

COTTONWOODS, ELK, AND WOLVES IN THE LAMAR VALLEY OF YELLOWSTONE NATIONAL PARK

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Abstract. In September 2001, the diameter at breast height (dbh) of all cottonwood (*Populus* spp.) ≥ 5 cm in diameter was measured within a 9.5-km² section of the Lamar Valley (elevation ~ 2000 m), in northeastern Yellowstone National Park. A total of 700 trees were measured of which 71% were narrowleaf cottonwood (*P. angustifolia*) and 29% were black cottonwood (*P. trichocarpa*). Slightly more than half of the narrowleaf trees were growing on point bar landforms at three major meander bends of the Lamar River, with the remainder occurring in small groves spread across various floodplain surfaces within the valley. Almost all of the black cottonwood occurred on point bars at only two of the meander bend locations. Tree diameters for both species ranged mostly between 30 and 110 cm with a nearly total absence of cottonwoods between 5 and 29 cm in diameter. Age vs. diameter relationships were developed and used as a basis for estimating establishment dates for all narrowleaf cottonwoods. These relationships, in conjunction with the dbh data, indicated an absence of cottonwood recruitment (i.e., growth of seedlings/suckers into ≥ 5 -cm diameters trees) over approximately the last 60 years. The paucity of cottonwood recruitment appears to have occurred independently of fire history, flow regimes, channel migrations, or factors affecting normal stand development, but over the same period of time that wolves (*Canis lupus*) had been extirpated from Yellowstone National Park. With the removal of this wide-ranging and keystone predator, elk (*Cervus elaphus*) populations were able to browse riparian plant communities unaffected by wolves.

Key words: cottonwood; elk; riparian; trophic cascades; wolves; Yellowstone National Park (USA).

INTRODUCTION

Over the last three decades, there has been growing recognition by the scientific community of the important functions and values of riparian systems (e.g., Johnson et al. 1985, Koehler and Thomas 2000, Wigginton and Beschta 2000, National Research Council 2002b). Functions provided by riparian plant communities include streambank stability (Rutherford et al. 1999), hydraulic resistance during overbank flows, enhanced deposition of organic matter and fine sediment (Sedell and Beschta 1991), allochthonous inputs and general food web support for aquatic and riparian organisms (Cummins 1974), thermal moderation of water temperatures and riparian microclimates (Beschta et al. 1987), large wood recruitment (Harmon et al. 1986, Maser et al. 1988), nutrient transformations and cycling (Gregory et al. 1991), and others (Knutson and Naef 1997). Even though riparian areas typically occupy a small percentage of a landscape, they are noted for their high biological productivity (Kauffman and Krueger 1984). For example, wildlife values of riparian habitats in the western United States, as indicated by measures of species density, richness, biodiversity, biomass, and number of rare species, are often much greater than those of adjacent uplands (Ohmart 1996).

The perpetuation of obligate riparian plant species along streams and rivers in the American West typically occurs in response to seasonal surface and groundwater regimes, availability of favorable surfaces for germination, and abundant seed sources (Patten 1998, 2000). Thus, variation in flows is central not only to the structuring of the physical environment of a riverine system, but also to the character and composition of their riparian plant communities (Baker 1990, Scott et al. 1997, Michener and Haeuber 1998). Early successional woody species, such as cottonwood (*Populus* spp.) typically regenerate on newly scoured/deposited alluvium because of their high seed production, seed release during seasons of normal high flow, lack of seed dormancy, intolerance of shade, and tolerance of nutrient scarcity and sediment accumulation (Braatne et al. 1996, Scott et al. 1997). In other instances, cottonwood may asexually reproduce by root sprouting and suckers.

Narrowleaf cottonwood (*P. angustifolia*) and black cottonwood (*P. trichocarpa*), the two species of principal interest in this study, are noted as prolific seeders during periods of seasonally high snowmelt runoff, with seedling establishment often occurring on bare alluvial substrates during the recession limb of a snowmelt hydrograph (Merigliano 1996, Dykaar and Wigginton 2000). Even though some seedling establishment may occur in most years, the likelihood of large numbers of seedlings growing into larger size classes

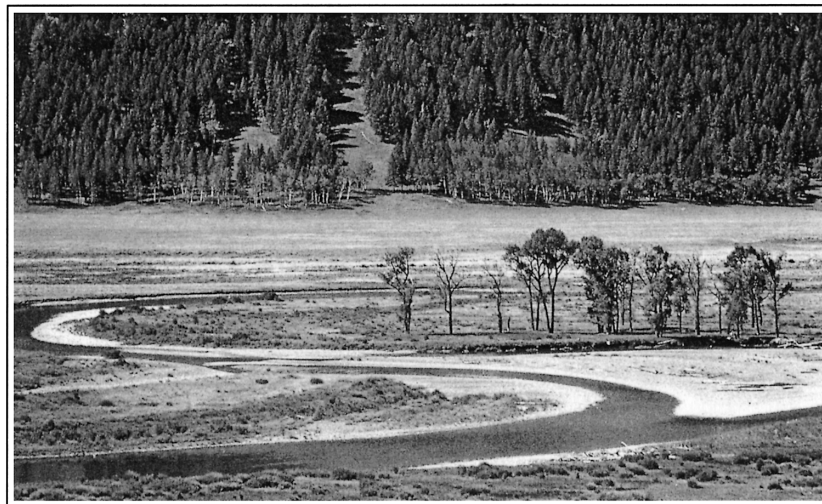


FIG. 1. Cottonwood grove along the Lamar Valley that has not reproduced successfully since early in the 20th century (no. YEL 35049, Yellowstone National Park photo archives).

