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Effects of bison on willow and cottonwood in northern Yellowstone National Park

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ABSTRACT

On the northern ungulate winter range of Yellowstone Park, willow (*Salix* spp.) and cottonwood (*Populus angustifolia* and *Populus balsamifera*) have increased in height and cover in some places since the reintroduction of wolves (*Canis lupus*) and the subsequent changes in elk (*Cervus elaphus*) behavior and population densities. However, in the Lamar Valley, an important part of this winter range, many plants are still intensively browsed and recruitment has been limited. As elk numbers have declined and their distribution has changed in recent years, bison (*Bison bison*) have increased on the northern range. To distinguish bison effects from those of elk, we measured browsing that occurred in summer. We found average summer browse rates of 84% for willow and 54% for cottonwood seedlings in the summer of 2010, demonstrating that bison have become significant browsers in the Lamar Valley. Plants were increasing in size except where intensively browsed by bison, suggesting that a release from elk browsing has occurred, and that a trophic cascade is occurring from wolves to plants, mediated by both elk and bison. Release of bison from competition with elk, low levels of predation on bison, and lack of opportunity for migration and range expansion may be factors contributing to a high concentration of bison, with resulting effects on plant communities and biodiversity.

1. Introduction

Some ecosystems of western North America were shaped in the past by bison (*Bison bison*) and the ecological effects of these iconic animals may again be a factor, with recent efforts to restore them to portions of their former range (Sanderson et al., 2008; Gates et al., 2010). In Yellowstone National Park, elk (*Cervus elaphus*) numbers have decreased following wolf (*Canis lupus*) reintroductions in 1995 and 1996, but the bison population has continued to grow, maintained below a peak of about 5000 by large-scale culling when bison leave the park in winter (White and Garrott, 2005; Plumb et al., 2009; White et al., 2010, 2011). White et al. (2011) reported that current management practices, in which bison are kept close to park boundaries in winter and hazed back into the park in early spring, are likely to lead to high population densities and density-dependence among bison, possibly causing deterioration of range resources and ecological processes.

Valleys in the northern part of Yellowstone National Park are used as winter range by elk, bison, and other ungulates (Fig. 1; Singer and Norland, 1994). In this area, called the northern ungulate winter range, or "northern range", willow (*Salix* spp.), cottonwood (*Populus angustifolia* and *Populus balsamifera*) and aspen (*Populus tremuloides*) declined in the 20th century, primarily due to browsing by elk in winter (Kay, 1994; Chadde and Kay, 1996; Singer, 1996; Keigley, 1997, 2000; Romme et al., 2001; National Research Council, 2002; Barmore, 2003; Singer et al., 2003; Beyer, 2006; Wagner, 2006). Beaver (*Castor canadensis*), which depend on these plants, also declined in number and range resulting in loss of wetlands and further decline of willows (Wolf et al., 2007; Bilyeu et al., 2008; Smith and Tyers, 2008). Since the return of wolves to the northern range, elk population size, spatial distribution, and foraging behavior have changed (Laundre et al., 2001; Hernandez and Laundre, 2005; White et al., 2010, in press). Probably as a result of these changes, woody browse plants have increased in height and cover in some places (Ripple and Beschta, 2006; Beschta and Ripple, 2007; Beyer et al., 2007; Ripple and Beschta, in press), and beaver have increased in number and range (Smith et al., 2003; Smith and Tyers, 2008). For example, few cottonwood trees grew to maturity on the northern range after the early 20th century (Beschta, 2005), and cottonwood saplings were kept short (<1 m) by browsing (Keigley, 1997; Beschta, 2003). Between 2001 and 2006 cottonwoods again began to grow tall enough to begin to escape elk browsing (>2 m) in places along the east edge of the Lamar Valley, on an island in the Lamar River, and on Soda Butte Creek (Ripple and Beschta, 2003; Beschta and Ripple, 2010). Willows also increased in height in some places (Ripple and Beschta, 2006; Beschta and Ripple, 2007). However, in most of the Lamar Valley, west of the Soda Butte Creek confluence (Fig. 1), the median cottonwood sapling height remained the same or decreased, and many willows and young cottonwoods were intensively browsed (Beschta and Ripple, 2010).

