences between treatments based on a post hoc Tukey test ($P < 0.05$). See Fig. 1 for treatments and abbreviations

Impacts of cattle and bison on aspen were associated primarily with physical damage to saplings other than defoliation (Fig. 4), and which in turn, led to mortality. This is not surprising given that cattle and bison are known to preferentially feed on graminoids (Plumb and Dodd

1993). However, our stocking rates may also have been too low to instigate greater browsing by these herbivores, as 81 % and greater use of aspen suckers has been observed with stocking rates up to 1.97 animal-unit-months (AUM) ha^{-1} (Alexander 1995), rates well above those examined here (Table 1). Despite limited browsing, our reductions in aspen sapling height are similar to other studies with cattle (Alexander 1995), and are consistent with the notion that both cattle (Asamoah et al. 2003) and bison (Didkowsky 2006) will voluntarily occupy this habitat when available. Given that bison prefer open grassland habitats (Reynolds et al. 1978; Hudson and Frank 1987), our findings suggest that bison (and likely cattle) may be using the small area of aspen forest (~7.6 %) within these savanna landscapes for other purposes in addition to foraging, potentially the provision of shade given the timing of our study in mid-summer when temperatures were near their peak for the year.

Our results also provide evidence that the impacts of bison on aspen mortality may be tied to stocking density (Fig. 2). Greater ungulate densities can reduce selection of habitats by herbivores through greater competition among individual animals (Launchbaugh and Howery 2005), with increased bison activity in aspen stands likely to lead to greater physical damage and associated mortality. Although our densities remained relatively low across all herbivory treatments, density effects could be exacerbated for herding animals such as bison, which alter foraging behavior (Launchbaugh and Howery 2005). Similar effects have been observed in studies employing cattle herbivory at high densities (e.g., up to 300 cow/calf pairs in 25 ha) to deliberately control aspen regrowth in the Parkland of Central Alberta (Fitzgerald and Bailey 1984; Alexander 1995). Consequently, the use of longer herbivory periods, including repeated use over multiple years, could further reduce aspen regeneration (Alexander 1995), and ultimately compromise the ability of these forests to regenerate, as reported elsewhere for wildlife (Bork et al. 1997; Kay and Bartos 2000) and livestock (Bailey et al. 1990). Although aspen mortality observed in our study (≤14 %) remained at moderate levels, repeated exposure over extended periods is likely to further increase mortality and may reduce aspen regeneration in the long term.

While cattle exhibited no herbivory of aspen, bison did consume small amounts of aspen (Fig. 3). Although bison are considered a bulk feeder with a preference for graminoids (Plumb and Dodd 1993), our observations of bison use on aspen occurred in mid-summer when ample alternative forage was available. Thus, our results emphasize that bison will voluntarily consume aspen when available, and in doing so can reduce aspen vigor and survival. Suppression of similar tree species has been observed in Yellowstone, where bison herbivory occurred on 84 % of willow saplings and 54 % of cottonwood saplings (Painter and Ripple 2012). Moreover, given that our stocking rates of bison within the native ungulate treatments (~1 AUM ha^{-1}) were below those in the cattle-alone treatment (>1.6 AUM ha^{-1}), our comparison of the differential impacts of bison and cattle on aspen is likely an underestimation, with bison potentially more willing than cattle to utilize this plant under free-range conditions. Notably, this conclusion lends support to the notion that the replacement of bison by cattle since European settlement may have exacerbated aspen encroachment by reducing biological control of this tree species (Campbell et al. 1994).

Specific impacts of deer and elk on aspen were limited compared to those of bison and cattle, and are expected given that their contribution to overall stocking rates within the native ungulate treatments were more modest, particularly for deer. Thus, potential impacts of deer and elk on aspen should be interpreted cautiously. Nevertheless, important observations were made regarding the impacts of elk on aspen saplings. Unlike other ungulates, elk contributed the most to browsing on aspen (Fig. 3), though this impact did not translate into elevated mortality (Fig. 1). High defoliation by elk was associated with both greater time spent in aspen forest compared to other habitats, as well as the inclusion of moderate amounts of woody vegetation (though less than deer) within their diet (Didkowsky 2006).

Native ungulate sequencing

Our results also demonstrated mixed responses to the hypothesis that the sequence of native ungulate herbivory within the rotational treatments may alter impacts on aspen saplings. In contrast to our hypothesis on the expected role of bison in facilitating use by other ungulate species, browsing impacts from elk were consistent in the rotational treatments regardless of whether elk followed deer or bison (Fig. 3), suggesting our results were neither indicative of facilitation nor high-grading. Instead, impacts of bison on aspen varied depending on whether saplings were exposed during spring (early June) or mid-summer (early July), with more negative impacts from bison during the early growing season.