(e.g., saplings, mature trees) tends to be infrequent. Peak flows with a ≥ 5 -yr return period are commonly associated with widespread cottonwood seedling establishment (Baker 1990, Wondzell 1992, Mahoney and Rood 1998), although long-term survival of seedlings also depends on the maintenance of seasonally high water tables (Patten 2000). For riparian plant communities that have developed with relatively unpaired flow and sediment regimes, such as along the Lamar River in the northeastern portion of Yellowstone National Park (YNP), periods of high flow would generally provide a disturbance regime important to their long-term establishment, growth, and sustainability.

Since cottonwoods may live longer than many of the deciduous woody species found in riparian areas, they provide an opportunity for developing a long-term perspective regarding patterns of recruitment, as well as factors affecting these patterns. Such assessments could also have important implications for associated riparian species that are shorter lived. Furthermore, in recent years it has been observed (Keigley 1997, 1998, Yellowstone National Park 1997) that cottonwood recruitment (i.e., the growth of established seedlings/suckers into trees) was no longer occurring in the northeastern portion of YNP (Fig. 1). Thus, this study was undertaken (1) to identify the extent to which cottonwood recruitment has not been occurring and (2) to better understand potential linkages between patterns of cottonwood recruitment and environmental factors such as fire, weather patterns, normal stand development, ungulate herbivory, and wolves (*Canis lupus*).

STUDY AREA

This study was conducted along a 9-km reach of the Lamar River (elevation ~ 2000 m) in northeastern YNP (Fig. 2). The study area extends from ~ 3 km downvalley of the Lamar Ranger Station (also known as

Buffalo Ranch) to 6 km upvalley of the ranger station and encompasses ~ 9.5 km² of valley bottom terrain. The ranger station (elevation, 1970 m) has an average annual precipitation of ~ 35 cm and an average 1 April snowpack water equivalent of 7 cm. In contrast, the Parker Peak SNOTEL site (elevation, 2865 m) at the head of the catchment has an average annual precipitation of 81 cm and an average 1 April snowpack water equivalent of 55 cm (Farnes et al. 1999).

Along the study reach, Pleistocene outwash deposits have created an expansive valley floor that ranges from 1 to 2 km in width. Within this broad valley setting, various groves of cottonwood reside on point bars or extend across existing and former floodplain surfaces. Floodplain soils are of sandy texture and variable thickness (mostly 0.5–1.5 m), and overlay coarse-textured (gravel and cobble) alluvium. Floodplain surfaces occur interspersed among glacial outwash deposits; the later typically characterized as having thin soils and a high proportion of gravel and cobble particles at or near the soil surface.

Historical aerial photographs taken between 1954 and 1998 indicate that portions of the Lamar River have undergone accelerated lateral migration and changes in channel morphology in recent decades; hence, the degree of hydrologic connectivity (i.e., the relative frequency of overbank flows) associated with floodplain landforms may have been similarly changing over this period. Although some floodplain surfaces continue to experience frequent overbank flows, others experience them less frequently or not at all because of channel migration and other channel adjustments (e.g., widening or incision).

METHODS

Since hydrologic disturbance regimes have been widely recognized as an important factor influencing

