

REDUCED COTTONWOOD RECRUITMENT FOLLOWING EXTIRPATION OF WOLVES IN YELLOWSTONE'S NORTHERN RANGE

ROBERT L. BESCHTA¹

College of Forestry, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. Cottonwoods (*Populus* spp.) represent an important tree component of riparian plant communities within the winter range of the northern Yellowstone elk (*Cervus elaphus*) herd, yet young cottonwoods are highly palatable to ungulates. To assess potential herbivory impacts associated with wild ungulates following the removal of gray wolves (*Canis lupus*), long-term cottonwood recruitment and stand dynamics were studied. While results indicated that the establishment of young cottonwoods is an ongoing process in Yellowstone's northern range, their relatively small stature and hedged appearance were indicative of high browsing pressure by wild ungulates, principally elk. At five study sites, the diameter at breast height (dbh) of all cottonwood trees ≥ 5 cm was determined; increment cores were also obtained for developing tree age vs. dbh relationships. At the La Duke Spring and Devils Slide Sites, which represent refugia sites since elk have limited access (due to local terrain conditions and cultural developments), cottonwood recruitment has been occurring during the last half century, indicating that climatic factors have not prevented cottonwood recruitment during that time. However, over this same period cottonwood recruitment no longer occurred at sites within the Soda Butte and Lamar Valleys. The overall decline in cottonwood recruitment at these locations occurred following the extirpation of wolves from Yellowstone National Park in the 1920s. At the Buffalo Ranch Site, where ranching of buffalo [bison] (*Bison bison*) and activities associated with culling of elk were centered, cottonwood recruitment continued after the loss of wolves but stopped following the curtailment of ungulate management activities at these facilities in the late 1960s. Taken together, data from the five sites reported herein along with the results of other studies provide compelling evidence that the absence of wolves in the northern Yellowstone has had a major impact on the recruitment of cottonwood and other woody browse species.

Key words: cottonwoods; elk; riparian vegetation; trophic cascades; wolves; Yellowstone National Park.

INTRODUCTION

The role of riparian plant communities has become increasingly recognized in recent years (NRC 2002b). Along streams and rivers, these communities help stabilize stream banks, provide hydraulic resistance during overbank flows, enhance deposition of organic matter and fine sediment on stream banks and floodplains, moderate water temperatures and riparian microclimates via shade, cycle nutrients, produce organic carbon that is an essential component of food webs for riparian and aquatic organisms, and maintain biodiversity (Cummins 1974, Beschta et al. 1987, Gregory et al. 1991, Sedell and Beschta 1991, Ohmart 1996, Wigington and Beschta 2000, Kauffman et al. 2001, Dobkin et al. 2002, NRC 2002b).

Cottonwoods (*Populus* spp.) are often a particularly important component of riparian flora along Western streams and rivers as they are widely distributed, represent the tallest deciduous woody species found along

many of these systems, and provide physical habitat and food web support for a wide range of wildlife species, including ungulates. Since cottonwoods are relatively long lived compared to other deciduous woody species that frequent riparian systems, their stand structure is amenable to historical assessment (via tree aging) and may be indicative of long-term climatic, hydrologic, land use, or other factors (e.g., Merigliano 1996, Beschta 2003).

The potential for wild (and domestic) ungulates to severely browse deciduous woody plants has been widely recognized and documented (Braatne et al. 1996, Clayton 1996, Heilman 1996, Whitham et al. 1996, Kay 1997, Barmore 2003). Yet the role of wild ungulates, principally elk (*Cervus elaphus*), with respect to aspen (*P. tremuloides*), willow (*Salix* spp.), cottonwood, and other woody species has been a controversial scientific and management issue within Yellowstone's northern winter range (e.g., NPS 1956, 1959, Houston 1982, Kay 1990, 1997, 2000, Romme et al. 1995, Keigley 1997, 1998, Meagher and Houston 1998, Shafer 2000, NRC 2002a). While multiple hypotheses have been proposed regarding the long-term

Manuscript received 10 June 2004; accepted 16 July 2004; final version received 19 July 2004. Corresponding Editor: D. A. Spiller.

¹ E-mail: Robert.Beschta@oregonstate.edu



FIG. 1. Cottonwoods (a) in winter (photo credit: Yellowstone National Park; circa 1970s) and (b) in summer (photo credit: R. L. Beschta; August 2000) in the Lamar Valley; note the lack of small and intermediate size classes of cottonwoods in both photos.

demise of deciduous woody species in the northern range, including fire regimes, climate, plant succession, disease, insects, and others, high levels of herbivory often have been considered a major contributor to this problem. More recently, the extirpation of a keystone predator in the mid-1920s, the North American gray wolf (*Canis lupus*), has been identified as having an important ecosystem linkage (via trophic cascades) with the depletion of aspen (Ripple and Larsen 2000), cottonwood (Beschta 2003), and other browse species (Ripple and Beschta 2004).

Both narrowleaf cottonwood (*P. angustifolia*) and, to a lesser degree, black cottonwood (*P. trichocarpa*) are often components of riparian systems within the northern winter range (Fig. 1), yet they have received little study. This research builds upon earlier work by

Keigley (1997, 1998) and Beschta (2003), and was undertaken to provide a broader understanding of the temporal dynamics of northern range cottonwoods. Specific objectives included the following:

1) Determine the number of young cottonwoods (seedlings and/or root sprouts) at two geomorphically different sites (i.e., floodplain and alluvial fan) to see if cottonwood reproduction is limiting recruitment.

2) Evaluate the history of cottonwood recruitment at five sites, as reflected in existing stand structure and establishment dates, to assess the relative importance of various factors (e.g., climate, peak flows, herbivory) that might explain historical patterns of recruitment.

STUDY AREA

In the upper portions of the northern Yellowstone elk herd's winter range (elevation ≈ 2000 m), wide val-