Observations of varying impacts of bison at different times (Fig. 4) are similar to studies examining cattle impacts on aspen regeneration following clear-cutting where greater damage occurred earlier in the summer (Dockrill et al. 2004). Although consistent with our hypothesis on the importance of timing of use, changes in the impact of bison at different times are unlikely to reflect interactions with other ungulates in this study, particularly given the limited stocking rates of deer and elk. Instead, other mechanisms may account for the reduced impact of bison in mid-summer, including increased aspen resistance to damage with advancing stem lignification (Dockrill et al. 2006). Bison may also spend more time in aspen stands early in the summer due to the limited growth of adjacent grasslands at that time, which may limit foraging opportunities or result in rapid forage depletion, either of which would lead to greater use of aspen. Similar early summer use patterns of aspen forest have been observed in cattle (Arthur 1984; Asamoah et al. 2003).

Finally, reductions in aspen growth and vigor were greatest within paddocks exposed to a simultaneous combination of bison, elk, and deer within the mixed treatment (Fig. 5), and coincided with the greatest aspen leaf defoliation, likely by elk based on observations in the other treatments. These findings partially support the last hypotheses proposed at the outset of this study on the potential additive impact of simultaneous exposure to multiple ungulates on aspen saplings. One explanation for this outcome is that bison may spatially displace elk and deer from grasslands and other open habitats, in turn leading to greater impacts by elk and deer on aspen. Moreover, with aspen habitats occupying less than 10 % of the landscape, localized intensities of aspen forest use by elk and deer may be greater than expected. This notion is further supported by the type of impacts observed on aspen in the mixed treatment, which involved defoliation rather than other forms of damage, including mortality. Repeated defoliation in the absence of mortality would ultimately account for the poor performance of aspen saplings in this treatment (Fig. 5).

Conclusion

Both cattle and native ungulate guilds increased mortality of aspen saplings during summer in this savanna environment of the Northern Great Plains, while only native ungulates caused a reduction in aspen growth, leading us to partly reject our hypothesis that the replacement of native herbivores with cattle has increased aspen presence. Aspen survival and growth is particularly important to aspen regeneration given the large-scale dieback of this species that has occurred in some regions due to the combined effects of drought and insects such as forest tent caterpillars (Hogg et al. 2008; and see Alexander 1995).

Our results suggest that despite similar mortality among herbivore treatments, cattle may contribute less to the suppression of aspen because of functional differences between cattle and those species in the native ungulate guild. That is, the specific mechanisms influencing aspen saplings varied depending on herbivore identity and timing. While elk impacts on aspen occurred primarily through defoliation, bison and cattle impacted aspen through physical damage. Impacts of bison on aspen were also greater during the early growing season. As mortality within the native ungulate treatment was linked primarily to the presence of bison, cessation of bison herbivory is likely to increase aspen survival (and thus, forest regeneration), particularly if combined with the absence of cattle. While deer and elk presence may impact aspen saplings, their impact is unlikely to alter aspen regeneration, and instead reduces the vigor of aspen populations. Overall, our results reinforce and clarify the importance of wild ungulates and contemporary cattle herbivory in regulating aspen regeneration, forest succession, and potentially grassland encroachment by this tree species in the Northern Great Plains.

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References

Alexander MJ (1995) The response of mature decadent and healthy sapling aspen forest communities to prescribed burning and controlled livestock grazing. M.Sc. thesis, Department of Plant Science, University of Alberta, Edmonton, Alberta

Anderegg WL, Plavcová L, Anderegg LDL, Hacke UG, Berry JA, Field CB (2013) Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. Global Change Biol. doi:10.1111/gcb.12100

Arthur RL (1984) Plant community and forage preferences of cattle on native Aspen Parkland range. M.Sc. thesis, Department of Plant Sciences, University of Alberta, Edmonton, Alberta

Asamoah SA, BorkEW Irving BD, Price MA, Hudson RJ (2003) Cattle herbage utilization patterns under high-density rotational grazing in the Aspen Parkland. Can J Anim Sci 83:541–550

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J Wildl Manage 62:1165–1183

Bailey AW, Irving BD, Fitzgerald RD (1990) Regeneration of woody species following burning and grazing in the aspen parkland. J Range Manage 43:212–215

Bird RD (1961) Ecology of the Aspen Parkland of western Canada in relation to land use. Publication no. 1006. Research Branch, Canadian Department of Agriculture, Ottawa

Bork EW, Hudson RJ, Bailey AW (1997) *Populus* forest characterization in Elk Island National Park relative to herbivory, prescribed fire and topography. Can J Bot 75:1518–1526

Campbell ID, Campbell C (2000) Late Holocene vegetation and fire history at the southern boreal forest margin in Alberta, Canada. Palaeogeogr Palaeoclimatol Palaeoecol 164:263–280

Campbell C, Cambell ID, Blyth CB, McAndrews JH (1994) Bison extirpation may have caused aspen expansion in Western Canada. Ecography 17:360–362

Didkowsky MG (2006) Scales of forage selection by ungulates in Aspen Parkland. M.Sc. thesis, Department of Biological Sciences, University of Alberta, Edmonton, Alberta