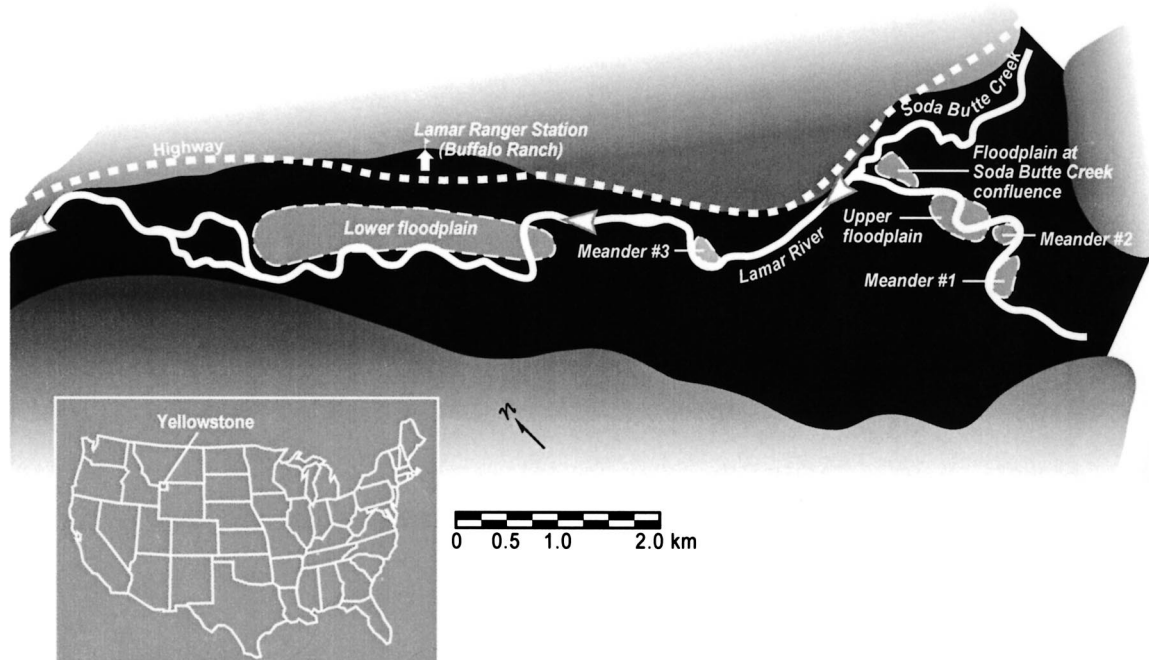


FIG. 2. Generalized study area map with approximate locations of the cottonwood groves evaluated in this study.

the establishment and growth of cottonwoods, flow records from two U.S. Geological Survey gaging stations were obtained to help evaluate long-term patterns of peak flows, with comparisons focusing primarily on flows having a ≥ 5 -yr recurrence interval. These stations include (1) the Lamar River near Tower Falls Ranger Station, Wyoming (no. 061880, elevation, 1830 m; drainage area, 1710 km²), and (2) the Clarks Fork of the Yellowstone River near Belfry, Montana (no. 062075, elevation, 1215 m; drainage area, 2990 km²). The Clarks Fork drains mountainous terrain immediately adjacent to and east of the Lamar River catchment. All field data were collected in September 2001.

Five belt transects were established across the study area to provide a general characterization of seedling densities (no./ha) and heights (m) that were commonly present in the Lamar Valley in 2001; the transects were not intended to provide a population estimate of total seedling numbers. Each transect was 2×30 m and typically oriented parallel to the river.

The species and diameter of all riparian cottonwoods ≥ 5 cm in diameter within the study area were also determined. Diameter at breast height (dbh), in centimeters, was measured using a Bitterlick Stick (Avery and Burkhart 2002); two measurements were made for each tree and then averaged. For a subset of 52 cottonwoods (ranging in dbh from 10 to 130 cm), tree circumferences were also measured using a diameter tape to assess the relative accuracy of the Bitterlick Stick methodology. Linear regression analysis indicated a nearly 1:1 relationship (slope of 0.98; $r^2 = 0.99$) for the two methods.

Since tree age (TA) is of primary importance in trying to understand historical patterns of cottonwood recruitment in the Lamar Valley, four independent approaches were used in an attempt to establish "TA vs. dbh" relationships. First, previously unreported tree ages (from analysis of increment cores) and circumferences for 56 open-grown narrowleaf cottonwood trees in the Lamar Valley, located near the confluence with Soda Butte Creek, were provided by R. Keigley (*unpublished data*). These previously unpublished data, obtained at a height of 0.3 m above the ground, were collected in 1992 from a cottonwood stand that has subsequently been lost because of lateral channel erosion associated with the Lamar River. Tree diameters at a height of 0.3 m ($D_{0.3}$) were calculated from the circumference measurements, and regression analysis was used to establish a relationship between TA and $D_{0.3}$.

In the second approach, 13 beaver-killed cottonwoods at the third meander site (Fig. 2) provided an opportunity to obtain, in a noninvasive manner, estimates of diameter growth rates. The cottonwood trees had been dead for some time, as indicated by characteristics of the bark (e.g., weathered appearance, easily dislodged, missing) and wood (e.g., sometimes partially rotted and decomposed, loss of structural integrity). However, weathering of the exposed beaver-cut surfaces also accentuated visual differences in winter/summer wood, so that groups of individual growth rings were often clearly evident. Ring counts made with a $10\times$ hand lens were obtained along short sections (usually 5–15 cm of radial distance) of the cut surface;

the radial distance (cm) of the center of each group of rings to the center of the tree was also measured. The measured rate of radial growth was doubled to obtain diameter growth rate for the woody portion of the bole, and then increased by 10% (based on measurements of narrowleaf cottonwood bark thicknesses at the site) to represent outside-bark diameter growth rates. Most beaver cutting occurred at a height of ~ 0.5 m, hence estimated growth rates represent diameter growth at this height. Regression analysis was used to establish a relationship between the diameter growth rate (G , cm/yr) and tree diameter at a height of 0.5 m ($D_{0.5}$, cm). Since $1/G$ represents the number of years required for a tree to accumulate 1 cm of diameter growth (i.e., yr/cm) at a given diameter, the regression equation was solved for $1/G$ at 1 cm diameter increments up to a $D_{0.5}$ of 45 cm (the maximum radial distance measured). The number of years associated with the $D_{0.5}$ for a given tree was then calculated by summing the number of years for each 1 cm of diameter less than or equal to the $D_{0.5}$ of interest. From these calculated tree ages and their respective $D_{0.5}$ measurements, regression analysis was again used to establish a relationship between TA and $D_{0.5}$.