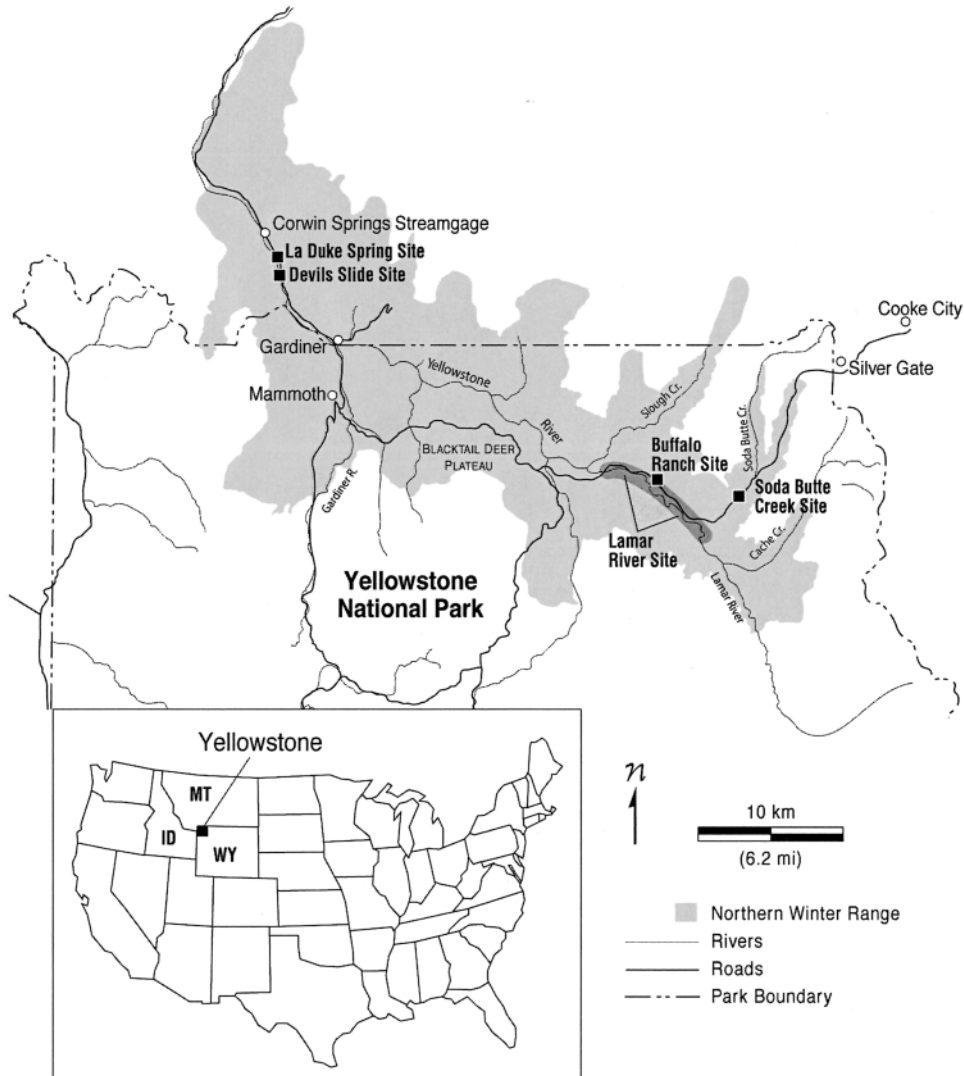


FIG. 2. Location of study sites within the northern Yellowstone elk winter range.

leys associated with the Lamar River and major tributaries, such as Slough Creek and Soda Butte Creek, are found, while at the lowest extent of the winter range (elevation ≈ 1600 m) is a broad valley associated with the Yellowstone River (Fig. 2). Located between these two areas are the Blacktail Plateau and the rugged Black Canyon of the Yellowstone River. All streams and rivers in the study area are unregulated (i.e., free flowing).

Summers are short and cool; persistent snow cover and subfreezing temperatures are common during the winter months. Snowfall averages in excess of 350 cm at elevations of 2100–2600 m, while snow depths on level sites within the open valleys typically do not exceed 80 cm (Barmore 2003). Depending upon the severity of winter conditions (e.g., snow depths and cover) and seasonal patterns of elk movement, the amount

and location of foraging and/or browsing by wild ungulates within the northern range varies from winter to winter.

Sagebrush (*Artemisia tridentata*) grasslands form expansive open areas of winter range on hillslopes interspersed with sedge- (*Carex* spp.) and grass-dominated meadows on gentle sloping sites and floodplains of the major valleys. Scattered cottonwood groves are found on various sites including floodplains, point bars, stream banks, and alluvial fans. Historically, aspen occurred in scattered stands across the winter range, and willows were found along streams and rivers; both have experienced major declines in abundance during the 20th century (Houston 1982, Chadde 1989, Kay 1990, 2001, Chadde and Kay 1996, NPS 1997, Meagher and Houston 1998, Ripple and Larsen 2000, Barmore 2003, Larsen and Ripple 2003).

NORTHERN RANGE MANAGEMENT HISTORY

Yellowstone National Park was established in 1872. In 1886, the U.S. Cavalry was assigned management of the park and a policy of ungulate protection was initiated. The Park Service continued this policy when it assumed management control of the park in 1918. However, during this period of federal control, wolves in and out of the park were hunted and poisoned, with the last recorded wolf removals occurring in the mid-1920s (Weaver 1978, Schullery and Whittlesey 1992).

In the 1920s, park administrators became concerned about the "bad condition" of the northern winter range due to high levels of herbivory by elk (Grimm 1939). Thus began a program of removing elk in an attempt to control their impacts. Even with reductions in elk numbers, impacts to vegetation in the winter range continued, and by the late 1950s management plans for the northern Yellowstone elk herd (NPS 1956, 1957, 1958) indicated that:

The cumulative effects of grazing and trampling by excessive numbers of elk for many decades are obvious today. Meadows once covered by lush thickets of willows now have a grass-type aspect; likewise former stands of aspen now have only a few trees that cannot be replaced while elk consume reproduction. Sagebrush has disappeared from ridges and other places where snow lies shallow, and even bunchgrasses, which comprises the bulk of the elk's diet, is in poor condition.

Similar impacts to plant communities and soils in the winter range of the upper Gallatin elk herd, along the northeastern portion of the Park, were also reported (Peek et al. 1967, Lovaas 1970).

Park Service assessments (NPS 1959, 1961) acknowledged the continuing need to control animal numbers given that "the herd was larger than the range could support." The early optimism for using the park as a producer of large numbers of ungulates had given way to the realization that, in doing so, unacceptable impacts were occurring to upland and riparian vegetation, soils, and food web support for various wildlife species. While park biologists and administrators apparently understood the gravity of changes occurring on the northern range of Yellowstone and a need to control elk impacts, they had inherited a legacy of wolf eradication as accepted practice and were unable to consider the potential role of wolves as a solution to resource management concerns. Thus, the only avenue seemingly open to them was to physically reduce elk numbers.

From a population size in excess of 10 000 elk (>7 elk/km²) in the 1930s, control efforts by the National Park Service eventually reduced elk numbers to 3000–4000 animals (2–3 elk/km²) in the mid-1960s. However, due to increasing public and political pressure against the culling of elk within a national park (Allin

2000), control efforts were no longer undertaken after 1968. This occurred even though the park's long-standing policy of controlling elk numbers was based on extensive research and observation that had confirmed elk were creating severe impacts to vegetation and soil resources on the northern range (e.g., NPS 1956, 1959, 1961).

With the cessation of control efforts after 1968, northern range populations quickly began to increase from their historical low in the mid-1960s to an average of 10 350 in the 1970s, 15 550 in the 1980s, and 16 570 in the 1990s. These increases occurred even though public hunting of northern range elk (i.e., those that left the park in winter) continued to occur. The post-1968 period has been identified by the Park Service (NPS 1997) as one of "natural regulation." However, from 1969 until 1995 natural regulation unfolded, much like the previous four decades, in the absence of predation from wolves. Under protection of the 1973 federal Endangered Species Act, wolves were reintroduced into Yellowstone National Park during the winter of 1995–1996. More detailed accounts of 20th-century park management can be found in Kay (1990), NPS (1997), Shafer (2000), NRC (2002a), and Beschta (2003).

The unique management history at Buffalo Ranch, in the north side of the Lamar Valley, is also of interest since it represents one of the field sites utilized for this study. In the early 1900s, an initially small, semidomesticated herd of buffalo was established on the northern range and intensively managed from the facilities at Buffalo Ranch. As part of the management effort to increase numbers of buffalo, exotic grasses were introduced for growing feed, pastures were irrigated from Rose Creek, and fences were constructed across the Lamar Valley and around the ranch buildings. These facilities were used for manipulating animal movements, undertaking a variety of ranching and animal husbandry practices, and for supporting elk culling operations from 1923 to 1968, during which 26 400 elk were removed from the park (NPS 1997).

NORTHERN RANGE EXCLOSURE STUDIES

Fenced exclosures have long been used in the northern range for studying ungulate browsing effects upon deciduous woody species and other plants. For example, in the early 1930s an exclosure was established near Mammoth Hot Springs where aspen root sprouts (suckers) had been continually suppressed by browsing. When remeasured in 1965, aspen sprouts inside the exclosure had grown into a dense stand of trees up to 11 m in height and 13.2 cm in diameter at breast height, whereas those on the outside remained only 40 cm tall. Based on these studies and others, Barmore (2003) concluded that "browsing by wild ungulates can cause deterioration and elimination of aspen clones by suppressing sucker growth and by barking older trees."

Additional exclosures were installed in the northern range in 1957 to study potential browsing effects upon willows. When remeasured in 1965, willows inside the exclosures had attained average heights of 130–200 cm, while those on the outside had average heights of only 40–60 cm, essentially unchanged over the period of measurement (Barmore 2003). In another northern Yellowstone study, Singer (1996) indicated willows inside exclosures were 200–400% taller than those on the outside.

