Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 184 (2003) 299–313

Forest Ecology and Management

www.elsevier.com/locate/foreco

# Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park

William J. Ripple[a,*], Robert L. Beschta[b]

[a]Environmental Remote Sensing Applications Laboratory (ERSAL), Department of Forest Resources,
Oregon State University, Corvallis, OR 97331, USA
[b]Department of Forest Engineering, Oregon State University, Corvallis, OR 97331, USA

Received 16 January 2003; received in revised form 12 March 2003; accepted 1 April 2003

## Abstract

We studied young riparian cottonwoods (*Populus* spp.) and associated woody plants along Soda Butte Creek and the Lamar River in northeastern Yellowstone National Park (YNP) to examine the potential influence of wolf/elk interactions upon plant growth. After a period of approximately 70 years without wolves in YNP, they were reintroduced in the winter of 1995–1996. When we compared woody plant heights shown in photographs taken prior to 1998 with those shown in 2001–2002 photos, we found an increase in the height of riparian woody plants for six of the eight sites within the study area. Plants were tallest (1–4 m) at point bar, stream confluence, and island sites, while heights remained relatively low (<1 m) along straight river reaches in a wide valley setting. We measured differences in both browsing intensity and cottonwood height for sites with relatively high predation risk (low visibility and/or the presence of escape barriers) and compared them to nearby sites with relatively low predation risk (open areas). In general, the high-risk sites had lower browsing intensities (percent of stems browsed) and taller plants than low-risk sites. Although the young cottonwoods on high-risk sites were growing taller each year over the last 4 years, there was little change in the plant heights for low-risk sites. For a stand of young cottonwoods growing adjacent to a gully (potential escape barrier), we found a linear correlation ($r^2 = 0.76$) between cottonwood height and adjacent gully depth; as gully depth increased, the percent of stems browsed decreased and cottonwood height increased. While the release of cottonwood and willows within the study area is in a very early stage, results provide rare empirical evidence illustrating the indirect effects of a top carnivore in a terrestrial food chain and supports theories on: (1) predation risk effects and (2) trophic cascades (top-down control). Wolf reintroductions into the Yellowstone environment may thus represent a management action that was needed to help insure the restoration of riparian species and preservation of biodiversity.

*Keywords:* Predation risk; Wolves; Elk; Cottonwoods; Trophic cascades; Yellowstone

## 1. Introduction

Deciduous woody species, such as aspen (*Populus tremuloides*) in terrestrial systems, and cottonwoods (*Populus* spp.) and willows (*Salix* spp.) in riparian systems, have been unable to successfully regenerate over extended periods of time in various forest and range landscapes of the western United States (Romme et al., 1995; Baker et al., 1996; Braatne et al., 1996; Kay, 1997; Yellowstone National Park, 1997; Brookshire et al., 2002; Zeigenfuss et al., 2002; Larsen and Ripple, 2003). Potential causes for this

---

[*] Corresponding author. Tel.: +1-541-737-3056;
fax: +1-541-737-3049.
*E-mail address:* bill.ripple@orst.edu (W.J. Ripple).

0378-1127/$ – see front matter © 2003 Elsevier Science B.V. All rights reserved.
doi:10.1016/S0378-1127(03)00154-3

lack of recruitment and plant community sustainability include weather patterns and climate, long-term fire suppression, overgrazing by domestic or wild ungulates, natural plant community dynamics, or some combination of these factors. Preliminary research in the greater Yellowstone ecosystem indicates that the extirpation of wolves (*Canis lupus*) may be linked to the long-term demise of certain deciduous woody species (Ripple and Larsen, 2000; Berger et al., 2001; Beschta, in press).

Wolves cause mortality and can influence the distribution and behavior of herbivores. Thus, when a top trophic level predator interacts with the next lower level herbivore and this interaction in turn alters or influences vegetation, a ‘‘trophic cascade’’ occurs. Trophic cascade effects involving wolves and elk (*Cervus elaphus*) were identified as a potentially important factor affecting aspen growth in Jasper National Park, Canada (White et al., 1998) and woody browse species in Yellowstone National Park (YNP) (Laundré et al., 2001). The National Research Council (2002) further highlighted trophic cascades as an important topic in a recent evaluation of ungulate issues in Yellowstone's northern range and indicated research was needed to evaluate the role of wolves in the trophic dynamics of the northern Yellowstone ecosystem.

Research on trophic cascades involves studying the effects of predators across successively lower trophic levels. Recent review articles suggest that observations of trophic cascades have largely occurred in aquatic systems, whereas the role of trophic cascades in terrestrial systems has often remained ambiguous (Pace et al., 1999; Estes et al., 2001). However, evidence is growing on how the removal of top predators from terrestrial ecosystems leads to profound disruptions in vegetative communities (Terborgh et al., 1999). If one accepts a three-level trophic cascade, involving wolves and elk at the upper two levels, as a working model for northern Yellowstone, then predator–prey interactions could potentially influence vegetation growth and spatial distributions at the lowermost level.

Two theories of predator–prey interrelationships have been reported (Schmitz et al., 1997). The first, and most common, involves a predator's influence on the size of a prey population via direct mortality. This, in turn, may influence total foraging pressure on individual plants, specific plant species, or plant communities. For example, Mclaren and Peterson (1994) found depressed growth rates of balsam fir (*Abies balsamea*) when wolves were rare and moose (*Alces alces*) densities were high. In the case of northern Yellowstone, if significant reductions in elk numbers occurred because of wolves, this situation might provide more favorable conditions for the regeneration of woody browse species (e.g., cottonwood, willows, berry-producing shrubs, aspen). The second theory emphasizes indirect effects that carnivores may have upon prey species, such as changes in behavior caused by predators frightening prey animals away from specific foraging areas (Brown et al., 1999). In this later situation, the reintroduction of long absent apex predators (e.g., wolves) might have widespread behavioral effects upon prey species (e.g., elk) by altering their habitat preferences and foraging patterns (Laundré et al., 2001). Plant establishment and growth responses would thus reflect any such shifts in foraging behavior. Interestingly, Schmitz et al. (1997) indicate that behavioral effects of predators upon prey species may be more important to patterns of herbivory than direct mortality effects.