To avoid coring cottonwoods within YNP and yet still attain information on representative growth rates, the third approach involved coring narrowleaf cottonwood trees outside of the YNP. The nearest narrowleaf cottonwoods outside of the park occur along the Clarks Fork of the Yellowstone River (elevation ~ 2100 m), ~ 30 km east of the Lamar Valley. The cottonwoods on the Clarks Fork site generally occupied sandy textured floodplain soils, although some of the smallest diameter classes had established on recent alluvial deposits with high gravel content. In contrast to cottonwood sites in the Lamar Valley where conifer competition is nearly nonexistent, an understory of dense conifer vegetation was present at this site and was beginning to overtop and suppress some of the existing cottonwood trees. A total of 34 increment cores were obtained; these cores were mounted onto wooden holders, air-dried, and sanded (400 grit). Annual rings were counted with a $10\times$ magnifying lens. Inspection of each dried core resulted in its exclusion whenever growth rings could not be clearly distinguished over most of the core length, or where cores were incomplete (e.g., heart rot).

Last, an age vs. diameter relationship for narrowleaf cottonwoods along the South Fork of the Snake River (elevations ~ 1530 – 1630 m) in eastern Idaho (M. F. Merigliano and M. L. Scott, *unpublished report*) was used to compare the results of locally derived data (the approaches described above). The Merigliano and Scott relationship was based on increment core analysis of over 550 trees.

The time required for an establishing narrowleaf cottonwood seedling to reach breast height (i.e., a height of 1.4 m) can be highly variable because of factors such as seasonal moisture and weather patterns, shad-

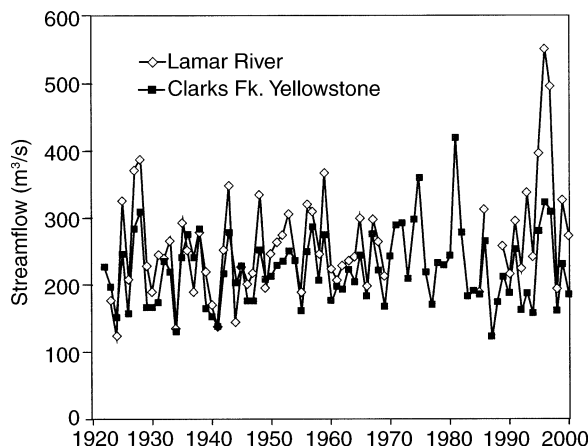


FIG. 3. Time series of annual peak flows for the Lamar River near Tower Falls stream gage and the Clarks Fork of the Yellowstone River stream gage over their respective periods of record.

ing and competition from adjacent plants, and intensity of browsing. Under conditions of severe browsing pressure, an average of approximately seven years was required for 0.3 m tall cottonwood seedlings to reach 1.0 m at the Soda Butte Creek confluence (Keigley 1997). Along the Salmon River in Idaho, where browsing was not a factor, six to eight years was generally required for black cottonwood seedlings to reach a height of 1.4 m (Merigliano 1996). Since all cottonwood tree diameters were measured at breast height in this study, an additional seven years was included in the age vs. diameter equations used for estimating establishment dates.

With the exception of a single tree from the Clarks Fork of the Yellowstone River data set of increment cores, none of the age vs. diameter relationships discussed above included any measurements of black cottonwood. Although the dbh of all black cottonwoods in the study area was measured, without an age/diameter relationship for this species I was thus unable to estimate establishment dates.

Finally, historical photographs from Meagher and Houston (1998) and Yellowstone National Park (1997) were used to help understand trends in the occurrence of riparian plant communities in the Lamar Valley over time. These photographs also provided an opportunity to qualitatively compare estimated cottonwood establishment dates (see *Results*) associated with some of the cottonwood groves in the Lamar Valley.

RESULTS

Peak flow history

Prior to the 1988 fires that burned large portions of the Lamar River watershed, the temporal pattern of peak flow magnitudes (Fig. 3) for the Lamar River and the Clarks Fork of the Yellowstone River gaging stations are similar. Before the fires, the Lamar River peak

TABLE 1. Cottonwood seedling densities and range of seedling heights for five belt transects (2×30 m) in the Lamar Valley study area, September 2001.

Transect no.	Approximate location and site description	Seedling density (no./ha)	Range of seedling heights (m)	Comments
1	point bar deposits adjacent to Lamar River at first meander site	13 200	0.2–1.2	nearby willows are 1.5–2.0 m tall
2	gravel deposits along Soda Butte Creek near confluence with Lamar River	4 000	0.1–0.5	approximately 20% of seedlings have been browsed over a period of several years
3	side-channel deposits within Lamar River floodplain, upvalley of Lamar Ranger Station	30 100	0.1–0.9	nearby cottonwood seedlings up to 1 m tall
4	gravel deposits along Lamar River, downvalley of Lamar Ranger station	11 200	0.2–0.7	many seedlings have been browsed during summer of 2001
5	gravel deposits along Lamar River, downvalley of Lamar Ranger Station	71 200	0.1–0.8	many seedlings have been browsed during summer of 2001

Note: Only cottonwood seedlings ≥ 0.1 m in height were counted in each transect.

flows averaged 114% of the Clarks Fork of the Yellowstone River. However, since 1988 the Lamar River peak flows have averaged 125% (an 11% increase) relative to those of the Clarks Fork of the Yellowstone River, indicating a hydrologic response following from the fires. Exceptionally high runoff from the Lamar River drainage, relative to the Clarks Fork of the Yellowstone River, occurred during 1995–1997 when peak flows for the Lamar River averaged nearly 137% (a 23% increase) relative to those for the Clarks Fork of the Yellowstone River. Based on annual series frequency analysis of all Lamar River peak flows prior to the 1988 fires ($n = 49$ yr), a 5-yr event is represented by a flow of ~ 305 m³/s.