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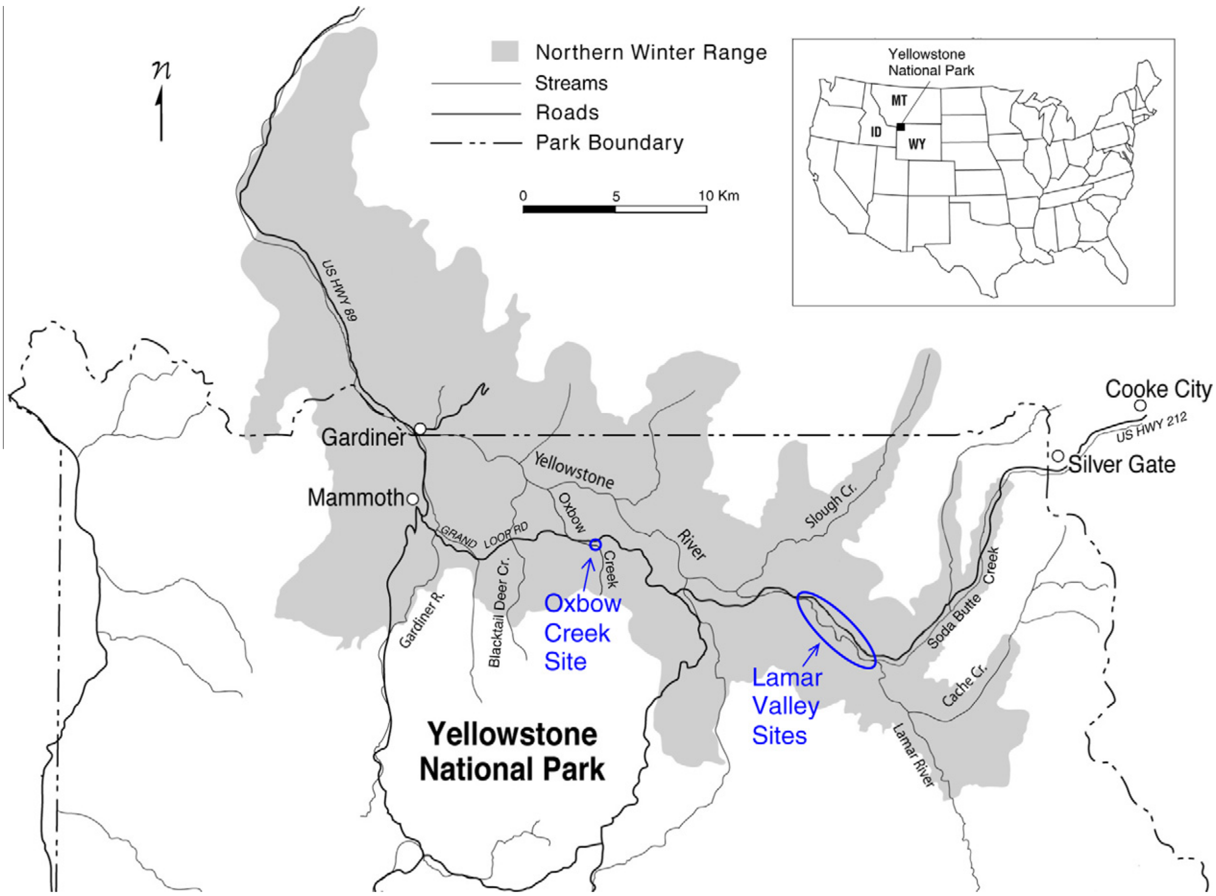

Fig. 1. Map of northern Yellowstone National Park, showing the location of study sites at Lamar Valley and Oxbow Creek.

Use of the Lamar Valley by wintering elk has declined since wolf reintroduction, due to lower elk numbers and a decrease in the proportion of the elk population wintering on the east side of the range (White et al., 2010, in press). Meanwhile, bison on the northern range increased from 455 in the summer of 1997 (following the removal of 725 the previous winter), to 2070 bison in 2007, the highest count on the northern range in the history of the park (Meagher, 1973; White et al., 2011). Since 1984 bison have congregated in the Lamar Valley in summer as well as winter, and some bison have moved from central Yellowstone to the northern range (Taper et al., 2000; Gates et al., 2005; Fuller et al., 2007). Ripple et al. (2010) hypothesized that the bison increase on the northern range may be part of a secondary trophic cascade, where wolves reduced elk density, thereby releasing bison from interspecific competition, resulting in higher bison densities and greater effects from bison on forage plants. Researchers reported seeing bison browsing in the summer season (Beschta, 2003; Beschta and Ripple, 2010), and found willow height to be inversely related to the density of bison fecal piles (Ripple and Beschta, 2006). Significant browsing in summer on the northern range had not previously been reported, nor has browsing by bison (winter or summer) been regarded as an important factor in the ecology of the area by most researchers, who have generally assumed that bison had little effect on browse plants (Singer et al., 1994; Singer and Norland, 1994; Keigley, 1997).

Are bison affecting the growth of willow and cottonwood in the Lamar Valley? Summer browsing can distinguish the effects of bison from those of elk, because elk are scarce in the valley in summer. Also, tall willows may be used to compare browsing between heights accessible only to elk, and heights accessible to both bison and elk (Fig. 2). We measured the effects of browsing, differentiated by height and season, to answer three questions regarding willow and cottonwood in the Lamar Valley: (1) are these plants suppressed by browsing, (2) how much browsing occurs in summer, and (3) what proportion of browsing can be attributed to bison?

1.1. Study area

The northern ungulate winter range in the Greater Yellowstone Ecosystem is comprised of open valleys with steppe and sagebrush–steppe vegetation, bordered by slopes with coniferous forest interspersed with aspen groves (Singer and Norland, 1994; Barmore, 2003; Gates et al., 2005). Willow bushes are present in riparian areas and wet meadows throughout the northern range, but cottonwood trees are limited to the larger river valleys (National Research Council, 2002; Beschta, 2005; Beyer, 2006; Beschta and Ripple, 2010). Elk and bison share the winter range with smaller numbers of moose (*Alces alces*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*) and bighorn sheep (*Ovis canadensis*) (Singer and Norland, 1994; Barmore, 2003).

Study sites were located in the Lamar Valley, a floodplain of the Lamar River about 1–2 km wide, extending about 9 km from the area of the confluence with Soda Butte Creek on the east to a small canyon called Lamar Canyon on the west (Fig. 1). All study sites were west of the Soda Butte Creek confluence. Willow study sites were in wet meadows on the river floodplain, with an additional site along Oxbow Creek about 20 km west and north of Lamar Valley, near where the creek crosses Grand Loop Road (Figs. 1 and 3).