Based on measurements obtained outside of northern range exclosures (i.e., Kay 1990, Singer 1996, Barmore 2003), aspen heights averaged 31 ± 10 cm (mean ± 1 SD, $n = 39$) from 1935 to 1989, willow heights averaged 44 ± 20 cm ($n = 31$) from 1959 to 1988, and the heights of other deciduous woody species averaged 40 ± 17 cm ($n = 11$) in 1988. While seasonal snow accumulations likely provided some over-winter browsing protection for young plants and allowed them to persist in a hedged condition over long periods, since measurements were begun in 1935 the attainment of heights >100 cm for woody browse species growing outside of exclosures has not been observed in any of the long-term northern range studies.

In contrast to the historical record of browsing-suppressed woody species, Ripple and Beschta (2003) reported increased height growth in recent years for young cottonwoods and willows growing at several locations in the Soda Butte and Lamar Valleys. Following the reintroduction of wolves into Yellowstone National Park in the winter of 1995–1996, decreased browsing pressure from elk and increased height growth appear to have begun in 1999–2000 at locations with high predation risk. Even so, young cottonwoods were still not above the browse level of elk, since the tallest plants measured in 2002 were only 300–400 cm in height on an island in the Lamar River and 200–300 cm high at several other sites.

METHODS

Relatively large peak flows often create bare substrates and hydrologic conditions amenable to widespread cottonwood seedling establishment (Braatne et al. 1996, Mahoney and Rood 1998). Thus, peak flow frequency analysis of the Yellowstone River at Corwin Springs (USGS No. 06191500, elevation 1550 m, Fig. 2) was undertaken to identify the occurrence of peaks having return periods ≥ 10 yr.

Five sites within the winter range of Yellowstone's northern elk, each with one or more cottonwood stands, were selected for undertaking cottonwood measurements (Fig. 2):

1) *La Duke Spring*.—This cottonwood stand ($n = 241$ trees ≥ 5 cm in diameter at breast height [dbh]; elevation ≈ 1560 m) occupies an active pointbar deposit, bordered on one side by the Yellowstone River and on the other by a steep, 7 m high glacial outwash

terrace; U.S. Highway 89 occurs along the top of the terrace (Fig. 3a).

2) *Devils Slide*.—This cottonwood stand ($n = 111$ trees ≥ 5 cm dbh; elevation ≈ 1570 m) occupies the steep sideslope of a 7 m high glacial outwash terrace. The Yellowstone River runs just at the base of the sideslope, and a paved turnout associated with U.S. Highway 89 occurs at the top (Fig. 3b).

3) *Soda Butte Creek*.—This cottonwood stand ($n = 146$ trees ≥ 5 cm dbh; elevation ≈ 2020 m) occurs along the floodplain of Soda Butte Creek ~ 4 km upstream of its confluence with the Lamar River.

4) *Lamar River*.—Multiple stands of cottonwoods occur within a broad valley setting at this site ($n = 700$ trees ≥ 5 cm dbh; elevation ≈ 2000 m) and occupy floodplains and pointbars along the Lamar River (Fig. 1). The valley is 1–1.5 km wide and ~ 10 km long.

5) *Buffalo Ranch*.—Rose Creek, entering the Lamar Valley from the north, splits into three distributaries at this site that flow across an alluvial fan; cottonwoods occur along each channel ($n = 108$ trees ≥ 5 cm dbh; elevation ≈ 2010 m). Various Park Service buildings (e.g., educational classroom and housing facilities), a barn, corrals, and an access road occur among the distributaries.

Two of the sites, La Duke Spring and Devils Slide, were selected as “refugia” sites from elk herbivory (Ripple and Beschta, *in press*) since access was obstructed by terrain and cultural features. The remaining three sites encompassed all major cottonwood stands occurring within the Soda Butte and Lamar Valleys (Fig. 2), but excluded a few isolated trees along highway right-of-ways.

In 2002, the number of young cottonwoods (i.e., ≥ 20 cm in height and < 5 cm dbh) was determined at the Lamar River (floodplain) and Buffalo Ranch (alluvial fan) sites. At the Lamar River Site, a systematic sampling approach was utilized. Starting immediately above a canyon section (≈ 4 km downstream of Buffalo Ranch) and heading up-valley, a 4 m wide belt transect was established perpendicular to the river at every 250 m of channel distance (48 transects in total). Within each transect, all young cottonwoods were counted. These transects were of variable length since they extended away from both sides of the river until young cottonwoods were no longer encountered. In addition, when traversing from one transect to the next, the heights of the three tallest young cottonwoods (< 5 cm dbh) were recorded within each 50 m of channel distance. In total, over 700 height measurements (i.e., the three tallest plants within each 50 m of channel distance) were obtained when traversing between belt transects along the Lamar River. At the Buffalo Ranch Site, where distributary channels of Rose Creek cross the alluvial fan, the heights of all young cottonwoods were measured; each plant was also categorized as either (1) a seedling or (2) a root sprout based on its proximity to a mature cottonwood, presence of exposed

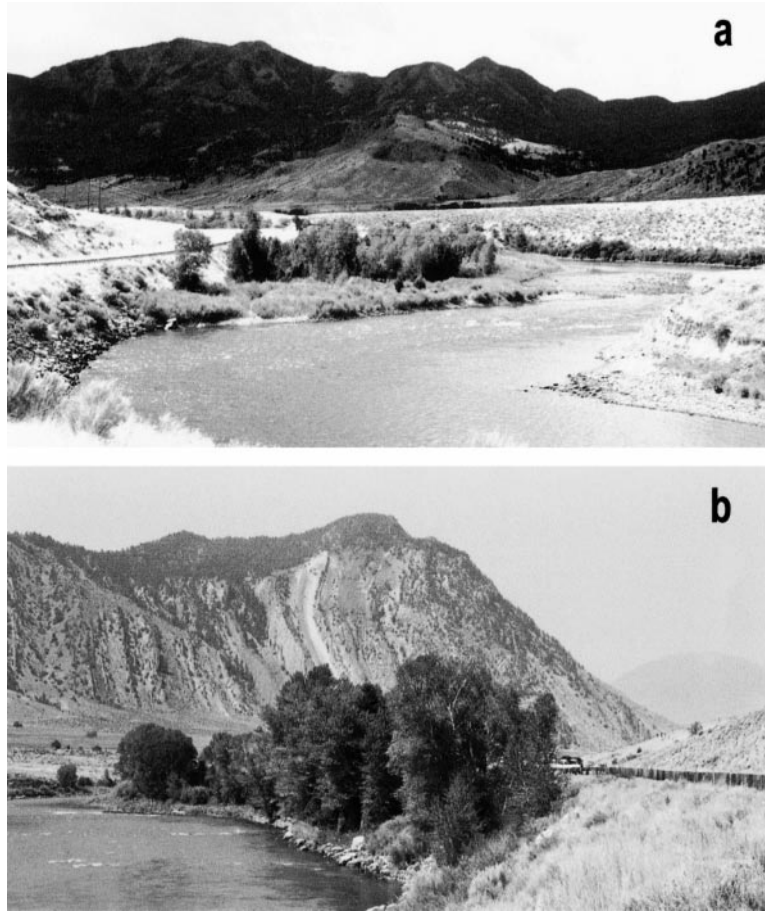


FIG. 3. (a) La Duke Spring (looking north) and (b) Devils Slide (looking south) refugia sites along the Yellowstone River (photo credit: R. L. Beschta; August 2003); small and intermediate size classes of cottonwood are common at both sites.

tree roots, occurrence of recent alluvial deposits, soil conditions, and others.

The dbh for all cottonwoods ≥ 5 cm was determined at each of the five study sites. For each tree, two dbh measurements were made at right angles using a Bitterlich Stick (Avery and Burkhart 2002) and then averaged. Measurements of dbh occurred in the summer of 2001 at the Lamar River and Buffalo Ranch Sites, in the summer of 2002 at the Soda Butte Creek Site, and in the summer of 2003 at the La Duke Spring and Devils Slide Sites. The Lamar River Site was revisited in 2002 and 2003 to evaluate tree mortality that had occurred during intervening years. Histograms of tree frequency vs. 5 cm dbh classes were developed to evaluate differences in stand structure between sites.