Foraging theory suggests that wild herbivores must balance demands for both food and safety (Lima and Dill, 1990). For example, when foraging under conditions of high predation risk, herbivores would be relatively vigilant, move to safer habitats, or both. In contrast, when foraging under conditions of low predation risk, herbivores would be more likely to heavily browse/graze palatable species thus reducing height growth or regeneration success. However, since wolves have been largely absent from most of United States for many decades, little information exists on how adaptive shifts in prey behavior—a trophic cascade—might be reflected in plant community composition and structure.

The history of wolf control, eradication, and reintroduction in YNP provides an important context for evaluating predator–prey relationships and their effects on woody browse species. After an intense period of wolf control in the late 1800s and early 1900s, wolves were finally eliminated from YNP in the mid-1920s (Weaver, 1978). Thus, wolves have been largely absent from the Park for much of the last century. Following the reintroduction of 31 wolves into YNP in the mid-1990s, their numbers have steadily increased so that by the end of 2001 at least 220 wolves lived in 21 packs in the greater Yellowstone ecosystem (Smith and Guernsey, 2002).

During the last half of 20th century, and perhaps longer, there has been a dramatic decline in the abundance and distribution of aspen, cottonwood, and willows for the winter range of wild ungulates in northeastern YNP. The decline of woody browse species apparently started following wolf extirpation in the 1920s and has been attributed to heavy browsing pressure, primarily by elk (Jonas, 1955; Chadde and Kay, 1996; Yellowstone National Park, 1997; Ripple and Larsen, 2000; National Research Council, 2002). Before wolf reintroductions in the winter of 1995–1996, nearly all deciduous woody species available to elk in the winter range were heavily browsed, resulting in a pattern of suppressed species of low stature (Houston, 1982; Keigley, 1997; Meagher and Houston, 1998; Singer et al., 1998). Concurrent with the decline of woody browse species during the first half of the 20th century was a drastic decline in the northern range beaver (*Castor canadensis*) population (Jonas, 1955).

In their review article, Lima and Dill (1990) describe how previous studies suggest that animals have an ability to assess their risk of being preyed upon and to incorporate such information into a decision making process. Two major subcomponents of predation risk are: (1) the likelihood of a prey animal detecting predators and (2) the availability of escape routes. Thus, potential changes in prey behavior related to the detection and escape from predators include spatial changes in habitat use and choices of feeding sites (Lima and Dill, 1990). For example, since wolf reintroduction into YNP, female elk have, over time, increased their vigilance levels during foraging in response to the expanding presence of wolves (Laundré et al., 2001). In a similar vein, elk may be adjusting foraging locations due to the presence of the reintroduced keystone predator (Ripple et al., 2001).

This investigation focused on the potential cascading effects of wolf reintroduction upon previously suppressed riparian plant communities. Although these plant communities are comprised of various woody species utilized by elk, we focused primarily on young cottonwoods since seedlings of both narrowleaf (*P. angustifolia*) and black (*P. trichocarpa*) are abundant along valley streams in the northern range. However, ungulate browsing has effectively prevented these rapidly growing species from attaining tall sapling and tree forms over a period of many decades (Beschta, in press). Furthermore, our capability to utilize "plant architecture" assessment techniques on cottonwood for deciphering past browsing history and height growth, the importance of this species to the composition and structure of riparian plant communities, and its role as a general indicator of browsing pressure on other woody riparian species were important considerations in the selection of young cottonwood for more detailed investigation. The principal objectives of this study were to:

(1) Collect base-line data on young small-stature cottonwoods and determine if they have begun to release (i.e., increase in total height) following wolf reintroductions.
(2) If young small-stature cottonwoods are increasing in height, assess whether increased height growth is associated with predation risk.

An underlying hypothesis of this study is that the growth of young cottonwoods would be greatest in areas where the predation risk of wolves on elk was relatively high (sites with a low likelihood of elk detecting wolves and with limited escape routes for elk). The relatively recent return of wolves into northern YNP provided a rare opportunity to study responses in the terrestrial food chain to a restored keystone predator.

## 2. Study area

The study area is located in valley-bottom terrain in the northeastern portion of YNP, the wintering ground for Park's largest elk herd. Data collection occurred along a portion of lower Soda Butte Creek and a segment of the Lamar River downstream of the Soda Butte Creek confluence (Fig. 1). Valley-bottom vegetation in this part of the Park consists of sagebrush steppe, primarily big sagebrush (*Artemisia tridentata*), and grassland interspersed with small stands of trees, primarily Douglas-fir (*Pseudotsuga menziesii*) and aspen (Despain, 1990). Herbaceous plants include sedges (*Carex* sp.) along stream channels and floodplain meadows dominated by grass. Interspersed along

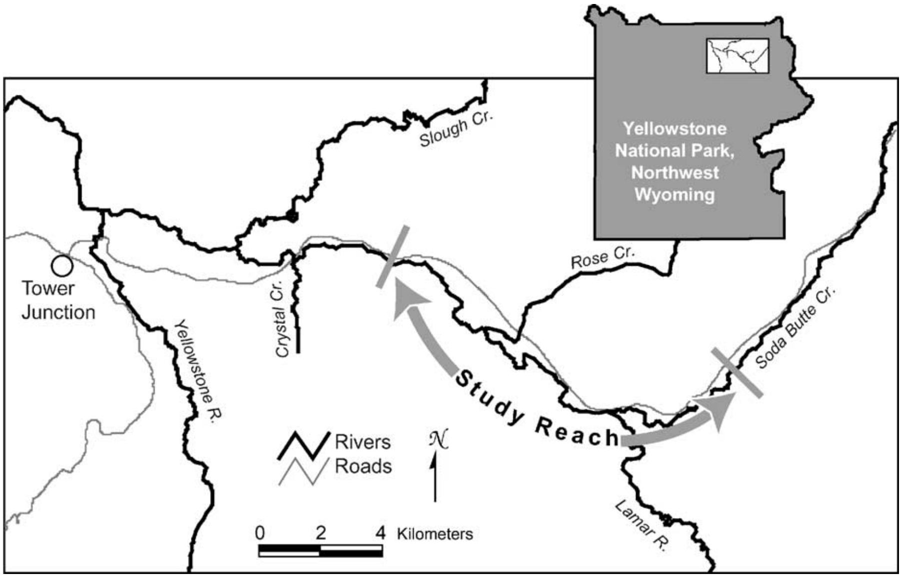

Fig. 1. Location map of study reach along Soda Butte Creek and the Lamar River, in northeastern YNP.

floodplains and along the channels are scattered groves of mature cottonwood trees; cottonwood seedlings and willows are common.