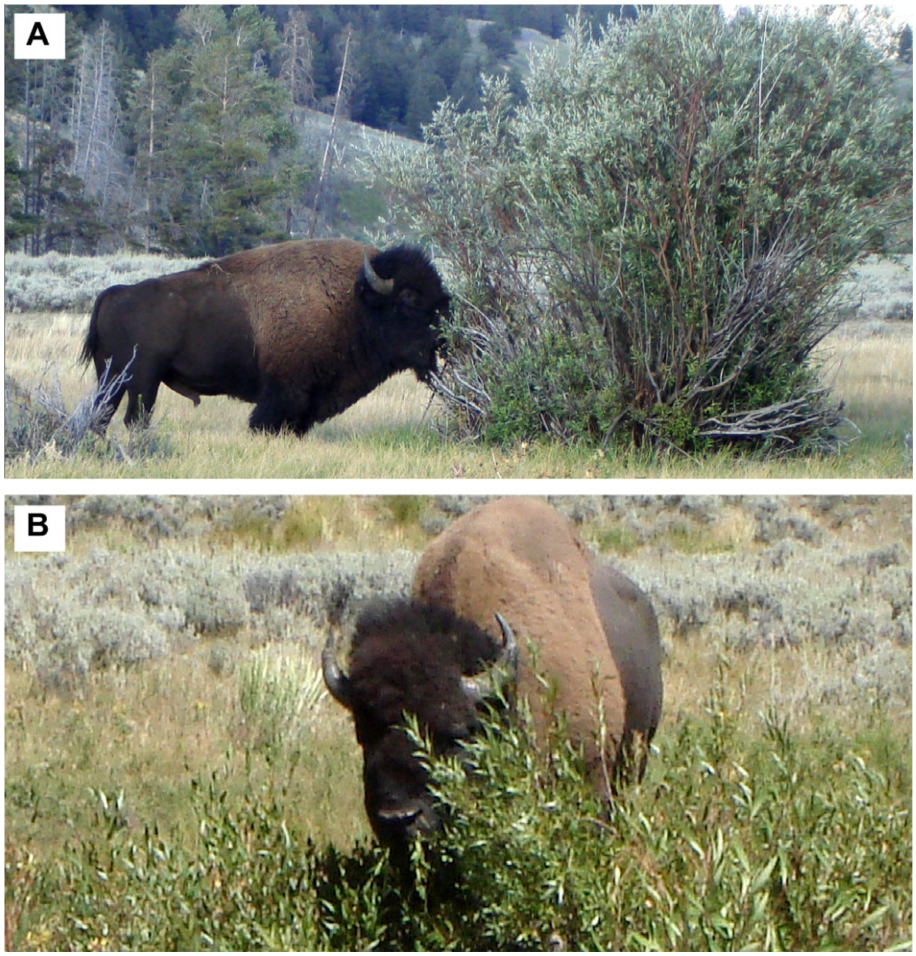

Fig. 2. Summertime browsing by bison of (A) a willow clump in the Lamar Valley; (B) young cottonwood plants on the bank of the Lamar River. Photos from August 2010.

Cottonwood study sites were within the active channel of the Lamar River, where thousands of cottonwood seedlings grow on gravel bars in the wide, shallow, meandering river bed, flanked by meadows of grasses and sedges on the sides of the river (Fig. 4). All study locations were within the winter ungulate range.

2. Methods

Field data were collected between August 20 and September 9, 2010. Plant measurements were similar for willow and cottonwood, but sampling methods were different. Browsing intensity was measured by the percentage of browsed leaders (browsing rate) in the current summer and previous year, the mean length of leader growth since last browsing (growth-since-browsing), and for cottonwood saplings, the mean spring height. We also noted damage from horning (bison thrashing bushes with their horns), and the height of browse-killed stems, defined as a dead stem with at least three terminal twigs at least one of which was pruned by browsing (Keigley, 1997). Season of browsing and growth-since-browsing were determined by examining plant growth architecture, following Keigley and Frisina (1998) and Keigley et al. (2002). Season of browsing was determined by counting the terminal bud scars on the stem. Growth-since-browsing (Keigley's Live–Dead index) was calculated as the difference between the spring height of a stem (the base of current annual growth) and the most recent browse height of the stem, as indicated by the browsed stub (spring height – browse height = growth-since-browsing). Growth-since-browsing compares the current (spring 2010) height of the plant to the height at which it was previously clipped by browsing. This indicator of growth suppression is independent of the height or age of the plant. A strong positive number indicates plants that are growing larger and not suppressed, whereas a negative or small positive number indicates plants suppressed by browsing, because the new growth is lower than or similar to the previous browse height. This occurs when a stem starts a new leader below a leader that was killed by browsing.

2.1. Willow methods

There were few tall willows in the Lamar Valley, so it was possible to locate all willows taller than 2 m on the Lamar Valley floor (between Lamar Canyon and the confluence with Soda Butte Creek, to the toe of the slope around the valley), and collect data on growth and browsing for all that met the sampling criteria. Height was measured as the spring height, at the base of current annual growth. Willow sites, both in Lamar Valley and Oxbow Creek, were in flat, wet meadows watered by groundwater. Willows within 20 m of a road, in the active channel of the river, or in areas inundated by recent spring river floods were not included, because these factors could affect accessibility and browsing, and flood damage could obscure browsing effects. Most tall willows had a large canopy, but some had few live stems, or were severely damaged by horning, and these were not included. For comparison to the Lamar Valley, we also measured willows on Oxbow Creek, where summer bison use appeared to be very slight (confirmed by scat counts, see Section 3). All willows shorter than 1 m within