Relationships between tree dbh and age were used as a basis for estimating establishment dates of individual trees and for developing frequency distributions of tree numbers vs. establishment date, by decade. To determine tree ages, increment cores were extracted at breast height (≈ 1.4 m) with a 125 mm diameter increment corer, and the dbh of each cored tree was measured with a diameter tape. The increment borer was

immersed in isopropyl alcohol prior to coring each tree to reduce the possibility of transmitting disease organisms from one tree to another. Cores were individually stored in polypropylene tubes, oven dried, sanded (400 grit), and ring counts made with a 10 \times binocular microscope.

At the Soda Butte Creek, Lamar River, and Buffalo Ranch Sites, a 5% random sample of trees between the 40th and 90th percentiles of tree diameter were cored in 2002. This selection strategy emphasized sampling the larger (i.e., older) trees within a stand but avoided the very oldest trees, which often had rotten interiors. When a significant amount of heart rot was encountered during coring, thus preventing accurate age determination, the nearest tree of a similar diameter was substituted. Additional cores from downed black cottonwood trees, due to bank erosion in the spring of 2002, were obtained at the Lamar River Site. At the La Duke Spring and Devils Slide Sites where large trees were infrequent, cores from five randomly selected cottonwoods within a 25–30 cm dbh range were obtained from each site in 2003. Increment cores from 61 cottonwoods (41 narrowleaf and 20 black) were ultimately

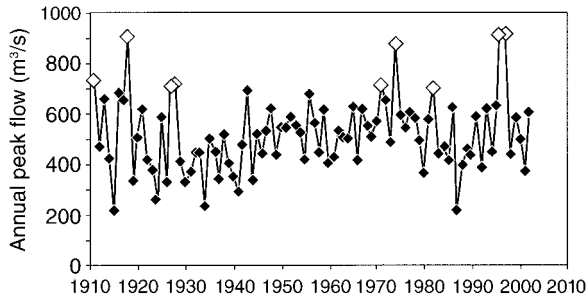


FIG. 4. Long-term patterns of annual peak flows from 1911 to 2002 for the Yellowstone River at Corwin Springs, Montana (open diamonds indicate flows with ≥ 10 -yr recurrence interval).

used in regression analysis to establish relationships between tree age and tree diameter.

The time required for a seedling to reach breast height can be highly variable due to multiple factors such as local site quality, competition from adjacent plants, browsing pressure, climate, and others. For the South Fork of the Snake River, Merigliano (1996) found that 6–8 years were required to reach a height of 1.4 m. Keigley (1998), in his study of young cottonwoods at the confluence of Soda Butte Creek and the Lamar River, found that a 30 cm tall seedling, experiencing severe browsing pressure, required from 1 to 20 years to reach a height of 100 cm. For purposes of this study, the time from germination to breast height was assumed to be seven years.

RESULTS

Flow regimes

Over the period 1911–2002, annual peak flows for the Yellowstone River at Corwin Springs averaged $18\,100 \pm 5170$ m³/s (mean \pm 1 SD). The pattern of relatively low peak flows during the 1930s (Fig. 4) is consistent with the occurrence of drought conditions that were common throughout much of the western United States. Relatively large peak flows (i.e., ≥ 10 -yr return periods), potentially important for widespread cottonwood establishment, occur in two periods: four events from 1911 to 1928, none from 1929 to 1970, and five events from 1971 to 1997.

Young cottonwoods

At the Lamar River Site, the number of young cottonwoods (≥ 20 cm tall and < 5 cm dbh) varied greatly along the river. For example, from the downstream end of the Lamar River valley to the confluence of the Lamar River and Soda Butte Creek, a river distance of ≈ 10 km, the estimated number of young cottonwoods averaged 5000 plants/km. However, from this confluence upstream to where the broad valley ends at a canyon reach, the estimated number of young cottonwoods averaged 48 500 plants/km, a 10-fold increase. In total, nearly 150 000 young cottonwoods were estimated to

be present along the Lamar River in 2002. Of the > 700 measurements of young cottonwood heights obtained between transects along the Lamar River, only 87 plants ($< 0.1\%$ of the estimated population) were > 100 cm in height. The maximum height observed for young cottonwoods at the Lamar River Site was 260 cm. A hedged growth form, as a result of browsing, was commonly observed.

Nearly all of the young cottonwoods at the Lamar River Site appear to have established as seedlings, since they typically occurred tens and hundreds of meters from the nearest trees, were arrayed in narrow strips paralleling the river, and occurred on bare alluvial deposits. Although major channel adjustments have occurred along the upper portion of the Lamar Valley in recent years, creating large areas of bare substrates, similar conditions existed in the lower portions of the valley (e.g., across from and downstream of Buffalo Ranch) where the occurrence of seedlings was comparatively lower.

Along the distributaries of the Buffalo Ranch Site, 585 young cottonwoods (≥ 20 cm tall and < 5 cm dbh) were found. Of these, 72% were categorized as having initiated from root sprouts and the remaining 28% from seeds. The tallest young cottonwood at this site had a height of 250 cm; nearly 95% of all young cottonwood had heights < 150 cm and most had a hedged condition, indicating heavy browsing.

Stand structure and recruitment

Several patterns of stand structure occurred at the five sites, as represented in frequency distributions of tree diameters (tabulated by 5 cm dbh classes) (Fig. 5). The La Duke Spring and the Devils Slide Sites have many small-diameter trees and a relatively consistent decrease in tree frequency with increasing diameter. In contrast, small tree sizes (e.g., the 5–25 cm dbh classes) are nearly absent for the Soda Butte Creek and Lamar River Sites, and relatively low for the Buffalo Ranch Site. Fig. 1 illustrates the general lack of small-diameter trees for cottonwood stands within the Lamar River Site. While narrowleaf cottonwoods comprised nearly all of the trees ≥ 5 cm dbh at four of the study sites, the Lamar River Site was notable in that black cottonwoods represented 29% of the 700 trees present at this site.

In general, the scatter of age vs. diameter data for narrowleaf and black cottonwoods, as illustrated in Fig. 6, was similar across all sites except for cores obtained from the Soda Butte Creek Site. Data from this site plotted “higher” than data from the other sites, indicating trees were growing comparatively slower. Many of the cored trees at the Soda Butte Creek Site had rotten interiors, indicating that disease, insects, or some other factor may be affecting growth rates. Furthermore, the foliage of cottonwood trees at this site generally had a chlorotic appearance. As a result, two regression equations were developed for tree age and

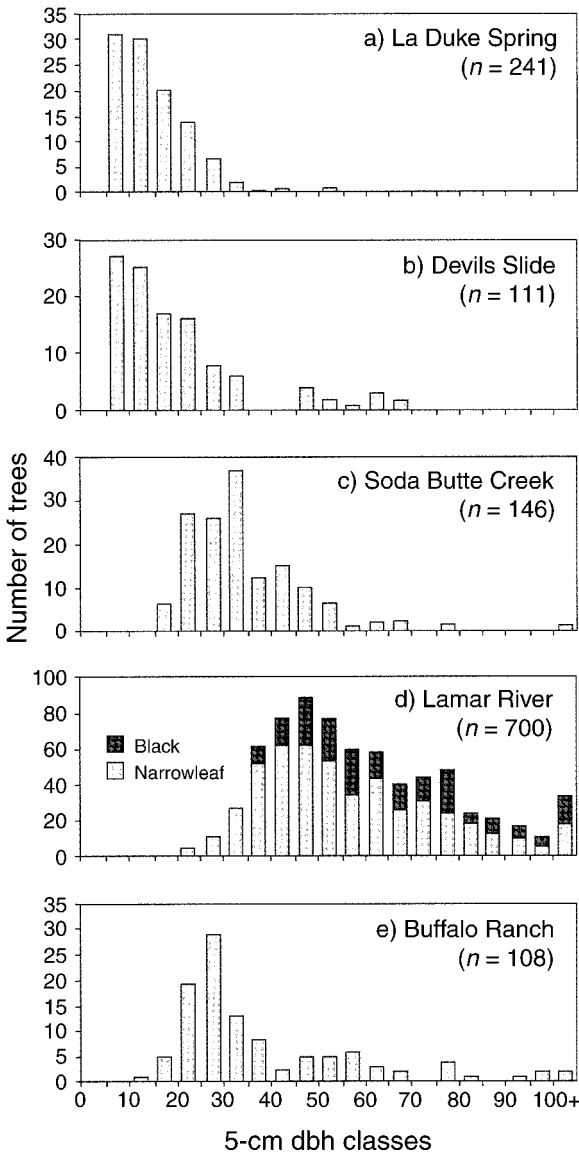


FIG. 5. Frequency distributions of narrowleaf cottonwood (and black cottonwood in panel d) diameters for trees ≥ 5 cm in diameter at breast height (dbh) at five study sites in the northern Yellowstone elk winter range.