## 3. Methods

Color photographs of riparian areas taken before 1998 were rephotographed in 2001 or 2002. We categorized the height of the woody vegetation into one of the three general height classes: <1, 1–2, and 2–4 m for both sets of photos using field measurements or photo measurements and observations.

In 2002, we conducted a field search of young cottonwoods 2–4 m in height (all were <5 cm diameter at breast height). Even though nearly 450 cottonwoods greater than 20 cm in diameter occur along the study reach, cottonwoods 5–20 cm diameter were entirely absent (R.L. Beschta, unpublished data). Our search started along Soda Butte Creek, approximately 5 km above its confluence with the Lamar River, and extended approximately 8 km down the Lamar River enters a canyon reach. We placed a 2 m × 30 m belt transect in each stand where young cottonwoods 2–4 m tall occurred. The young cottonwood stands were long and narrow and typically slightly larger than 2 m × 30 m. Whenever a stand was longer or wider than the 2 m × 30 m transect, we placed the transect in the part of the stand with the highest cottonwood stem density. Along the length of each belt transect, the height of the tallest leader was measured within each 1 m segment (30 in total). Using plant architecture methods presented by Keigley (1997), Keigley and Frisina (1998) and Keigley et al. (2003), the recent history of total plant height and browsing intensity were assessed. For unbrowsed plants, inspection for terminal bud scars allowed us to determine annual leader heights for up to four of the previous years. To determine elk utilization, we assessed whether each measured leader had been browsed during each of the previous years. Since ungulates typically consume segments of the stem from the current year's growth, browsing removes the terminal bud causing growth to arise from a lateral bud. If this happens each year, the stem grows in a zigzag manner leaving behind stubs representing annual segments which can be counted and measured (Keigley et al., 2003).

The level or degree of predation risk associated with a particular site was estimated from two primary terrain factors: (1) wolf detection potential (visibility or viewshed) and (2) the presence of escape barriers which could potentially slow fleeing elk. Examples of escape barriers include high cut banks, stream terraces, gullies, and to a lesser extent the stream channels themselves at confluence and point bar sites, all of which could slow fleeing elk (Bibikov, 1982; Lima and Dill, 1990; Dekker, 1997; Kunkel and Pletscher, 2001).

Field observations indicated that sites with young cottonwoods 2–4 m in height occurred at locations characterized by a high level of predation risk as indicated by limited viewshed, the presence of escape barriers, or both. Thus, for each belt transect established at a site with high predation risk (a total of two sites), an additional 2 m × 30 m belt transect was established at the nearest location, which was hydrologically similar to the initial site, but where the predation risk was assessed to be ‘‘low’’ (i.e., relatively open terrain with few escape barriers). The elevations of low and high-risk sites above the water surface of the adjacent stream were measured in early September 2002. These elevations provided an indicator of moisture availability (approximate depth to the water table) at these sites.

Finally, a third group (approximately 60 m long) of young cottonwoods 2–4 m in height was found growing along a gully bordering the Lamar River. While a suitable hydrologically matched site was not available, we nevertheless measured the height of the tallest young cottonwood plants within each 1 m segment along a 2 m × 60 m belt transect as well as the depth of the adjacent gully (to index the magnitude of the potential escape barrier). Linear regression was used to relate cottonwood height to gully depth.

Assessments were done in late summer of 2002 when riparian plants had largely attained their maximum annual growth. At the time measurements were made, the current year’s growth had not experienced any effects from winter browsing. Keigley (1997) indicates that when assessing plant responses to ungulate browsing, it is only appropriate to present data for plants that have actually had an opportunity to experience the effects of browsing. Thus, data presented in this paper are for 2001 and earlier since measurements for those years reflect the effects of both growth and browsing. Most of the browsing on cottonwood occurs during the winter season.

Selected environmental variables (maximum annual snowpack water equivalent, annual peakflow, and July streamflow) were obtained for measurement stations within the study area (i.e., streamflow) or nearby (i.e., snowpack data). These data were used to assess whether accelerated young cottonwood height growth in recent years might be related to annual patterns of moisture availability.

## 4. Results

A total of nine sets of paired color photographs dating from 1977 to 1997 were obtained for sites within our study reach; five of the photo pairs were for Soda Butte Creek and the remaining four were for the Lamar River. One of the photo pairs on Soda Butte Creek was removed from the analysis due to extensive overlap with another Soda Butte Creek photo pair. No other pre-1998 color photos were located. Historical black and white photos were not considered in this analysis. Visual inspection of the eight photo pairs indicated that woody species (e.g., cottonwood, willow) in riparian areas were suppressed (<1 m tall) in all of the pre-1998 photos (Table 1). However, when compared to photos taken in 2001 and 2002, there was an increase in plant height for six of the eight photo pairs (Table 1 and Figs. 2–4). Based on both field observations and inspection of the photos, riparian woody plants were tallest in 2001–2002 on point bar, stream confluence, and island sites, while plant height remained low for river reaches along the Lamar River, which mostly flows through a relatively wide and open valley (Table 1). Since wolf reintroduction, locations along Soda Butte Creek appear to have experienced more cottonwood and willow growth, overall, than for locations along the Lamar River. All four photo pairs for Soda Butte Creek showed increases in plant height in recent years, while only two of the four photo pairs along the Lamar River showed similar responses.