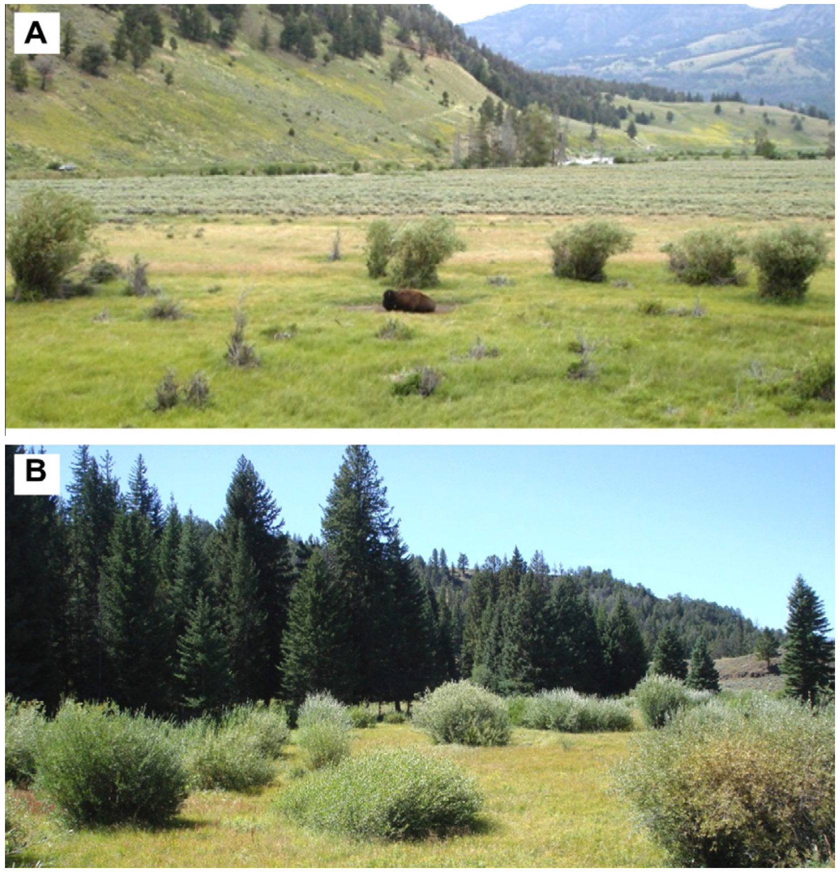

Fig. 3. Tall willow sites on the Yellowstone northern ungulate range. (A) In the Lamar Valley a bison rests in a wallow among tall willows. Willow growth is constricted by browsing below about 1 m, but expanding above that height, resulting in a mushroom shape. Most willows are short, with many dead branches (as in foreground). Tallest willows in the photo are approximately 5 m in height. (B) On Oxbow Creek, willow growth at low height is not suppressed and willows have a full, hemispherical shape. Most are tall, few are short. Tallest willows in the photo are approximately 4 m in height. Photos from August 2010.

the tall willow sites were also measured, using the same methods detailed above for tall willows. Willow bushes in a clump were sampled as a unit if their canopies merged. In the sampled locations willows did not form continuous thickets.

To help distinguish the influences of bison and elk, each tall willow bush or clump was divided into two browsing height zones, a lower zone below 1 m accessible to all ungulates, and an upper zone from 1.5 to 2 m easily accessible to elk but not bison. A pilot study showed that almost all bison browsing occurs below 1 m (authors' unpublished data). Stems between 1 and 1.5 m are unlikely to be browsed by bison, but could have a small amount of bison browsing; therefore, measures in this middle height zone would be ambiguous as indicators of browsing by bison, and were not used.

In each height zone we measured four leaders, for a total of eight leaders per bush. Sampled leaders were representative of those most accessible to browsing ungulates, and leaders that were inaccessible to browsers due to dead stems or other obstructions were not included. For those few stems that had never been browsed, the height at which the stem grew beyond browsing obstructions was substituted for the most recent browse height. We sampled an additional 12 leaders in each height zone to estimate the browsing rate for the current summer (2010) and for the previous year (summer 2009 to spring 2010), so browsing rates were based on 16 leaders in each height zone. For each bush we also measured the height of three of the oldest browse-killed stems (Keigley, 1997). Variables were averaged for each bush or clump for each height zone, with 95% confidence intervals (t distribution), and compared between the two height zones. Because this comparison was between upper and lower heights on the same plants, topographic site variables were ruled out as confounding factors. Browse rates and growth-since-browsing were also compared between willow sites at Lamar and those at Oxbow Creek; these sites were all within the winter range of elk and bison, and were similar in slope, elevation, and water availability.

2.2. Cottonwood methods

Young cottonwood seedlings and saplings occurred in dense "stands" in discrete sites on alluvial bars along the Lamar River. These sites were relatively homogeneous in age and density, with hundreds of seedlings distributed in a long band on a gravel bar (Fig. 4). Many plants were short (<1 m) and hedged, with a bush growth form. We sampled all stands that were longer than 50 m and with most plants older than 3 years, based on the growth visible above the ground. Each stand was a separate study site and sampling unit. For each site, data collected included length, width, distance from river bank, and height above water.