Annual peak flows for the Clarks Fork of the Yellowstone River are included in Fig. 3 since (1) the period of record is nearly 30% longer than that of the Lamar River (i.e., 79 yr vs. 61 yr for Lamar River gage), (2) the period of record is continuous from 1922 to 2000, and (3) the year-to-year patterns of peak flow magnitudes are similar for the pre-1989 period of overlapping record (linear regression of peak flows prior to 1989 indicates an $r^2 = 0.71$). Based on annual series frequency analysis of all peak flows ($n = 79$) for the Clarks Fork of the Yellowstone River, a 5-yr event is ~ 275 m³/s.

Belt transects of seedling establishment

Five spatially distributed belt transects were established across the study area to indicate the general range in densities and heights of cottonwood seedlings (≥ 0.1 m in height) that existed in September of 2001. Since sites were selected based on the presence of cottonwood reproduction, they cannot be used to provide a population estimate of total seedling numbers within the study area or the proportion of gravel bars with seedlings.

Results from the belt-transect measurements (Table 1) indicate seedling densities varied from ~ 4000 – $70\,000$ seedlings per hectare. Cottonwood seedlings

usually occurred in relatively narrow bands, typically parallel to the river, and on exposed gravel deposits along channel margins and point bars. For example, two parallel bands, one 4–5 m wide and 50 m long and an adjacent band 4–5 m wide and 60 m long, were observed along the Lamar River in the downstream portion of the study area. The elevation of these and other bands of cottonwood seedlings relative to that of the Lamar River varied, but most occurred ~ 0.75 – 2 m above the baseflow water levels present in September 2001. Seedling heights were commonly in the range of 0.1–0.6 m. Rarely were cottonwood seedlings with heights of 1–2 m, or higher, encountered anywhere in the study area. Inspection of selected seedlings within each transect indicated that they were typically from one to five years in age. Seedlings that had begun growing in the spring/summer of 2001 were not included in the seedling counts.

Both narrowleaf and black cottonwoods are extensively clonal. However, the belt transects were located several tens or hundreds of meters from existing cottonwood groves and thus these transects represent seedling counts. Reproduction by suckering within existing cottonwood groves was seldom observed in the field.

Cottonwood diameter measurements

A total of 700 cottonwood trees with ≥ 5 cm dbh were measured within the study area. Of this total, 495 trees (71%) were narrowleaf cottonwood and 205 trees (29%) were black cottonwood (Table 2). Over half of the narrowleaf cottonwoods (i.e., 261 trees) occurred in relatively dense stands on point bar landforms associated with three major river meanders. The remaining narrowleaf cottonwoods occurred mostly on floodplain surfaces in relatively open groves consisting of 10–40 trees per grove. These groves, as well as several smaller groups and some isolated trees, were distributed spatially throughout much of the valley. General locations of the narrowleaf and black cottonwood sites

TABLE 2. General characteristics of riparian cottonwood sites in the Lamar Valley study area of northeastern Yellowstone National Park (see Fig. 2 for general site locations), September 2001.

Species, valley location	Site	Groves (no.)	Trees (no.)	Dbh, mean \pm SD (cm)	Estimated establishment dates, mean \pm SD (yr)
Narrowleaf cottonwood (<i>Populus angustifolia</i>)					
Upstream	first meander	4	135	53 \pm 17	1860 \pm 59
↓	second meander	1	26	41 \pm 8	1901 \pm 25
↓	upper floodplain	3	32	54 \pm 23	1910 \pm 36
↓	floodplain near Soda Butte Creek confluence	3	78	57 \pm 19	1905 \pm 29
↓	third meander	2	100	52 \pm 15	1866 \pm 53
Downstream	lower floodplain	~9	124	67 \pm 21	1889 \pm 32
Black cottonwood (<i>Populus trichocarpa</i>)					
Upstream	first meander	2	113	59 \pm 21	...
↓	second meander	2	87	69 \pm 16	...
↓	upper floodplain	1	3	64 \pm 9	...
↓	floodplain near Soda Butte Creek confluence
↓	third meander	1	2	83 \pm 14	...
Downstream	lower floodplain

Note: Dbh is diameter at breast height.

identified in Table 2 are shown in Fig. 2; each floodplain site contained more than one grove of trees.

Histograms of dbh for the narrowleaf and black cottonwoods in the Lamar Valley (Fig. 4) show that <2% of all measured cottonwoods had diameters between 5 and 29 cm; most diameters were between 30 and 110 cm. Narrowleaf cottonwoods with the largest diameters, and potentially the oldest trees, were typically found on floodplain sites. The vast majority of black cottonwoods, almost 98%, were found at the first and second meander sites (i.e., point bars) near the upstream end of the study area (Fig. 2).

Tree age (TA) and diameter (D) relationships

Regression analysis was used to establish general relationships between tree age and diameter for narrowleaf cottonwoods. Those relationships are summarized in Fig. 5 and individually discussed in the following paragraphs.