Along the 13 km study reach, we found only three stands of young cottonwoods that had attained heights of 2–4 m. These included a point bar along Soda Butte Creek, a mid-channel island of the Lamar River, and a point bar along the Lamar River (Table 1). The Soda Butte Creek point bar had a 6.5–7.5 m high terrace (detection and escape barrier) on the opposite side of the river and the mid-channel island had 2.4–3.2 m high cutbanks on both sides (escape barriers). We located comparable low-risk sites to match both the Soda Butte Creek point bar and the island site on

Table 1
General characterization of cottonwood and willow height classes in pre- and post-1998 photographs

| Stream, geomorphic setting | Primary species | Pre-1998 | | Post-1998 | |
|---|---|---|---|---|---|
| | | Photo year | Tallest height class (m) | Photo year | Tallest height class (m) |
| Soda Butte Creek, point bar | Cottonwood | 1991 | <1 | 2002 | 2–3 |
| Soda Butte Creek, straight reach | Willow | 1993 | <1 | 2002 | 1–2 |
| Soda Butte Creek, confluence 1 | Willow | 1997 | <1 | 2001 | 2–3 |
| Soda Butte Creek, confluence 2 | Willow | 1997 | <1 | 2001 | 1–2 |
| Lamar River, point bar | Cottonwood | 1977 | <1 | 2002 | 2–3 |
| Lamar River, island | Cottonwood, willow | 1977 | <1 | 2002 | 3–4 |
| Lamar River, straight reach 1 | Cottonwood, willow | 1991 | <1 | 2002 | <1 |
| Lamar River, straight reach 2 | Cottonwood, willow | 1991 | <1 | 2002 | <1 |

the Lamar River (Table 2). We found differences in both browsing intensity and cottonwood height when comparing high-risk sites with their nearby low-risk sites. In general, the high-risk sites had lower browsing intensities and taller plants than low-risk sites, especially in the most recent years of 2000 and 2001 (Fig. 5). While young cottonwoods on high-risk sites were typically growing taller each year, there was little change in plant heights for the low-risk sites. Based on site elevations relative to the water surface of the adjacent stream (Table 2), low-risk sites probably had slightly higher water tables than high-risk sites during the summertime growing season.

At the third site with cottonwoods above 2 m tall, we discovered a 0.1–1.2 m deep gully adjacent to the stand (potential escape barrier). We found a direct linear correlation between depth of the adjacent gully and cottonwood height (Fig. 6B); as the gully became deeper, the percent of stems browsed decreased (Fig. 6A) and cottonwood height increased.

Since wolf reintroductions in the winter of 1995–1996, their population numbers on the northern range have experienced a general upward trend through 2001 (Fig. 7A). During the years immediately before wolf introductions (i.e., 1990–1995), total elk numbers for the northern winter range averaged 15,500 (S.D. = ±2800), whereas total elk numbers for 1998–2001 averaged 12,700 (S.D. = ±1250), representing approximately 18% fewer elk than in the pre-wolf period (Fig. 7B). Unfortunately, elk inventory data for the years 1996 and 1997 were not available since it appears that the 18% drop in elk numbers occurred principally in those years.

Environmental factors that might influence the seasonal growth of young cottonwood, and for which there are historical records, include snowpack water equivalent (affecting the protection of small cottonwoods from winter browsing and the availability of springtime soil moisture), annual peakflow (indexing the relative the amount of inundation and soil saturation for riparian

Table 2
Estimated levels of predation risk based on variables affecting the capability of a wild ungulate to detect a predator (viewshed) and terrain features that reduce the capability of a prey animal to escape (once detected)[a]

| Site, geomorphic setting | Risk level | Viewshed[b] (%) | Cut bank/terrace height (m) | Height of site above summer baseflow (cm) |
|---|---|---|---|---|
| Soda Butte Creek, straight reach | Low | 100 | 0–0 | 60 |
| Soda Butte Creek, point bar | High | 69 | 6.5–7.5 | 73 |
| Lamar River, island 1 | Low | 100 | 0–1.0 | 70 |
| Lamar River, island 2 | High | 100 | 2.4–3.2 | 120 |

[a] The variable in the right column is an indicator of moisture availability and shows the height of the site (cm) above the adjacent stream's water surface in early September 2002.

[b] Viewshed percentage represents the percentage of a 360° field-of-view that is visible from a site to a distance of 100 m.

Fig. 2. Comparison photographs taken in 1991 (top) and 2002 (bottom) illustrating cottonwood growth on a point bar along Soda Butte Creek. In 1991, the plants were suppressed due to high levels of elk herbivory. In 2002, following wolf reintroductions that began in the winter of 1995–1996, cottonwoods have increased in height. The pole in the center of the lower photo is 2 m tall; the photo was taken from on top of a 6.5–7.5 m high terrace (a major visibility blockage and escape barrier for prey animals on the point bar).

Fig. 3. Comparison photographs taken in 1997 and 2001 near the confluence of Soda Butte Creek with the Lamar River illustrating the stature of willow plants during suppression (left photo of A and top photo of B) from long-term browsing and their release (right photo of A and bottom photo of B) following wolf reintroductions that began in the winter of 1995–1996. This appears to be a high-risk site due to significant topographic and stream barriers as well as the close proximity to a long-term den used by the Druid Peak wolf pack.

Fig. 4. Comparison photographs taken in 1994 (top) and 2002 (bottom) across the Lamar valley illustrating continued suppression of riparian vegetation by wild ungulate browsing. This continued suppression of riparian woody species following wolf reintroductions, that began in the winter of 1995–1996, appears to be due to a relatively low level of predation risk that is characteristic of this wide and open valley.