A line transect was placed through the centroid along the long axis of each site, and every 5 m the plant nearest to the line was measured. For the shortest site, 75 m in length, the sampling interval was shortened to 2.5 m. If the nearest plant was covered with debris above the base of current annual growth, or had less than 3 years of growth visible, or appeared diseased or dying, the next closest plant was chosen. In addition, the tallest cottonwood bush in each 50 m segment (25 m in the smallest site) was measured, as an indication of the leading edge of growth. For each plant we measured the leader with the tallest spring-time height. The field data were used to calculate browsing rate, mean height, mean height of

Fig. 4. Cottonwood saplings at two sites in the Lamar Valley. (A) Cottonwood Site 4, typical of sites in the Lamar Valley, with hundreds of saplings hedged and stunted by browsing. (B) Cottonwood Site 6, the exception in Lamar Valley with lower browse rates and taller saplings. Inconvenient location away from foraging areas, shading by the adjacent slope in winter, and flooding in spring are possible factors reducing browsing in this site. All browsing in 2009–2010 was at heights below 1 m. Photos from September 2010.

browse-killed stems, and mean growth-since-browsing for each of the seven sites. These quantities were compared using 95% confidence intervals (t distribution) to ascertain significant differences among sites, and between height and browse-killed stem height within the same site. The relationship between mean plant height and height above water was analyzed using simple linear regression, to assess the possible influence of water availability. In Site 6, where cottonwood saplings were taller with a single-stem growth form (Fig. 4B), the browse status and height for previous years were also recorded.

2.3. Indications of ungulate use

The amount of use the study sites received by bison, elk or other ungulates was evaluated based on counts of fecal piles, along with other evidence such as the presence of tracks, wallows and hair, and sightings of the animals. Fecal piles were counted in plots (belt transects) 2 m wide, extending for the length of the wet meadow or cottonwood site. For willows, plots were spaced 10 m apart to the edge of the wet meadow containing the willows. For cottonwood, there were two plots in the site and two on the adjacent bank, separated by 4 m. Fecal piles were categorized as from the current summer or a previous season, as determined by color, state of decomposition, and relationship to growing vegetation.

3. Results

3.1. Willow

Of 53 tall willow clumps found in wet meadows on the floor of the Lamar Valley, 18 were rejected because of extensive horning damage (almost all had some horning damage), and three were rejected because their few leaders were protected from browsing by dead branches. Some tall willows growing along the river bank near the east end of the valley were excluded by the decision to limit sampling to wet meadows. The sampled willows included 20 tall willow bushes or clumps in the largest wet meadow and 12 from five additional locations, for a total of 32 in the Lamar Valley (Fig. 3A). The largest clump was 8.6 by 4.3 m, the smallest 1.7 by 0.5 m (the widest extent of live branches). The Oxbow Creek site contained 14 tall willow clumps that met the sampling criteria (Fig. 3B). Unlike Lamar, none were rejected due to horning damage and all had full canopies with many leaders. Height ranged from 2.2 to 5.2 m in Lamar (mean 3.5, standard error 0.1), and from 2.3 to 4.2 m in Oxbow (mean 3.1, standard error 0.1). All tall willows and most short willows sampled were Geyer willow (*Salix geyeriana*); some short willows were Booth (*Salix boothii*) or Bebb (*Salix bebbiana*) willow species.

Measures of browsing intensity at low height in Lamar Valley were significantly different (t test, 95% confidence) from the upper height in Lamar, and also different from either height in Oxbow. These differences were very pronounced (Fig. 5). Differences in browsing intensity between upper and lower heights in Oxbow were small, but still statistically significant for growth and previous year browse rate.

In the Lamar Valley willow sites, short willows far outnumbered tall willows (196 short/32 tall), but in Oxbow there was a much smaller proportion of short willows (26 short/14 tall). For short willows, the summer browsing rate was 88% in Lamar and 0% in Oxbow. Previous year browsing was 100% and 72%, respectively; growth-since-browsing was −3 and 7 cm.