Lamar Valley floodplain near Soda Butte Creek confluence, YNP.—Regression analysis of ring counts (from increment cores) and tree circumference measurements collected in 1992 for open-grown narrowleaf cottonwood trees ranging from 13 to 75 cm in diameter

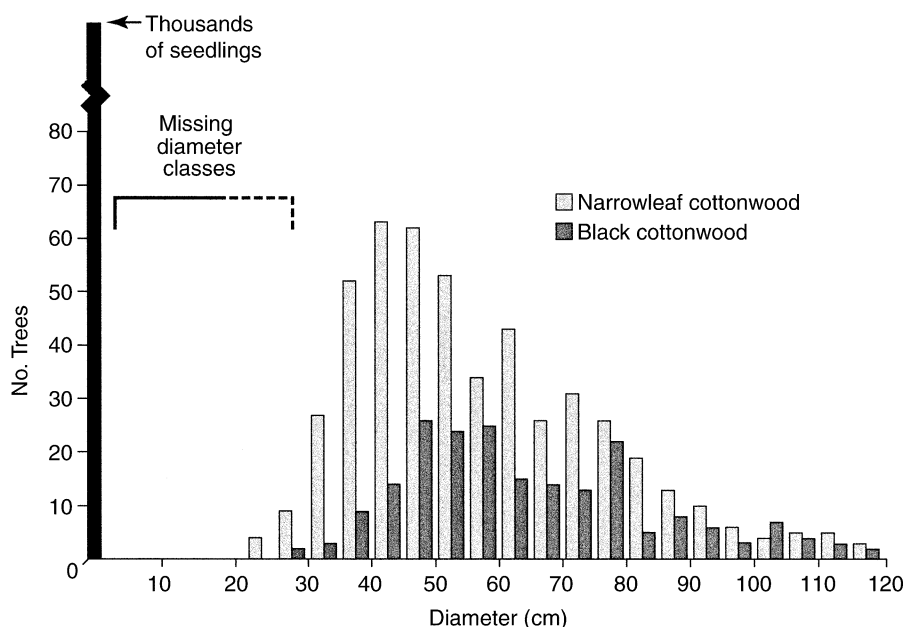


FIG. 4. Frequency distributions of cottonwood diameters (in 5-cm classes) for trees ≥ 5 cm in dbh (diameter at breast height) for the 9.5-km² Lamar Valley study area.

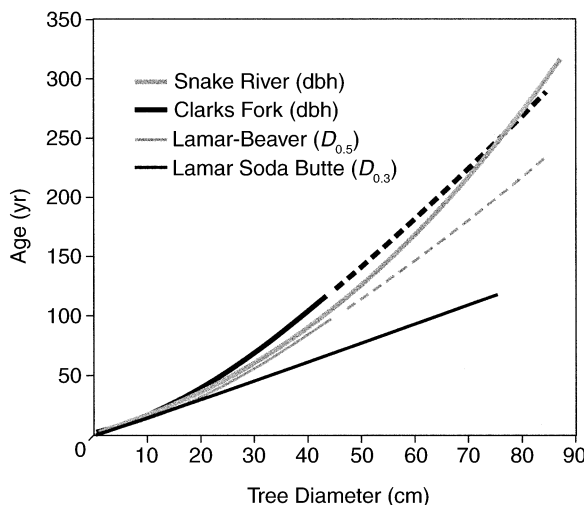


FIG. 5. Tree age (yr) as a function of tree diameter (cm) based on four different data sets (see *Methods* for detailed explanation). Solid lines represent the range of diameters used in development of an equation; dashed lines represent an extrapolation beyond that range.

resulted in the following relationship: $TA = 1.55 D_{0.3}$, $r^2 = 0.33$, $n = 56$.

Third meander site, Lamar Valley, YNP.—Regression analysis of growth ring counts and radial distance measurements from beaver-killed trees resulted in the following relationship between rate of diameter growth (DG, cm/yr) and tree diameter at a height of 0.5 m ($D_{0.5}$, cm): $DG = 0.90 e^{-0.03(D_{0.5})}$; $r^2 = 0.47$, $n = 27$. After this equation had been solved for $1/G$ at 1-cm increments of $D_{0.5}$ to determine the total number of years associated with a given tree diameter, regression analysis was used to obtain the following TA vs. $D_{0.5}$ relationship for tree diameters between 7 and 45 cm (the range of diameters represented in the original field measurements): $TA = 0.56 D_{0.5}^{1.37}$.

Clarks Fork of the Yellowstone River, Wyoming.—Of the original 34 cores, six cores eventually were considered unusable. For example, cores for the two largest trees (i.e., 49 and 61 cm dbh) were not used because the trees had rotten centers and the resultant core lengths were inadequate for estimating tree age. For the remaining 28 cottonwood cores (27 narrowleaf and 1 black cottonwood), ranging between 8 and 43 cm in dbh, regression analysis was used to establish the following relationship: $TA = 0.66 dbh^{1.37}$, $r^2 = 0.88$, $n = 28$.

South Fork of the Snake River, Idaho.—A TA vs. dbh relationship for narrowleaf cottonwoods (M. F. Merigliano and M. L. Scott, *unpublished report*) provided an opportunity to compare the preceding results with a data set that was much larger (both in number of trees and the overall range of diameters evaluated); the range of dbhs represented in their analysis was from 2 to 87 cm. Their relationship was as follows: $TA = 2.62 dbh + 0.191 dbh^2$, $r^2 = 0.56$, $n = 551$.