dbh: one equation for the Soda Butte Creek Site and the other to represent cottonwoods at the remaining sites (Fig. 6). Establishment dates (ED, in years) for individual trees were estimated as follows: $ED = 2002 - (0.56 \text{ dbh}^{1.36} + 7)$ for cottonwoods at all sites except the Soda Butte Creek Site; at that site $ED = 2002 - (0.93 \text{ dbh}^{1.36} + 7)$. Estimated establishment dates for individual trees at a given site were "binned" by 10-yr increments from 1750 to 1990, a period of nearly two and one-half centuries.

Histograms of tree frequencies by establishment date at the La Duke Spring Site (pointbar; Fig. 7a) and the Devils Slide Site (steep sideslope of glacial outwash

terrace, Fig. 7b) along the Yellowstone River indicate a relatively uniform decrease in tree frequency with earlier establishment dates. However, both of these refugia sites confirm cottonwood recruitment (i.e., cohorts of young cottonwoods growing into trees) has been ongoing every decade for at least half a century.

The histogram of tree frequency and establishment date at the Soda Butte Creek Site (Fig. 7c) indicates several features regarding historical stand dynamics. For example, the recruitment peak during the 1860s may have represented a generally favorable period of cottonwood establishment and growth along Soda Butte Creek. Furthermore, cottonwood recruitment was successfully occurring for the decades prior to the 1920s. Finally, there was a significant lack of cottonwood recruitment during recent decades—much reduced in the 1930s and essentially none from the 1940s to 1990s. Histograms of establishment dates for narrowleaf and black cottonwoods at the Lamar River Site, much like the Soda Butte Creek Site, indicated that cottonwood frequencies have decreased since the early 1900s; very low frequencies were indicated for black cottonwoods after the 1920s and for narrowleaf cottonwoods after the 1930s (Fig. 7d). The histogram of tree frequency vs. establishment date at the Buffalo Ranch Site (Fig. 7e) indicates that cottonwoods were also able to establish and grow into trees from the 1750s to 1920s and that recruitment continued through the 1920–1970s, with a maximum occurring in the 1940s. This pattern of recruitment was considerably different than that obtained for either of the nearby Lamar River or Soda Butte Creek Sites.

Tree mortality measurements at the Lamar River Site from 2001 to 2003 indicated that 73 trees were lost

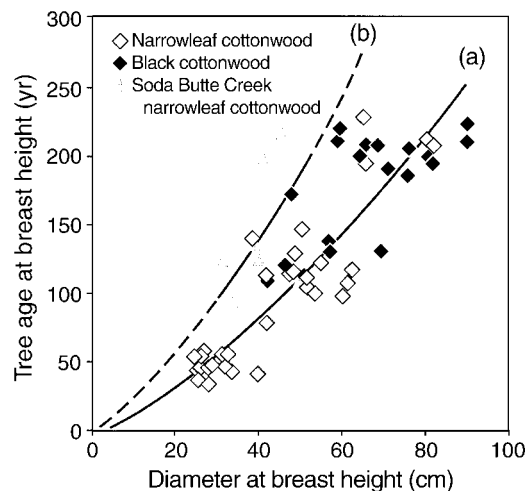


FIG. 6. Tree age (TA, yr) at breast height and diameter at breast height (dbh, cm) relationships for cottonwoods from (line a) the La Duke Spring, Devils Slide, Lamar River, and Buffalo Ranch Sites ($TA = 0.56 \text{ dbh}^{1.36}$, $r^2 = 0.82$, $n = 54$) and (line b) the Soda Butte Creek Site ($TA = 0.93 \text{ dbh}^{1.36}$, $r^2 = 0.12$, $n = 7$).

between 2001 and 2002, with an additional six trees lost by the summer of 2003. A major channel adjustment at the head of the Lamar River Site occurred during snowmelt flows in the spring of 2002 and removed 68 trees, nearly all of which were black cottonwoods. An additional five cottonwoods were eroded from this location in the spring of 2003. Of the remaining tree mortality, four died because of bank erosion at a downstream location, one was killed by beaver (*Castor canadensis*), and another had a shattered bole (due to a large amount of interior decay). Thus, of the original 700 cottonwoods ≥ 5 cm dbh, 11% have been lost in only two years.

DISCUSSION

Consistent with the long-term declines in woody browse species (e.g., upland aspen and riparian willows) that have been well documented for Yellowstone's northern range (Kay 1990, NPS 1997, Meagher and Houston 1998, Ripple and Larsen 2000, NRC 2002a, Barmore 2003), results of this study indicate that cottonwoods in the Soda Butte and Lamar Valleys have had a similar outcome. Below, I consider the potential roles of several factors that might have contributed to this decline: (a) disturbance regimes associated with climate and their potential effect on the establishment of young cottonwoods, and (b) the intertwined roles of park management, wolves, and ungulate herbivory upon long-term cottonwood recruitment in the northern range.

Disturbance regimes and cottonwood recruitment

Long-term shifts in climate and weather patterns have often been highlighted as a possible mechanism for causing reduced establishment of willows and aspen in the northern range (Houston 1982, Singer et al. 1994, Romme et al. 1995, NPS 1997, Singer et al. 1998). Others, however, have been unable to demonstrate a climate/weather effect or have concluded that suggested changes in climate are insufficient to have a major influence on deciduous woody species (Wagner et al. 1995, Chadde and Kay 1996, Kay 1997, Ripple and Larsen 2000, NRC 2002a, Beschta 2003, Larsen and Ripple 2003). While a number of interacting atmospheric variables (e.g., temperature, humidity, snowfall, precipitation) comprise regional climatic patterns, ecological processes associated with high flows (e.g., hydrochory, geomorphic disturbance, water availability, vegetation exclusion) often have an important influence on the establishment of riparian cottonwoods (Braatne et al. 1996, Patten 1998, Rood et al. 2003). Thus, annual peak flows were utilized in this study to index short- and long-term climate effects upon cottonwood reproduction over the period of recorded flows (i.e., from 1911 to 2002).