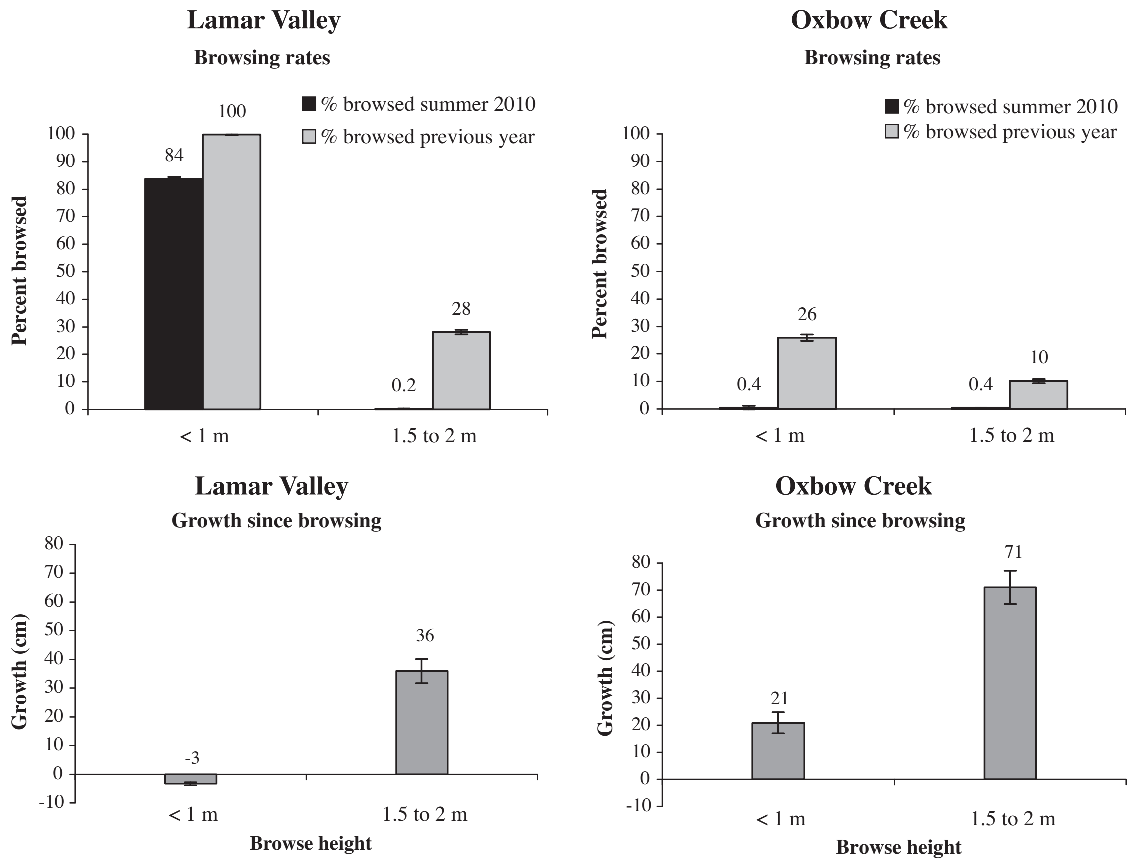

Fig. 5. Willow browsing rate and growth-since-browsing (spring height – browse height = growth-since-browsing). Summarized data show browsing rate is very high in Lamar below 1 m, but low otherwise, and this difference is reflected in growth (bars show standard error). Summer browsing is near 0% except in Lamar Valley at low height.

3.2. Cottonwood

There were seven cottonwood sites that met the sampling criteria (at least 50 m long with most saplings older than 3 years) along the Lamar River from near the confluence with Soda Butte Creek to the beginning of Lamar Canyon (Table 1). These seedling patches ranged in length from 75 to 250 m, and in width from 11 to 52 m. All were in the active channel of the river, and drift accumulations indicated that four of the seven sites were flooded in the spring of 2010. Most plants were in the form of small bushes (Fig. 4A), an indication of intensive browsing (Keigley, 1997), and the mean summer browsing rate was 54%. Plants were generally shorter than 1 m except in Site 6 (Fig. 4B), but even there the mean spring height was shorter than 1 m (Table 1, Fig. 6). Growth-since-browsing was strongly and inversely correlated with summer browsing rate, with both variables log transformed in a linear regression ($r^2 = 0.92$, $p < 0.001$, $n = 7$); height was also strongly correlated with summer browsing ($r^2 = 0.69$, $p < 0.02$, $n = 7$). Most of the top leaders were browsed in the summer of 2010 preventing direct measurement of current annual growth and productivity, but all of the sites were in a similar landscape position in the active river channel, and there was no significant relationship between mean spring height and height of the plants above water (Table 1; linear regression, $r^2 = 0.03$, $p = 0.70$). Mean spring height was not significantly different (t test, 95% confidence) from the mean height of browse-killed stems, except in Sites 1 and 6 where the summer browse rate was low, and this difference was much greater in Site 6, with the lowest summer browse rate. Of the selected saplings in cottonwood Site 6, 19% were too damaged by horning to be measured for browsing, so the next closest sapling was used.

Table 1
Mean data values for seven cottonwood sites in the Lamar Valley.

Site	Browse rate (%) summer	Spring height (cm)	Browse-killed height (cm)	Growth since browse (cm)	Three tallest height (cm)	Height above water (cm)	Count
1	23	46	39	6.2	60	138	44
2	68	41	37	−1.4	78	109	44
3	92	26	23	−0.7	40	77	36
4	56	27	27	−0.9	37	73	55
5	27	56	51	6.2	121	75	30
6	13	94	49	35.4	199	74	32
7	100	40	43	−1.7	68	129	30
Grand mean	54	47	38	6	86	96	39