Summary of tree age vs. diameter relationships.—Regardless of measurement height or site conditions, all relationships provide similar estimates of narrowleaf cottonwood tree ages at the smaller diameters (e.g., generally those <30 cm). However, for larger diameter trees, the relationship for the open-grown floodplain trees along the Lamar River floodplain (near the Soda Butte Creek confluence) diverges from the other relationships (Fig. 5).

Cottonwood establishment dates

Because the tree age vs. diameter relationship obtained at the third meander site was locally derived from narrowleaf cottonwood trees at a meander site, and represents a relationship very similar to those based upon increment core data sets for both (1) the Clarks Fork of the Yellowstone River and (2) the South Fork of the Snake River, it was used in conjunction with field measurements of dbh to estimate establishment dates (ED) for narrowleaf cottonwood at all meander sites: $ED = 2001 - (0.56 dbh^{1.37} + 7)$. For the remaining floodplain sites, where narrowleaf cottonwoods occurred in open-grown stands, the relationship developed for the Lamar River floodplain near the Soda Butte Creek confluence was used: $ED = 2001 - (1.55 dbh + 7)$. A histogram of establishment dates, by 20-yr periods (Fig. 6), illustrates the general historical pattern of narrowleaf cottonwood recruitment in the Lamar Valley.

Historical photographs

Historical photographs can sometimes be useful for bracketing the general establishment age of prominent woody species, such as cottonwood. Meagher and Houston (1998) provide chronosequences of historical landscape photographs throughout YNP, two of which include portions of the Lamar Valley study reach. One chronosequence begins ~1885 with a northerly view toward the third meander site (Fig. 2) from the top of Specimen Ridge and is followed by retakes in 1970 and 1991 (Meagher and Houston 1998:128–129). Mature cottonwoods are clearly visible on the north end of the third meander site in the ~1885 photograph. Although the condition of the vegetation is not as clearly evident along the center and southern portion of the meander in the ~1885 photograph, scattered groups of relatively small cottonwoods appear to occur in an upstream direction (i.e., farther south) along the meander's point bar. In the most recent photograph of this site, 106 years later, the large cottonwoods to the north remain clearly visible, with increasing numbers of large cottonwood trees evident in a southerly direction along the meander. A total of 102 cottonwoods (100 narrowleaf and 2 black) were measured at this site in September of 2001. A sequential plot of cottonwood dbhs in a general north to south direction reveals a grouping of relatively large diameter trees at the north end of the meander, most likely the large cottonwoods visible

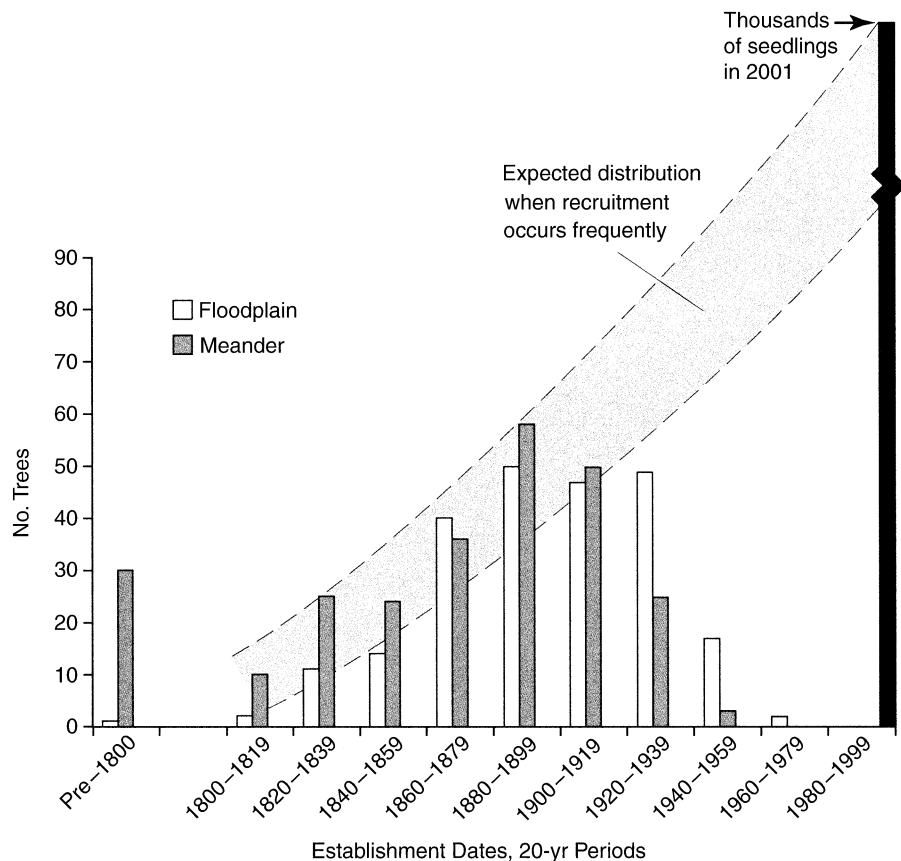


FIG. 6. Frequency distribution of estimated narrowleaf cottonwood establishment dates, by 20-yr periods, for the 9.5-km² Lamar Valley study area.

in all photographs. Based on the tree age vs. tree diameter relationship for point bar sites, the group of 26 relatively large trees at the northern end of the meander had an average establishment date of 1795 (± 1 SD = ± 51 yr), whereas the remaining 76 trees had an average establishment date of 1885 (± 35 yr). These results indicate that the larger trees became established nearly two centuries ago, with additional trees establishing in the late 1800s.