Dockrill CWM, Blenis PV, Bailey AW, King JR (2004) Effect of summer cattle grazing on aspen stem injury, mortality and growth. For Chron 80:257–261

Dockrill CWM, Bailey AW, Blenis PV, King JR (2006) Seasonal variation in resistance of aspen stems to shearing force. Rangel Ecol Manage 59:212–215

Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and fires as a cause of multiple stable states in the Serengeti-Mara woodlands. J Anim Ecol 59:1147–1164

England RE, DeVos A (1969) Influence of animals on pristine conditions on the Canadian grasslands. J Range Manage 22:87–94

Fitzgerald RD, Bailey AW (1984) Control of aspen regrowth by grazing with cattle. J Range Manage 37:157–158

Fuhlendorf SD, Engle DM (2001) Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51:626–632

Goheen JR, Keesing F, Allan BF, Ostfeld RS (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. Ecology 85:1555–1561

Goheen JR, Palmer TM, Keesing F, Riginos C, Young TP (2010) Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. J Anim Ecol 79:372–382

Hoffmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443–457

Hogg EH (1994) Climate and the southern limit of the western Canadian boreal forest. Can J For Res 24:1835–1845

Hogg EH, Brandt JP, Michaellian M (2008) Impacts of a regional drought on the productivity, dieback and biomass of western Canadian aspen forests. Can J For Res 38:1373–1384

Hudson RJ, Frank A (1987) Foraging ecology of bison in aspen boreal habitats. J Range Manage 40:71–75

Johnson BK, Kern JW, Wisdom MJ, Findholt SL, Kie JG (2000) Resource selection and spatial separation of elk and mule deer in spring. J Wildl Manage 64:685–697

Kay CE, Bartos DL (2000) Ungulate herbivory on Utah aspen: assessment of long-term exclosures. J Range Manage 53:145–153

Launchbaugh KL, Howery LD (2005) Understand landscape use patterns of livestock as a consequence of foraging behavior. Rangel Ecol Manage 58:99–108

Maclean JE, Goheen JR, Doak DF, Palmer TM, Young TP (2011) Cryptic herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree. Ecology 92:1626–1636

McNaughton SJ, Georgiadis NJ (1986) Ecology of African grazing and browsing mammals. Annu Rev Ecol Syst 17:39–65

Milchunas DG, Lauenroth WK (1989) Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55:82–86

Morgan RG (1980) Bison movement patterns on the Canadian plains: an ecological analysis. Plains Anthropol 25:143–159

Murry MG, Illius AW (2000) Vegetation modification and resource competition in grazing ungulates. Oikos 89:501–508

Nelson JG, England RE (1971) Some comments on the causes and effects of fire in the Northern Grasslands area of Canada and the nearby United States. C.A. 1750–1900. Can Geogr 15:295–306

Odadi WO, Abdulrazak SA, Karachi MM, Young TP (2011) African wild ungulates compete with or facilitate cattle depending on season. Science 333:1573–1755

Painter LE, Ripple WJ (2012) Effects of bison on willow and cottonwood in northern Yellowstone National Park. For Ecol Manage 264:150–158

Peterson EB, Peterson NM (1992) Ecology, management and use of aspen and balsam poplar in the prairie province. Special report no. 1. Forestry Canada, Northern Forestry Center, Environment Canada, Edmonton, Alberta

Plumb GE, Dodd JL (1993) Foraging ecology of bison and cattle on a mixed prairie—implications for natural area management. Ecol Appl 3:631–643

R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reynolds HW, Hansen RM, Peden DG (1978) Diets of Slave River lowland bison herd, Northwest Territories Canada. J Wildl Manage 42:581–590

Roe FG (1951) The North American Buffalo: a critical study of the species in its wild state. University of Toronto Press, Toronto

Scheffler EJ (1976) Aspen forest vegetation in a portion of the East Central Alberta Parklands. M.Sc. thesis, Department of Plant Science, University of Alberta, Edmonton, Alberta

Schier GA (1973) Origin and development of aspen root suckers. Can J For Res 3:45–53

Shepperd WD, Bartos DL, Mata SA (2000) Above- and below-ground effects of aspen clonal regeneration and succession to conifers. Can J For Res 31:739–745

Strong WL (1977) Pre- and post-settlement palynology of southern Alberta. Rev Palaeobot Palynol 23:373–387

Vance RE, Emerson D, Habgood T (1983) A mid-Holocene record of vegetative change in central Alberta. Can J Earth Sci 20:364–376

Voetin MM, Prins HHT (1999) Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 121:287–294

Wheeler GW (1976) Some grassland and shrubland communities in the Parklands of central Alberta. M.Sc. thesis, Department of Plant Science, University of Alberta, Edmonton, Alberta

Worrall JJ, Rehfeldt GE, Hamman A, Hogg EH, Marchetti SB, Michaelian M, Gray LK (2013) Recent declines of *Populous tremuloides* in North America linked to climate. For Ecol Manage. doi:10.1016/j.foreco.2012.12.033