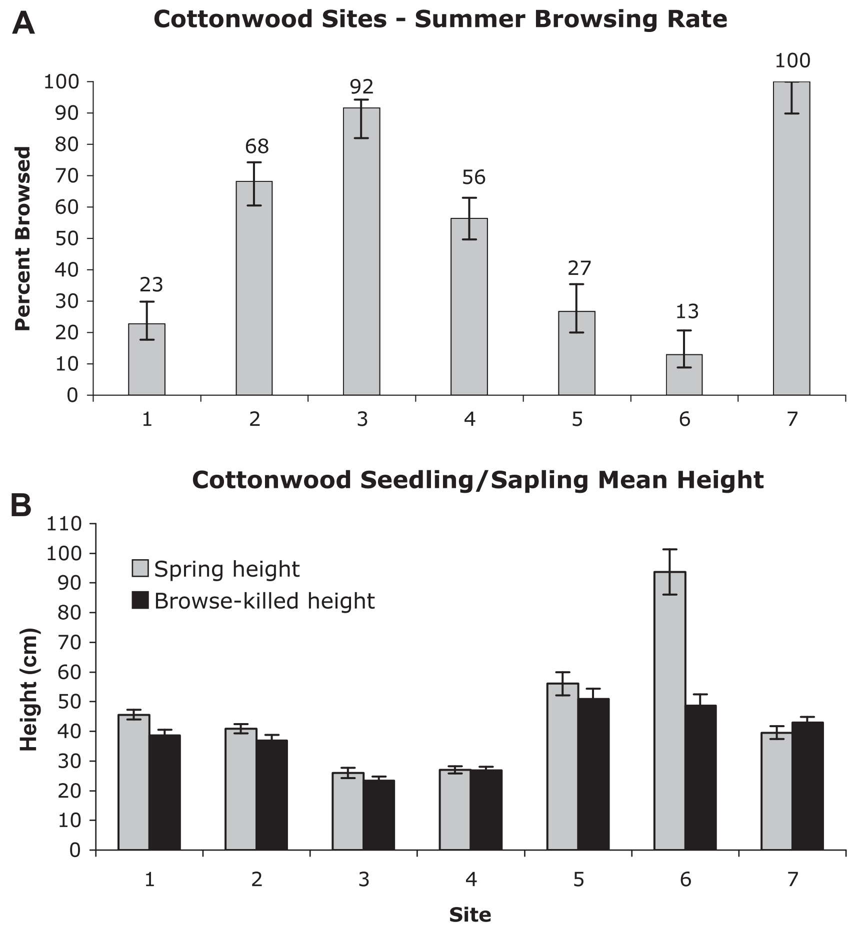

Fig. 6. Seven cottonwood sites in the Lamar Valley in summer 2010 (bars show standard error). (A) Four of seven sites had summer browsing rates >50%, with two greater than 90%. (B) Mean height was strongly suppressed except in Site 6, where summer browse rate was very low. Mean height was similar to the height of browse-killed stems except in Site 6, so plants have grown little beyond the height at which they were previously hedged by browsing except where summer browse rate was low.

3.3. Ungulate use

Bison fecal piles were abundant in sampling plots in the Lamar Valley (Table 2), along with wallows and many bison tracks, horned bushes, and clumps of bison hair; there were many bison in Lamar, sometimes browsing willows or cottonwoods (Fig. 2). In contrast, no elk pellet piles or tracks from the 2010 summer season were found in either the Lamar Valley or the Oxbow Creek study sites. All bison fecal piles counted in sample plots were found in Lamar, none in Oxbow. The difference in total number of scat piles counted for bison compared to other ungulates was very large in Lamar Valley (Table 2). In both Lamar and Oxbow some elk and bison scat piles from previous seasons were present in the area.

4. Discussion

Willows and cottonwoods in the Lamar Valley were browsed at a high rate, and much of this browsing occurred in the summer season, when herds of bison were present and elk were scarce. Most browsing occurred at low height, and browsing rates were much less at heights above the reach of bison (Fig. 5). The season, height, and rate of browsing demonstrate that browsing by bison in summer was common, and that bison were responsible for a large proportion of annual browsing of terminal leaders, enough to suggest a significant ecological effect. For both cottonwood and willow, high summer browsing rates were associated with severely restricted growth (Figs. 5 and 6). For tall willows in the Lamar Valley, mean growth-since-browsing was negative (−3 cm) at heights below 1 m, showing that stems have not grown back to the heights at which they were previously browsed, a characteristic of bushes that are severely hedged by browsing (Keigley and Frisina, 1998; Keigley et al., 2002). On the same bushes, growth-since-browsing was strongly positive (36 cm) at heights from 1.5 to 2 m, demonstrating that these same willows have been increasing in size at heights accessible to elk but not bison. Similarly for willows shorter than 1 m in the Lamar Valley sites, growth-since-browsing was −3 cm, indicating suppressed growth.

If elk were primarily responsible for browsing willows in the Lamar Valley, then the browsing rate would likely be similar in the lower part of a bush and the upper part, because elk can reach the entire height range. Also, the browsing rate should be very low in summer, because the study locations are in elk winter range, with few elk in summer. The summer browsing rate in Lamar was nearly zero in the upper height zone, but very high, 84%, at low height below 1 m (Fig. 5). The high summer browse rate is strong evidence that bison are eating most of the accessible leaders before the end of the summer. Browsing below 1 m was also very intensive

Table 2
Lamar Valley ungulate scat counts, for plots covering 12,620 m^2. In Oxbow, no scat piles were found in sample plots, but elk and bison scat from previous seasons were present near the site.

Species	Total fecal piles	Summer 2010	Older	Density (100 m^{-2})
Bison	1302	1079	223	10.3
Elk	1	0	1	0.0
Pronghorn	23	23	0	0.2

in the previous year (summer 2009 to spring 2010), with 100% of sampled leaders browsed, as compared to 28% above 1.5 m. Short willows had similar browsing rates, 88% in the summer. The severely hedged condition of willows in the low height range (Fig. 3A), and the negative growth-since-browsing (Fig. 5), indicate that the high browsing rate measured in the summer of 2010 may represent the typical browsing intensity for recent years.

For cottonwood, measurements were compared across the seven cottonwood sites (Fig. 6). Four sites had summer browsing rates greater than 50%, and two were greater than 90%, with an average of 54%. Growth was suppressed in six of the seven sites as indicated by short average height (<1 m), hedged growth form, and low growth-since-browsing. Only Site 6, with summer browsing rate of 13%, had saplings close to 2 m in height (Table 1 and Fig. 4). This site was farther out in the river channel than the other sites, and was shaded in winter by a tall adjacent slope, factors that may have reduced browsing and allowed cottonwood saplings to grow taller once pressure from elk was reduced.

There was no evidence of elk in the Lamar Valley in summer, either from pellet counts, field sightings, or other evidence, and the area is not considered part of elk summer range. Elk pellets from any season were rare; only 1 elk pellet pile was found in 12,620 m^2 of scat sampling plots (Table 2). Although detectability was poor in many of these plots, the low elk pellet density is consistent with a major reduction in elk use of the eastern portion of the northern range over the last decade, as reported by White et al. (2010, in press). It was probably during this period of declining elk density that the tall willows in the Lamar Valley grew beyond the reach of elk to their present height; tall willows were not reported in the area previously (Kay, 1990; Chadde and Kay, 1996; Ripple and Beschta, 2006; Beyer et al., 2007). This increased height of willows is evidence of a trophic cascade from wolves to plants; if the increase in bison density is a response to reduced elk density, then the bison increase and their resulting effect on plants would represent an additional pathway associated with this trophic cascade (Ripple et al., 2010).