If high flows are an influential mechanism for increased cottonwood seedling establishment, relatively high levels of establishment should have been expected

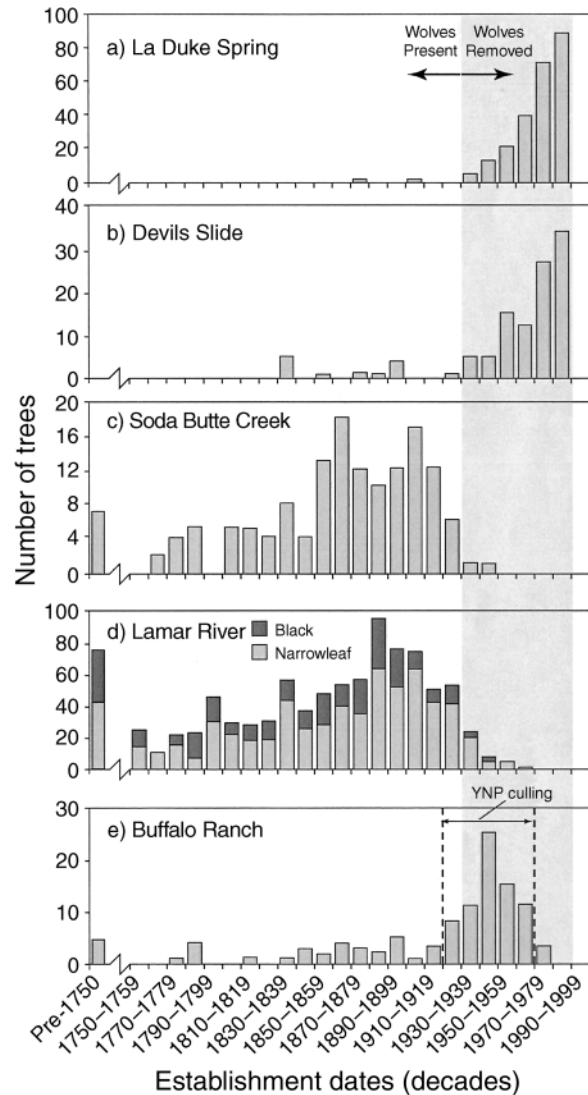


FIG. 7. Frequency distributions of cottonwood establishment dates for trees ≥ 5 cm in diameter at breast height (dbh) at five study sites in the northern Yellowstone elk winter range.

in the northern range during the periods 1911–1928 and 1971–1997 due to the occurrence of high peak flows (i.e., return periods of ≥ 10 yr, Fig. 4). However, relatively high rates of establishment were not found in the patterns of cottonwood recruitment for these two high-flow periods (Fig. 7), with the exception of the 1970s and 1980s for the La Duke Spring and Devils Slide Sites. While high flows during these two decades may have contributed to seedling germination at the La Duke Spring and Devils Slide Sites, Fig. 7a, b indicate cottonwood recruitment also occurred in earlier decades. When all sites are considered, regional climatic fluctuations or patterns (as indexed by the occurrence of relatively large peak flows) do not appear to represent an important or consistent mechanism for

explaining patterns of cottonwood recruitment in the northern range. Similarly, the NRC (2002) concluded that the effects of climate on vegetation in the northern range were of much less importance than the effects of herbivores.

Wildfire can also have an important effect on the processes, functions, and characteristics of forest and range ecosystems of the American West (Pyne 1982, Brown et al. 1995, Turner et al. 2003). However, for the decades prior to 1988, fires in the northern range were small, infrequent, and confined to upland areas. Even the major fires of 1988 that burned much of the upper Lamar Basin and other portions of the Park did not burn any of the sites used in this study (NPS 2001). Thus, it is unlikely that fire has been a significant factor affecting the historical patterns of cottonwood recruitment evaluated in this study.

Of the nearly 150 000 young cottonwood seedlings (≥ 20 cm in height and < 5 cm dbh) estimated to be present along the Lamar River in 2002, many may have become established during the large peak flow events of 1996 and 1997 that eroded channels and created large areas of bare alluvium. However, inspection of a chronosequence of historical aerial photographs of the Lamar Valley from 1954 to 1998 points to an increasingly common occurrence of channel changes and exposed alluvial substrates in the years preceding 1996. Similarly, Keigley (1998) found ~ 3000 young cottonwoods in a 1992 field study near the confluence of Soda Butte Creek and the Lamar River. Given that the periodic occurrence of high flows has been part of the flow history of the Yellowstone River and its tributaries prior to 1996, that aerial photos prior to 1996 indicate bare substrates suitable for cottonwood seedlings were commonly available, and that significant numbers of young cottonwoods were documented in the early 1990s (Keigley 1998) as well as more recently (this study), it would appear that cottonwood seedling establishment has likely been an ongoing occurrence for the Lamar River Site. For every cottonwood tree ≥ 5 cm dbh at this site, > 200 young cottonwoods ≥ 20 cm tall were present in 2002, indicating a high potential for future recruitment.

At the Buffalo Ranch Site, where young cottonwoods were also enumerated in 2002, inspection of the tributary channels on the alluvial fan indicated little evidence of widespread scouring or alluvial deposits from flow events of recent years. Most of the young cottonwood plants were classified as originating from root sprouts (over 70% of the total), indicating that asexual reproduction was the predominant mechanism for young cottonwood establishment. For every cottonwood tree ≥ 5 cm dbh at this site, approximately five young cottonwoods currently exist.

Field observations indicated that young cottonwoods were also common at the remaining three sites. Since cottonwoods are prolific seed producers and can also be proficient at growing root sprouts (Braatne et al.

1996), it is not surprising that large numbers of young cottonwoods were either measured or observed at all study sites.

Height measurements of young cottonwoods at the Lamar River and Buffalo Ranch Sites indicated all were < 260 cm in height, with the vast majority < 100 cm. These restricted heights occurred independently of whether seedlings or root sprouts predominated, of the geomorphic surface upon which young cottonwoods were growing (i.e., the floodplains and pointbars of the Lamar River vs. the steeper gradient distributary channels of the Rose Creek alluvial fan), or of time: the 1992 study by Keigley (1998) vs. this study. Apparently, persistent (year-after-year) herbivory has been able to prevent young cottonwoods from growing above the browse height of elk, and thus taller seedlings/saplings are absent from these sites.

Wolves, elk, and cottonwood recruitment

Ungulate exclosures, which have been used for assessing long-term effects of browsing on aspen, willows, and other hardwoods, were not available for assessing cottonwood recruitment in Yellowstone's northern range. However, the La Duke Spring and Devils Slide Sites had been selected as refugia sites, since ungulate access was impeded at each site by a combination of the Yellowstone River on one side and steep, terrace banks, and a highway with guardrails on the other. The relatively rapid decrease in number of trees with increasing diameter class at the La Duke Spring and Devils Slide Sites (Fig. 5a, b) reflects a balance between factors influencing rates of recruitment and tree mortality. Since both stands are located within a few meters of the Yellowstone River, it is not known what effects the periodic occurrence of high flows and associated erosion/deposition, the use of cottonwoods as a source of food by beaver (beaver cuttings were common at both sites), or additional factors were having on the observed diameter distributions. However, even though these sites represented very different geomorphic surfaces (pointbar vs. terrace side slope), results indicated that both have been able to successfully recruit cottonwoods in the 5–30 cm dbh classes.

In contrast to the La Duke Spring and Devils Slide Sites, cottonwood stands at the remaining three sites were relatively accessible by elk. A distinguishing feature of the diameter distributions at the Soda Butte Creek and Lamar River Sites (Fig. 5c, d), relative to the La Duke Spring and Devils Slide Sites, was the nearly total lack of trees in the 5–30 cm diameter classes. Since cottonwoods at the Soda Butte Creek and Lamar River Sites comprised multiple stands that were widely spaced and occupied a variety of geomorphic surfaces (e.g., pointbars, floodplains), the lack of small-diameter classes represents a major departure from normal stand development. The stand structure for the Buffalo Ranch Site (alluvial fan) similarly shows a general deficiency of small-diameter classes (Fig. 5e).

Although histograms of tree frequency vs. dbh class provide an important perspective of stand development patterns within and between sites, relationships between tree age and diameter were needed to identify temporal trends in tree recruitment. Since large-diameter trees were nearly absent from the La Duke Spring and Devils Slide Sites, trees in the range of 25–30 cm were utilized for increment coring at these sites. The sampling strategy employed at the Soda Butte Creek, Lamar River, and Buffalo Ranch Sites was to core relatively large trees to ensure any relationship between tree age and dbh was “well-anchored” with larger diameter classes. Given the large variability between tree age and dbh normally encountered for cottonwoods (e.g., Merigliano 1996, Beschta 2003), the application of an “age vs. diameter” relationship to uncored trees is not expected to provide a precise estimate of establishment dates for individual trees, especially older trees. However, the approach is relatively efficient for assessing general patterns of cottonwood recruitment over time when the entire population of tree diameters at a given site is measured, as in this study.