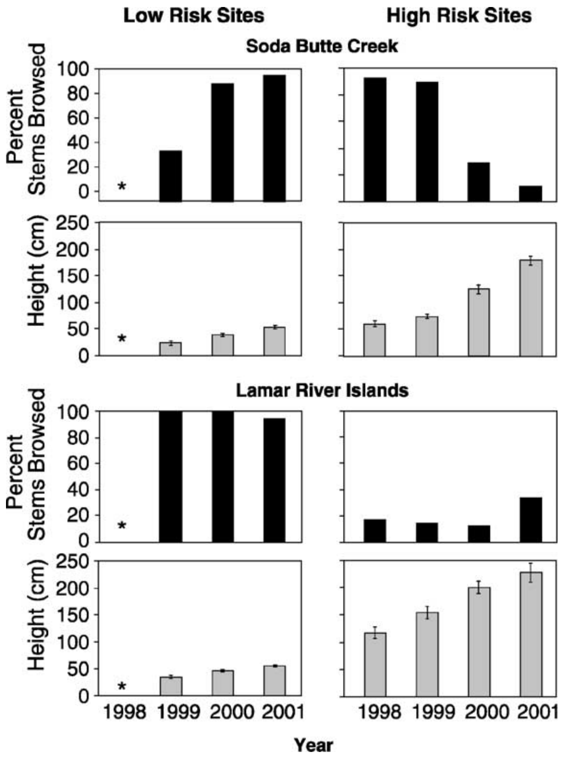

Fig. 5. Percent stems browsed (black bars) and mean plant height (gray bars) for young cottonwood plants on both low predation risk sites (left graphs) and high predation risk sites (right graphs) on two Soda Butte point bar sites and two islands in the Lamar River. High-risk sites show less elk browsing and taller cottonwoods than low-risk sites; vertical lines on the height bars represent standard errors. The maximum number of samples represented by each year's height or percent browsing value shown in the graphs is 30 which is based on 1 m segments on 30 m long transects. (*) We were unable to record browsing history and plant height data for 1998 on the low-risk sites because the plants were heavily browsed making it difficult to read the plant architecture that far back in time.

plant communities and floodplains during springtime runoff), and July streamflow (important for maintaining riparian water tables during summertime growth periods). Time trends for each of these environmental variables, respectively, are presented in Fig. 7C–E. While 1998 was a relatively low year for both snowpack accumulation and peak flows, summertime streamflows (as indexed by July data) were relatively high. During the following three years of 1999–2001, each of these environmental indictors show a trend of initially high moisture availability in 1999 that successively decreases in each of the following 2 years. If moisture availability is assumed to correlate with the growth of young cottonwood, then the last 3 years should represent a period of decreasing growth rates. Decreases in annual cottonwood height growth from 1999 to 2001 are not reflected in the chronological plant growth data presented in Fig. 5.

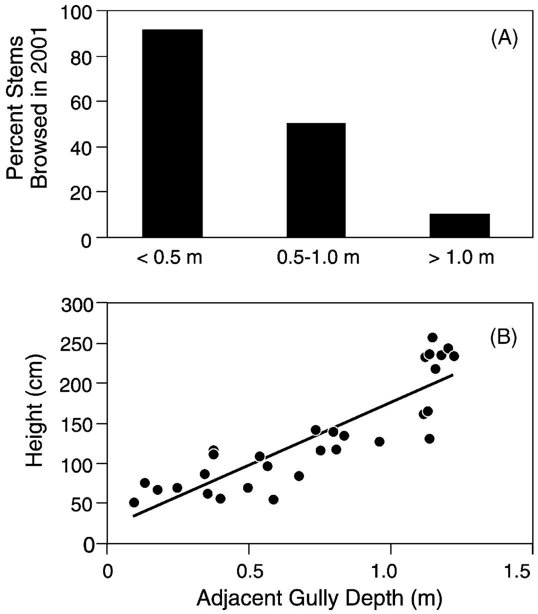

Fig. 6. Percent stems browsed for three gully depth classes (A) and the relationship between adjacent gully depth and cottonwood height (B) at a Lamar River point bar ($r^2 = 0.76$).

## 5. Discussion

The occurrence of young cottonwood plants 2–4 m in height is in stark contrast with the long-term suppression of woody browse species that has occurred in this area over much of the last century as illustrated by chronologically sequenced photos (Houston, 1982; Meagher and Houston, 1998) and field measurements (Ripple and Larsen, 2000; Beschta, in press). We hypothesize that this relatively recent release is related to predation risk interactions between wolves and elk. Overall, riparian vegetation (e.g., young cottonwoods and willows) in recent years has been growing taller along several portions of the study area but more so along Soda Butte Creek than along the Lamar River. The Lamar River valley bottom is a large open landscape (low predation risk). In contrast, Soda Butte

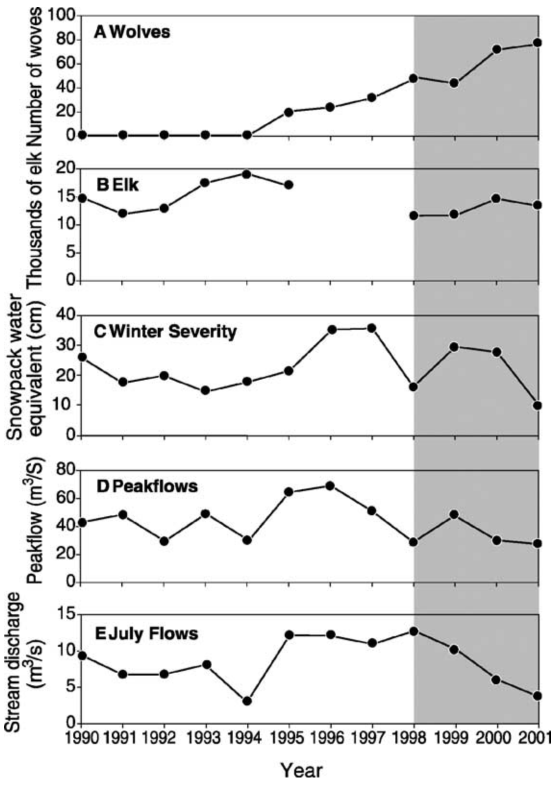

Fig. 7. The estimated total number of wolves by year on Yellowstone's northern range (A); the estimated total number of elk by year (average = 15,500 for 1990–1995 and 12,700 for 1998–2001; data for years 1996 and 1997 are not available) (B); annual maximum snowpack water equivalent for the northeast entrance snow course (average = 22.8 cm for 1947–2001) (C); annual peakflows (average = 43.2 $m^3/s$ for 1989–2001) (D); and July streamflow (average = 8.4 $m^3/s$ for 1989–2001) (E). The shaded portion of the figure represents years for which plant architecture evaluations provided measurements of ungulate browsing intensities and cottonwood plant heights. Data sources: (A) Smith and Guernsey (2002); (B) Yellowstone Center for Resources, Mammoth, WY; (C) National Resources Conservation Service, Northeast Entrance Snow Course, Montana; (D) and (E) US Geological Survey, Soda Butte Creek stream gage, Wyoming (USGS #06187950).