No evidence of moose or deer was found in the Lamar Valley study sites. At Oxbow Creek, deer trails and bedding areas were present among willows, yet summer browsing was minimal, 0.5%. Given the clear evidence of deer in Oxbow Creek with little summer browsing, and the lack of any evidence of deer in the Lamar Valley where browsing rates were very high, it is reasonable to conclude that deer were not responsible for the summer browsing of willow and cottonwood observed in the Lamar Valley. Pronghorn were present in the Lamar Valley in summer, in much smaller numbers than bison (Table 2). Studies of the diet and habitat selection of pronghorn on the northern range and elsewhere have found little evidence of willow or cottonwood consumption (Singer and Norland, 1994; Barmore, 2003; Jacques et al., 2006; Boccadori et al., 2008). Low numbers and dietary preferences make it unlikely that pronghorn are having a significant effect on growth or browsing rates of browse plants.

Where plants are intensively browsed in summer, as in Lamar Valley, tall willows are constricted below the height at which they are accessible, creating a clump with a mushroom shape. The lower stems are continually clipped but the upper stems continue to lengthen (Figs. 2 and 3A). This shape, called "highlining", is seen in many of the tall willows in the Lamar Valley, but where bison are less numerous, as at Oxbow Creek (Fig. 3B), willows become full with new growth in summer and have a roughly hemispherical shape. In the Lamar Valley, the low height of this growth suppression suggests that bison, not elk, are now the primary browsers.

All tall willows had browse-killed stems with browse brooms (clusters of browse-killed twigs), an indication of past suppression of growth. In the Lamar Valley the mean height of these stems was 147 cm (SE = 3.6), and in Oxbow 108 cm (SE = 8.3). The fact that these plants are now growing well beyond this previous growth limit is further evidence that they have experienced a release from elk browsing (Keigley and Frisina, 1998). They were previously suppressed by elk, but now are growing freely at those heights.

In six of the seven cottonwood sites, the spring height was very close to the height of browse-killed dead stems (Fig. 6). This strongly suggests cottonwood saplings at these sites are stunted by browsing, limited to about the same height as the old leaders killed by browsing. The exception is cottonwood Site 6, where live leaders were much taller than browse-killed stems, indicating that something has changed about the browsing and growth dynamics at this site (Fig. 4B). In the previous year (summer 2009 to spring 2010) in Site 6, stems shorter than 1 m were browsed at a rate of 45%, while those taller than 1 m, above the reach of bison, were not browsed at all, suggesting that recent browsing has been due to bison and not elk.

The results of this study make possible an evaluation of alternative explanations for the fact that willow and cottonwood growth in the Lamar Valley has been generally less than in some adjacent areas of the northern range, such as the upper Lamar River and Soda Butte Creek (Ripple and Beschta, 2003; Beschta and Ripple, 2010). One hypothesis could be that there has been no trophic cascade sufficient to release plants from elk browsing. The pronounced changes in height and cover of willow and cottonwood in areas peripheral to the Lamar Valley in conjunction with the recent decline in elk density make this "no-effect" explanation unlikely. An alternative hypothesis is that wolves have caused a release of vegetation by reducing elk browsing, but bison are having an increased effect on plants, counteracting the reduced effects of elk – a secondary trophic cascade (Ripple et al., 2010). The evidence from this research supports this second explanation, for three reasons: (1) plants grew larger and taller where they were beyond the reach of bison, demonstrating release from the effects of elk; (2) browsing rates were very high in summer, when elk were absent, therefore, elk could not have been responsible for most of the browsing of new leaders, because bison consumed them first; and (3) plant growth was suppressed by browsing where the summer browse rate was high, showing that browsing by bison has been affecting plant growth. This growth suppression, and the fact that browsing rates for the previous year were high, are evidence that the summer browsing rates observed in 2010 are indicative of a multi-year pattern. The comparison between the lower portion and the upper portion of the same willows shows that differences in site moisture or productivity were not significant factors, as does the similarity in landscape position of cottonwood sites.

The bison of Yellowstone today differ from their pre-settlement ancestors in two important ways. First, bison are prevented from moving freely or expanding their range outside the park (White et al., 2011). Second, bison in Yellowstone experience very low predation pressure, compared to what was likely in the past with hunting pressure from humans, and larger numbers of wolves focused on bison (Young and Goldman, 1944; Carbyn, 2003; Kay, 2007). Even if predation was compensatory in ancient times and bison numbers were high, it is likely that predation pressure would have caused bison herds to move, perhaps long distances, as occurs with Canadian bison and wolves (Carbyn, 1997). These differences – freedom to move and greater predation pressure from humans and wolves – make it unlikely that bison would have concentrated in the Lamar Valley in the past as they do today, even if they were present in the region in similar numbers.

The consequences of preventing bison movement may extend beyond the bison population to the ecology of the range, in summer as well as winter. The potential effects of bison and other large ungulates include suppression of woody plants and changes in plant communities (Meagher, 1973; Coppedge and Shaw, 1997; Baker, 2003; Gates et al., 2010; Martin et al., 2011). Bison have the potential to limit recovery of willow and cottonwood in the Lamar Valley, and possibly elsewhere in the Yellowstone area. Lack of willow and cottonwood could slow or prevent colonization by beaver and other species, with cascading effects on plant communities, stream morphology, and biodiversity (Kay, 1994; Smith and Tyers, 2008; Baril, 2009; Beschta and Ripple, 2010, 2011). Bison, cottonwood, willow and beaver evolved together, but the effects of bison may be more pronounced in Yellowstone today, where bison occur at higher densities and with less movement than was likely when they and the people and other predators that hunted them roamed freely across the landscape.

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