Increment cores obtained in this study included both narrowleaf and black cottonwood growing on a variety of geomorphic surfaces within the northern range. Since all trees ≥ 5 cm in dbh had been recorded at each site, regression equations of tree age vs. dbh were only useful for estimating establishment dates for the decades prior to 1990. With the exception of cottonwoods at the Soda Butte Creek Site, tree age vs. dbh data were incorporated into a single equation that was very similar to that used for narrowleaf cottonwoods at “meander sites” in an earlier study by Beschta (2003). However, the linear relationship for “open-grown” narrowleaf cottonwoods growing on floodplains (Beschta 2003) was not supported by the increment core data obtained in this study.

Histograms of tree frequencies and establishment dates at the La Duke Spring and Devils Slide Sites confirm that cottonwood recruitment has been occurring for at least a half-century prior to 1990 (Fig. 7a, b). This result is consistent with the hypothesis that cottonwood recruitment at refugia sites has not been prevented by either elk browsing or climate fluctuations. In contrast, a general lack of cottonwood recruitment was found at the Soda Butte Creek and Lamar River Sites from approximately the 1930s to the present (Fig. 7c, d). Results for these two sites are consistent with a hypothesis of increased browsing pressure by elk following the extirpation of wolves from Yellowstone National Park (Ripple and Larsen 2000, Beschta 2003, Ripple and Beschta 2004). Furthermore, even though elk numbers had been reduced to relatively low levels in the mid-1960s, in the hopes of minimizing impacts to vegetation and to improve general range conditions, cottonwood recruitment was unable to occur. With the loss of wolves, even a reduced population

of elk was apparently able to browse deciduous woody species unhampered by predation risk, and thus the recruitment of cottonwoods has been curtailed over a period of many decades.

At the Buffalo Ranch Site, the frequency distribution of tree numbers vs. establishment date indicates that the 1920–1960s represented a period of relatively high cottonwood recruitment (Fig. 7e). The timing of this recruitment also corresponds to a period of human activities associated with the ranching (of bison) and culling (of bison and elk) that apparently kept elk away from the Rose Creek alluvial fan (upon which the ranch buildings and corrals were situated) so that significant numbers of young cottonwood were able to “escape” above the browsing level of elk and to ultimately become trees.

It is important to note the pattern of cottonwood recruitment at all sites during the two decades (i.e., 1970s and 1980s) immediately following the stoppage of elk culling efforts by the Park Service. At the La Duke Spring and Devils Slide Sites where ungulate access was impaired by terrain and cultural features, high levels of cottonwood recruitment occurred during both decades (Fig. 7a, b). However, at the Soda Butte Creek and Lamar River Sites (Fig. 7c, d), where young cottonwood plants were easily accessible to ungulates and where large numbers of elk gathered during wintertime conditions (Fig. 1a), cottonwood recruitment was nonexistent. Similarly, at the Buffalo Ranch Site (Fig. 7e), where bison and elk management activities had been terminated after 1968, only three trees recruited during these two decades.

CONCLUSIONS

The widespread occurrence of young cottonwoods (measured at the Lamar River and Buffalo Ranch Sites as well as observed at the other three sites), earlier measurements of young cottonwoods by Keigley (1997, 1998), inspection of historical aerial photos for availability of sites with bare substrates, and the fact that cottonwoods generally are prolific producers of seed and have the capability to reproduce by root sprouts, indicate that a lack of young seedlings and/or root sprouts is unlikely to have been a factor limiting cottonwood recruitment in Yellowstone’s northern range. In addition, results from the La Duke Spring and Devils Slide refugia sites indicate that the climatic record (as indexed by peak flows) during the last half-century was not a major factor restricting young cottonwood establishment and eventual recruitment. Furthermore, results from these refugia sites are consistent with those from other northern range enclosure studies where woody browse species growing inside enclosures (protected from herbivory) have also been able to establish and grow into taller growth forms, regardless of climatic conditions (e.g., Kay 2001, Barmore 2003).

Because of the importance of cottonwoods for providing multiple riparian functions, the termination of

recruitment over a period of many decades not only represents a major ecological loss associated with riparian plant communities in the northern range, but is also indicative of browsing/grazing impacts to other riparian species. If cottonwood recruitment into the future continues to be prevented by high levels of ungulate browsing, the continued functional degradation of northern range riparian systems should be expected and, over time, the extirpation of cottonwoods from portions of the northern range is eventually likely to occur.

Overall, study results support a conclusion that the removal of wolves triggered a widespread reduction in the recruitment of riparian cottonwoods in the winter range of Yellowstone's northern elk herd. The suppressed/curtailed recruitment of this era is firmly etched in the histograms of tree frequencies, by diameter class and establishment date. The lack of small and intermediate size classes are also visually evident in many northern range cottonwood stands. Since the removal of wolves in the 1920s seems to have initiated the precipitous downturn in cottonwood recruitment via a trophic cascade involving wolves and elk, the return of this keystone predator in 1995–1996 may provide the greatest promise for renewed cottonwood recruitment and the eventual recovery of riparian plant communities.

ACKNOWLEDGMENTS

The author appreciates various comments/suggestions provided by J. Boone Kauffman, William J. Ripple, two anonymous reviewers, and an associate editor.

LITERATURE CITED

- Allin, C. W. 2000. The triumph of politics over wilderness science. Pages 180–185 in *Proceedings: Wilderness Science in a Time of Change*. Report RMRS-P-15, Volume 2. USDA Forest Service, Ogden, Utah, USA.
- Avery, T. E., and H. E. Burkhart. 2002. Forest measurement. McGraw Hill, New York, New York, USA.
- Barmore, W. J. 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park: research and synthesis 1962–1970. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.
- Beschta, R. L. 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. *Ecological Applications* **13**:1295–1309.
- Beschta, R. L., R. E. Bilby, G. W. Brown, L. B. Holtby, and T. D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Pages 191–232 in E. O. Salo and T. W. Cundy, editors. *Streamside management: fisheries and forestry interactions*, proceedings of a symposium, 12–14 February, 1986. Contribution 57. University of Washington, Institute of Forest Resources, Seattle, Washington, USA.
- Braatne, J. H., S. B. Rood, and P. E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. Pages 57–85 in R. F. Stettler, H. D. Bradshaw, Jr., P. E. Heilman, and T. M. Hinkley, editors. *Biology of Populus and its implications for management and conservation*. National Research Council, Ottawa, Ontario, Canada.
- Brown, J. K., R. W. Mutch, C. W. Spoon, and R. H. Wakimoto, technical coordinators. 1995. *Proceedings of the Symposium on Fire in Wilderness and Park Management*. USDA Forest Service, General Technical Report, INT-GTR-320. Ogden, Utah, USA.
- Chadde, S. 1989. Willows and wildlife of the northern range, Yellowstone National Park. Pages 168–169 in R. E. Gresswell, B. A. Barton, and J. L. Kershner, editors. *Practical approaches to riparian resource management: proceedings of an educational workshop*, 8–12 May 1989, Billings, Montana. U.S. Bureau of Land Management, BLM-MT-PT-89-001-4359. Billings, Montana, USA.
- Chadde, S., and C. E. Kay. 1996. Tall-willow communities on Yellowstone's northern range: a test of the "natural regulation" paradigm. Pages 165–184 in F. J. Singer, editor. *Effects of grazing by wild ungulates in Yellowstone National Park*. National Park Service Technical Report, NPS/NRYELL/NRTR/96-01. Denver, Colorado, USA.
- Clayton, S. R. 1996. Factors influencing black cottonwood (*Populus trichocarpa*) recruitment on the upper Clark Fork River, western Montana. Thesis. University of Montana, Missoula, Montana, USA.
- Cummins, K. W. 1974. Stream ecosystem structure and function. *BioScience* **24**:631–641.
- Dobkin, S. D., F. J. Singer, and W. S. Platts. 2002. Ecological condition and avian response in willow, aspen, and cottonwood communities of the National Elk Refuge, Jackson, Wyoming. High Desert Research Institute, Bend, Oregon, USA.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones: focus on links between land and water. *BioScience* **41**:540–551.
- Grimm, R. L. 1939. Northern Yellowstone winter range studies. *Journal of Wildlife Management* **8**:329–334.
- Heilman, P. E. 1996. Ecology and watershed functions of western cottonwoods. Pages 3–5 in *Natural Resource News Special Edition*. Eastern Oregon State College, La Grande, Oregon, USA.
- Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. Macmillan, New York, New York, USA.
- Kauffman, J. B., J. Mahrt, L. A. Mahrt, and W. D. Edge. 2001. Wildlife of riparian habitats. Pages 361–388 in D. H. Johnson and T. A. O'Neil, editors. *Wildlife-habitat relationships in Oregon and Washington*. Oregon State University Press, Corvallis, Oregon, USA.
- Kay, C. E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural-regulation" paradigm. Dissertation. Utah State University, Logan, Utah, USA.
- Kay, C. E. 1997. Viewpoint: ungulate herbivory, willows, and political ecology in Yellowstone. *Journal of Range Management* **50**:139–145.
- Kay, C. E. 2000. False gods, ecological myths, and biological reality. Pages 238–261 in C. E. Kay and R. T. Simmons, editors. *Wilderness and political ecology*. University of Utah Press, Salt Lake City, Utah, USA.
- Kay, C. E. 2001. Long-term aspen exclosures in Yellowstone ecosystem. Pages 225–240 in W. D. Shepperd, D. Binkley, D. L. Bartos, and T. J. Stohlgren, compilers. *Sustaining aspen in western landscapes: symposium proceedings*, 13–15 June 2000, Grand Junction, Colorado. USDA Forest Service, RMRS-P-18. Fort Collins, Colorado, USA.
- Keigley, R. B. 1997. An increase in herbivory of cottonwood in Yellowstone National Park. *Northwest Science* **71**:127–136.
- Keigley, R. B. 1998. Architecture of cottonwood as an index of browsing history in Yellowstone. *Intermountain Journal of Sciences* **4**:57–67.
- Larsen, E. J., and W. J. Ripple. 2003. Aspen age structure in the northern Yellowstone ecosystem, USA. *Forest Ecology and Management* **179**:469–482.
- Lovaas, A. L. 1970. People and the Gallatin elk herd. Montana Fish and Game Department, Helena, Montana, USA.

- Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. *Wetlands* **18**:634–645.
- Meagher, M., and D. B. Houston. 1998. *Yellowstone and the biology of time: photographs across a century*. University of Oklahoma Press, Norman, Oklahoma, USA.
- Merigliano, M. F. 1996. Ecology and management of the South Fork Snake River cottonwood forest. USDI Bureau of Land Management, Technical Bulletin 96-9. Boise, Idaho, USA.
- NPS (National Park Service). 1956. Management plan for northern elk herd, Yellowstone National Park, 30 November 1956. USDI, National Park Service, Yellowstone National Park, Wyoming, USA.
- NPS (National Park Service). 1957. Management plan for northern elk herd, Yellowstone National Park, 27 November 1957. USDI, National Park Service, Yellowstone National Park, Wyoming, USA.
- NPS (National Park Service). 1958. Management plan for northern elk herd, Yellowstone National Park, 21 November 1958. USDI, National Park Service, Yellowstone National Park, Wyoming, USA. 7 pp.
- NPS (National Park Service). 1959. Our wildlife legacy, 30 January 1959. USDI, National Park Service, Yellowstone National Park, Wyoming, USA. 5 pp.
- NPS (National Park Service). 1961. Management of Yellowstone's northern elk herd, 15 December 1961. USDI, National Park Service, Yellowstone National Park, Wyoming, USA.
- NPS (National Park Service). 1997. *Yellowstone's northern range: complexity and change in a wildland ecosystem*. National Park Service, Yellowstone National Park. USDI, Yellowstone National Park, Mammoth Hot Springs, Wyoming, USA.
- NPS (National Park Service). 2001. *Yellowstone National Park fire history*. National Park Service, Yellowstone National Park, Fire Management Office, Mammoth Hot Springs, Wyoming, USA.
- NRC (National Research Council). 2002a. *Ecological dynamics on Yellowstone's northern range*. National Academy Press, Washington, D.C., USA.
- NRC (National Research Council). 2002b. *Riparian areas: function and management*. National Academy Press, Washington, D.C., USA.
- Ohmart, R. D. 1996. Historical and present impacts of livestock grazing on fish and wildlife resources in western riparian habitats. Pages 245–279 in P. R. Krausman, editor. *Rangeland wildlife*. Society for Range Management, Denver, Colorado, USA.
- Patten, D. T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* **18**:498–512.
- Peek, J. M., A. L. Lovaas, and R. A. Rouse. 1967. Population changes within the Gallatin elk herd, 1932–65. *Journal of Wildlife Management* **31**:304–316.
- Pyne, S. J. 1982. *Fire in America: a cultural history of wildland and rural fire*. University of Washington Press, Seattle, Washington, USA.
- Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* **184**:299–313.
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk restructure ecosystems? *Forest Ecology and Management* **54**:755–766.
- Ripple, W. J., and R. L. Beschta. *In press*. Refugia from browsing as reference sites for restoration planning. *Western North American Naturalist*.
- Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* **95**:361–370.
- Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in the northern Yellowstone National Park. *Ecology* **76**:2097–2106.
- Rood, S. B., J. H. Braatne, and F. M. R. Hughes. 2003. Eco-physiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiology* **23**:1113–1124.
- Schullery, P., and L. Whittlesey. 1992. The documentary record of wolves and related wildlife species in Yellowstone National Park area prior to 1882. Pages 1–174 in J. D. Varley and W. G. Brewster, editors. *Wolves for Yellowstone? A report to the United States Congress*. Volume IV. Research and analysis. National Park Service, Yellowstone National Park. Mammoth Hot Springs, Wyoming, USA.
- Sedell, J. R., and R. L. Beschta. 1991. Bringing back the “bio” in bioengineering. *American Fisheries Society Symposium* **10**:160–175.
- Shafer, C. L. 2000. The northern Yellowstone elk debate: policy, hypothesis, and implications. *Natural Areas Journal* **20**:342–359.
- Singer, F. J. 1996. Differences between willow communities browsed by elk and communities protected for 32 years in Yellowstone National Park. Pages 279–290 in F. J. Singer, editor. *Effects of grazing by wild ungulates in Yellowstone National Park*. ISDI, National Park Service, Natural Resource Information Division, Denver, Colorado, USA.
- Singer, F. J., L. C. Mack, and R. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. *Journal of Range Management* **47**:435–443.
- Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: an assessment of a management of native ungulates by natural regulation, 1968–1993. *Wildlife Society Bulletin* **26**:375–390.
- Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment* **1**:351–358.
- Wagner, F. H., R. B. Keigley, and C. L. Wambolt. 1995. Comment: ungulate herbivory of willows on Yellowstone's northern winter range: response to Singer et al. (1994). *Journal of Range Management* **48**:475–477.
- Weaver, J. 1978. *The wolves of Yellowstone*. National Park Service, Yellowstone National Park, Natural Resources Report 14. Mammoth Hot Springs, Wyoming, USA.
- Whitham, T. G., K. D. Floate, G. D. Martinsen, E. M. Driebe, and P. Keim. 1996. Ecological and evolutionary implications of hybridization: *Populus*–herbivore interactions. Pages 247–275 in R. F. Stettler, H. D. Bradshaw, Jr., P. E. Heilman, and T. M. Hinckley, editors. *Biology of Populus and its implications for management and conservation*. NRC Research Press, Ottawa, Ontario, Canada.
- Wigington, P. J., Jr., and R. L. Beschta, editors. 2000. *Riparian ecology and management in multi-land use watersheds*. American Water Resources Association, TPS-00-2. Middleburg, Virginia, USA.