Creek has a narrower valley than the Lamar and is relatively close to a den site that is commonly occupied by the Druid Peak wolf pack (both of these conditions could contribute to greater predation risk). Should the differences in cottonwood and willow height responses continue between these two reaches, we would suggest that they represent landscape scale responses to predation risk. Such a conclusion is in concert with that of Dekker (1997) where he indicated that elk prefer to remain in more open country so they can both see wolves from afar and have adequate escape routes.

Our results of the paired high/low predation risk sites indicate that young riparian cottonwoods are growing tallest at localized sites where predation risk is relatively high—in essence representing local refugia from the effects of browsing. Field observations indicate similar responses are occurring with willows. At these high-risk sites, terrain features (e.g., high cutbanks, terraces) have the capability to limit the viewshed of elk, increasing the likelihood that they will not detect wolves. In addition, high terraces, steep cutbanks, riverbanks, gullies, dead and down trees, or other comparable features represent potential impediments to escape. Individually or in combination, these features represent a "terrain fear factor" which appears to index the degree of predation risk for a given site. Browsing intensity and height growth data from the paired transects illustrates that elk may assess predation risk at the scale of tens of meters or more. In contrast, the height and browse data collected along the gully of the Lamar River point bar illustrates that the level of predation risk recognized by elk may change significantly within only a few meters, apparently due to subtle changes in gully depth.

Although "plant architecture" measurements allowed us to assess plant browsing intensities and heights as far back as 3–4 years, it appears that the high-risk Lamar River island site began to experience increased height growth before that period (Fig. 5). In contrast, the high-risk Soda Butte Creek point bar appears to show increased height growth in only the last 3 years. These data suggest that the timing and magnitude of an altered herbivory pattern may occur somewhat differently at various sites, as predators and prey continually adjust to each other over time. Similarly, Laundré et al. (2001) found a lag time between when wolves were first reintroduced into Yellowstone and increased/stabilized vigilance levels by elk. These authors attributed this time lag to elk possessing imperfect information on the lethality of wolves and increases in encounter rates as the total number of wolves increased in recent years.

While broad open areas would generally be indicative of a landscape characterized as having low predation risk, the occurrence of microtopography within this broader landscape that restricts visibility or escape would represent a localized area of high-risk. This would imply that prey animals, as they move across a landscape, would be continually assessing predation risk at varying spatial scales. Thus, if decreased herbivory is occurring in a landscape where deciduous woody species have been widely suppressed by browsing over a long period of time, measurements of plant herbivory at a given site represent the appropriate gauge from which to assess whether that site is characterized as one with a relatively high or low level of predation risk.

This study provides empirical evidence on how predation risk may influence the release of previously suppressed riparian plant communities. Based on the predation risk hypothesis, elk will increasingly forage at sites that allow early detection, avoidance, and successful escape from wolves, a reintroduced keystone predator in the northern YNP that rely on elk as their primary source of food. Our data support the concept that elk may be increasingly avoiding riparian areas (except for the very large and open valley bottoms) and selecting higher ground, both to detect wolves and to escape from wolves. Such a ‘‘higher ground hypothesis’’ is also supported by daytime elk observations from the winter of 2001/2002 in terrain near both Soda Butte Creek and the Lamar River with elk use of hillslopes high and elk use of floodplains low (McIntyre, 2002, personal communication). In nearby Glacier National Park, stalking cover and the element of surprise were found to be important factors affecting the predation success of wolves (Kunkel and Pletscher, 2001). In addition, wolves made relatively large numbers of kills in ravines (limited detection of wolves and escape from wolves) and at sites close to water (limited escape routes for ungulates, travel corridors for wolves) (Bibikov, 1982; Kunkel and Pletscher, 2000, 2001). Bergerud and Page (1987) suggested that Caribou (*Rangifer tarandus*) place themselves at high elevations to increase distance between themselves and predators traveling in valley bottoms. Ferguson et al. (1988) also indicate that caribou may sacrifice high quality forage to avoid high-risk environments.

The chronosequence photo comparisons shows a more generalized recovery of riparian vegetation for both cottonwood and willow species in recent years. At the same time, plants growing at low-risk sites continue to experience heavy browsing and have not significantly increased their stature. Most importantly, increased heights of young cottonwood have occurred only since 1997, which coincide well with the wolf reintroductions in the winter of 1995–1996.

Since total elk numbers following wolf reintroduction average approximately 18% less than the average before wolf reintroduction, we considered this change in elk population as a possible explanation for the riparian plant growth that we observed. However, much of this decrease in elk numbers was most likely caused by the severe winter of 1996–1997 (Farnes et al., 1999) rather than wolf predation. The extent to which wolf predation may, or may not, have contributed to the relatively ‘‘flat’’ population curve for elk since 1998 (Fig. 7B) is not known.

The smaller post-wolf elk population alone cannot explain the plant growth we documented for two reasons. First, the plant growth that we observed was spatially patchy and mostly occurring at sites with low visibility and/or high escape barriers, thus supporting a predation risk hypothesis. While differences in site quality might represent a confounding factor regarding growth responses, we attempted to reduce the role of this factor by comparative high and low-risk sites that were hydrologically similar. Our results show that plants on the low-risk sites were actually growing closer to the water table than the plants at the high-risk sites (Table 2). Second, an elk population ranging from approximately 12,000–14,000 animals in recent years was much higher than the elk population of the late 1960s when numbers dropped below 4000 due to direct removal of elk by the National Park Service. Even with the lower elk numbers of the 1960s, there was not a general release of woody browse species (National Research Council, 2002). Thus, results of this study are supportive of a top-down trophic cascades effect involving wolves, elk, and cottonwoods due to changes in browsing habituation and not primarily because of direct mortality effects on prey animals.

Since the growth of young riparian vegetation may sometimes be attributed to environmental factors, particularly those which affect moisture availability, we considered the potential effects of the annual maximum snowpack water equivalent, annual peak flow, and July streamflow as potential contributing factors to the increased height growth that has occurred in recent years. In 1998, maximum snowpack water equivalent was about average, annual peakflows were slightly below average, and July streamflow was much higher than average. In 1998, the heights of young cottonwoods were relatively low for the high-risk sites (Fig. 5); we were unable to assess plant heights on the low-risk sites for 1998. While the amount of available moisture, as indexed by each of the three environmental variables, was relatively high in 1999, it incrementally declined in the succeeding years (Fig. 7C–E). This chronology of declining moisture availability is in contrast to a pattern of increased height growth on the high-risk sites. For the low-risk sites, where elk may browse with reduced concerns regarding predators, little change in plant height occurs over time (Fig. 5). Thus, for both high and low-risk sites, there appears to be little association between any of the three moisture variables and the height growth of young cottonwood. Similarly, Zeigenfuss et al. (2002) found that elk herbivory rather than water table depth was the primary factor driving willow productivity in Rocky Mountain National Park although they suggest that water tables may have been too high for a willow response.

For western cottonwoods, widespread seedling establishment often occurs on exposed substrates during periods of high runoff followed by continued growth for a subset of the seedling population into tall saplings and ultimately into mature trees. Since both Soda Butte Creek and the Lamar River are free-flowing (i.e., undammed), they have continued to experience a natural flow regime during the period of wolf extirpation. During this same time span, periodic channel changes and adjustments have insured the availability of bare alluvial substrates for cottonwood germination (see discussion, National Research Council, 2002, pp. 75–77). The common occurrence of seedlings along riparian areas of Soda Butte Creek and the Lamar River, evident in recent years, attest to the capabilities of young cottonwoods to establish throughout the study area (Beschta, in press). However, from a historical perspective, hydrologic disturbances have been of little assistance regarding cottonwood recruitment (i.e., the growth of young cottonwood seedlings/suckers into taller size classes). Even though natural variations in snowpack amounts, peakflows, and summer flows continued to occur during the multiple decades of wolf extirpation, cottonwood recruitment was largely absent (Beschta, in press).

Alternatives to our predation risk hypothesis might include, for example: (1) elk distributions are affected by snows that may accumulate in broken terrain and preclude elk use, while the more open Lamar Valley offers opportunities for snow to blow off of foraging areas, and (2) winter severity has altered elk distributions to where they remain at higher elevations or on sites other than in riparian zones. In addition, there are potential predation risk factors that we did not study such as those related to the senses of smell and hearing in elk and how these senses might be used in risk sensitive foraging strategies (wind speed and direction, sounds from rushing water, etc.).

If wolves had not been returned to YNP, the continued suppression of deciduous woody plants occupying riparian systems, by wild ungulate browsing, and the possible extirpation of some of these species would have been a likely legacy. However, the height growth of cottonwood and willow communities that is currently underway along Soda Butte Creek and portions of the Lamar River may eventually provide for the development of taller growth forms (i.e., tall shrubs and saplings, trees) that has not been able to occur for many decades. If the young cottonwoods and willows continue to increase in stature and expand their spatial occurrence along these riparian systems, this response may ultimately contribute to the biodiversity and sustainability of riparian plant communities characteristic of this ecosystem. Over time, the increased stature and spatial occurrence of riparian woody species may create additional predation risk effects related to decreased visibility and fewer escape routes available to the elk.

## 6. Conclusions

This study provides specific field evidence illustrating how the effects of a top predator can ripple through a system of three trophic levels. Results of the photo comparisons and vegetation measurements indicate that riparian systems in the northern range are very much in the early stages of a patchy “release” whereby some of the previously browse-suppressed plants (specifically those occupying high-risk sites) are seeing decreased levels of browsing and increased height growth. As an additional indicator of potential riparian recovery, a wintering beaver colony has recently become established on Soda Butte Creek, a rare occurrence over the past few decades. While such observations are hopeful of a more general recovery of riparian plant communities, it needs to be emphasized that in 2002 there were only three locations along the entire 13 km study reach where young cottonwood plants had accrued a height of 2–4 m in recent years. Conversely, the growth of previously suppressed willows appears to be more widespread in parts of the study reach (Figs. 2 and 3) and along other streams on the northern range such as portions of Crystal Creek, Blacktail Creek, and Slough Creek (author observations). Continued riparian plant community recovery and beaver presence may also depend upon future predator–prey dynamics and winter weather conditions which in turn influence elk distributions and utilization of riparian vegetation. Thus, even though vegetation responses are occurring at local and landscape scales, it is still too early to determine if the trends in cottonwood and willow release will continue into the future, the spatial scale of these responses, or if beaver will remain.

If the woody browse species do continue to grow taller and expand their spatial domain, numerous long-term ecological benefits will accrue to aquatic and riparian habitats such as increased shading and thermal moderation, large wood and litter inputs, increased rooting and streambank stability, improved food web support for a wide number of terrestrial and aquatic organisms, and others. Since the groves of mature narrowleaf and black cottonwoods that currently reside in the riparian systems of the Soda Butte Creek and Lamar River valleys have not successfully recruited either tall sapling or tree forms during the last half-century, or longer, the potential release of existing young cottonwoods due to predation risk effects following wolf reintroductions represent an opportunity for insuring the sustainability of these important riparian plant species. While the results of this study are specific to the wild ungulates and riparian systems in the northern range of YNP, it is possible that similar scenarios of overbrowsing and suppression of deciduous woody species comprising riparian plant communities following the widespread extirpation of wolves have been playing out across other streams and rivers of the American West. Thus, the reintroduction of wolves to at least some of their former range may be a necessary component of restoring western riparian ecosystems and increasing biodiversity.

## References

Baker, W.L., Munroe, J.A., Hessl, A.E., 1996. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20, 155–165.

Berger, J., Stacey, P.B., Bellis, L., Johnson, M.P., 2001. A mammalian predator–prey imbalance: grizzly bears and wolf extinction affect avian neotropical migrants. Ecol. Appl. 11, 947–960.

Bergerud, A.T., Page, R.E., 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Can. J. Zool. 65, 1597–1606.

Beschta, R.L., in press. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. Ecol. Appl.

Bibikov, D.I., 1982. Wolf ecology and management in the USSR. In: Harrington, F.J., Paquet, P.C. (Eds.), Wolves of the World: Perspectives of Behavior, Ecology, and Conservation. Noyes Publications, Park Ridge, NJ, pp. 120–133.

Braatne, J.H., Rood, S.B., Heilman, P.E., 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. In: Stettler, R.F., Bradshaw Jr., H.D., Heilman, P.E., Hinckley, T.M. (Eds.), Biology of Populus and its Implications for Management and Conservation, Part I. National Research Council of Canada, Ottawa, Ont., Canada, Chapter 3, pp. 57–85.

Brookshire, E.N.J., Kauffman, J.B., Lytjen, D., Otting, N., 2002. Cumulative effects of wild ungulate and livestock herbivory on riparian willows. Oecologia 132, 559–566.

Brown, J.S., Laundré, J.W., Gurung, M., 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. J. Mammal. 80, 385–399.

Chadde, S.W., Kay, C.E., 1996. Tall-willow communities on Yellowstone's northern range: a test of the "natural-regulation" paradigm. In: Singer, F.J. (Ed.), Technical Report No. NPS/NRYELL/NRTR/96-01. National Park Service, Natural Resource Information Division, Denver, CO, pp. 165–183.

Dekker, D.G., 1997. Wolves of the Rocky Mountains from Jasper to Yellowstone. Hancock House Publishers Ltd., Blaine, WA.

Despain, D.G., 1990. Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting. Roberts Rinehart, Boulder, CO.

Estes, J.A., Crooks, K., Holt, R., 2001. Predators, ecological role of. In: Levin, S. (Ed.), Encyclopedia of Biodiversity, vol. 4. Academic Press, San Diego, CA, pp. 280-1–280-22.

Farnes, P., Hyedon, C., Hansen, K., 1999. Snowpack distribution across Yellowstone National Park, Wyoming. Final Report. Department of Earth Sciences, Montana State University, Bozeman, MT.

Ferguson, S.H., Bergerud, A.T., Ferguson, R., 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. Oecologia 76, 236–245.

Houston, D.B., 1982. The Northern Yellowstone Elk: Ecology and Management. Macmillan, New York.

Jonas, R.J., 1955. A population and ecological study of beaver (*Castor canadensis*) of Yellowstone National Park. M.S. Thesis. University of Idaho, Moscow.

Kay, C.E., 1997. Is aspen doomed? J. For. 95, 4–11.

Keigley, R.B., 1997. An increase in herbivory of cottonwood in Yellowstone National Park. Northw. Sci. 71, 127–136.

Keigley, R.B., Frisina, M.R., 1998. Browse evaluation by analysis of growth form. Montana Fish, Wildlife, and Parks.

Keigley, R.B., Frisina, M.R., Fager, C., 2003. A method for determining the onset year of intense browsing. J. Range Manage. 56, 33–38.

Kunkel, K.E., Pletscher, D.H., 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Can. J. Zool. 78, 150–157.

Kunkel, K.E., Pletscher, D.H., 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. J. Wildl. Manage. 65 (3), 520–530.

Larsen, E.J., Ripple, W.J., 2003. Aspen Age Structure in the Northern Yellowstone Ecosystem: USA. For. Ecol. Manage. 179, 469–482.

Laundré, J.W., Hernandez, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the landscape of fear in Yellowstone National Park, USA. Can. J. Zool. 79, 1401–1409.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

McIntyre, R., 2002. Personal communication, Silver Gate, MT.

Mclaren, B.E., Peterson, R.O., 1994. Wolves, moose, and tree rings on Isle Royale. Science 266, 1555–1558.

Meagher, M.M., Houston, D.B., 1998. Yellowstone and the Biology of Time. Oklahoma State University Press, Norman, OK.

National Research Council, 2002. Ecological Dynamics on Yellowstone's Northern Range. National Academy Press, Washington, DC.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Tropic cascades revealed in diverse ecosystems. Trends Ecol. Evol. 14, 483–488.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol. Conserv. 95, 361–370.

Ripple, W.J., Larsen, E.J., Renkin, R.A., Smith, D.W., 2001. Trophic cascades among wolves, elk, and aspen on Yellowstone National Park's northern range. Biol. Conserv. 102, 227–234.

Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76, 2097–2106.

Schmitz, O.J., Beckerman, A.P., O'Brien, K.M., 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78, 1388–1399.

Singer, F.J., Zeigenfuss, L.C., Cates, R.G., Barnett, D.T., 1998. Elk, multiple factors, and persistence of willows in national parks. Wildl. Soc. Bull. 26, 419–428.

Smith, D.W., Guernsey, D.S., 2002. Yellowstone Wolf Project: Annual Report, 2001. YCR-NR-2002-04. USDI National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

Terborgh, J., Estes, J.A., Paquet, P., Ralls, K., Boyd-Heiger, D., Miller, B.J., Noss, R.F., 1999. The role of top carnivores in regulating terrestrial ecosystems. In: Terborgh, J., Soule, M. (Eds.), Continental Conservation: Scientific Foundations of Regional Reserve Networks. Island Press, Washington, DC, Chapter 3.

Weaver, J., 1978. The wolves of Yellowstone. Natural Resources Report No. 14. US Department of Interior, National Park Service.

White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildl. Soc. Bull. 26, 449–462.

Yellowstone National Park, 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. US Department of Interior, Yellowstone National Park, Mammoth Hot Springs, WY.

Zeigenfuss, L.C., Singer, F.J., Williams, S.A., Johnson, T.L., 2002. Influences of herbivory and water on willow in elk winter range. J. Wildl. Manage. 66, 788–795.