The second chronosequence of historical photographs represents a view looking south across the Lamar Valley toward Specimen Ridge (Meagher and Houston 1998:130–131); photographs were taken in 1898, 1970, and 1990. Although cottonwoods are not evident in any of the three photographs, the 1898 photos show a riparian shrub community of willows (*Salix* spp.) and mountain alder (*Alnus* sp.) along the river; this shrub community no longer exists in the 1970 photograph. Meagher and Houston (1998) also report a noticeable lack of aspen (*P. tremuloides*) reproduction along the valley sides in the 1970 and 1990 photographs relative to that observed in the 1898 photograph.

A Yellowstone National Park (1997) report provides a synthesis of scientific information and presents the agency's formal administrative position on grazing is-

suces in the northeastern portion of YNP. On page 83 of that report, a photograph taken in March 1933 (no. YEL35049) presents a southerly view toward the Lamar Ranger Station (foreground) and the lower valley floodplains of this study (background). The ranger station facilities were used to help manage bison (*Bison bison*) and elk (*Cervus elaphus*) populations in the northern winter range from the 1920s through the late 1960s. The 1950s and 1960s are particularly notable, because these decades represented a period of major herd reductions via hunting and trapping by the Park Service (Houston 1982). Sometime after the 1933 photograph was taken, recruitment of narrowleaf cottonwood occurred along a small stream on north side of the ranger station. In September 2001, the dbh of 33 narrowleaf cottonwood (not evident in the 1933 photo) were measured. Of these, 24 were alive, with an average dbh of 9.3 cm (range of 5–15 cm); heights generally ranged from 8 to 15 m, which is well above the normal browse level for elk. Nine dead cottonwoods were also measured (average dbh of 5.6 cm; range of 3–9 cm).

DISCUSSION

Observed declines in tall-willow and other riparian plant communities in northeastern YNP have been at-

tributed to various environmental and biotic factors (e.g., Chadde and Kay 1996, National Research Council 2002a). Below, I consider (a) fire, (b) weather patterns and hydrologic disturbance regimes, (c) stand development, (d) ungulate herbivory, and (e) the potential role of wolves relative to the long-term lack of cottonwood recruitment within the Lamar Valley study area.

Fire

Fire has an important effect on ecosystem processes and functions in the forested mountain terrain of YNP and throughout much of the American West (e.g., Berg 1989, Krammes 1990, Brown et al. 1995). In northeastern YNP, the decades prior to 1988 represent a period of relative quiescence as fires upstream of the study area were small (a few hundred hectares in total) and infrequent (<10 fire occurrences from 1930–1987). The major fires of 1988, which burned large areas of hillside in the Lamar River drainage, essentially bypassed the riparian cottonwoods in the study area (Yellowstone National Park 2001).

Weather patterns and hydrologic disturbance regimes

Changes in weather patterns (e.g., seasonal precipitation amounts, summer temperatures, Palmer Drought Severity Index) have been suggested as contributing mechanisms for explaining reduced establishment and growth of aspen and willows in the northern range (Houston 1982, Singer et al. 1994, Romme et al. 1995, Yellowstone National Park 1997, Singer et al. 1998). However, others (e.g., Wagner et al. 1995, Chadde and Kay 1996, Kay 1997, Ripple and Larsen 2000, Larsen and Ripple 2003) have been unable to demonstrate a climate/weather effect or have concluded that the suggested changes in climate are insufficient to have a major influence on woody species. Attempts to decipher ecosystem responses from shifting weather patterns over annual, decadal, or longer periods are often confounded by (1) an imperfect understanding of what constitutes a significant variation in weather/climate and (2) having a well-defined cause-and-effect mechanism that associates a specific weather pattern or climate shift to the plant communities of interest.

Interpretation of peak flows recorded at the Lamar River gage, relative to their potential for affecting seedling establishment and eventual recruitment of cottonwoods, is complicated since 18 years of record are missing in the 1970s and 1980s. While a ≥ 5 -yr peak flow event, a flow magnitude often associated with widespread cottonwood establishment, was not recorded during two decades (1930s and 1960s), all other decades from the 1920s to the present have experienced one or more such events (except for the 1970s, a period where flow records are entirely absent). For the Clarks Fork of the Yellowstone, every decade during the 79-yr period of record experienced at least one peak flow

with a ≥ 5 -yr recurrence interval. Collectively, these hydrologic records (albeit a partial record for the Lamar River gage) indicate it is unlikely that cottonwood seedling establishment would have been continuously prevented over the last 80 years due to a lack of high flow events. Even though seedling establishment during the last several years might have been augmented by a period of high peak flows in the mid- to late-1990s and the occurrence of bare substrates since the 1988 fires, historical aerial photos of the Lamar Valley between 1954 and 1998 indicate that channel changes have been common and that exposed alluvial substrates for cottonwood seedling establishment were plentiful prior to the 1988 fires.

Stand development

Measurements of 700 cottonwood trees within the study area indicated that the 5–29 cm diameter classes are almost entirely absent. This absence is remarkable for the abruptness in which it is observed in the histograms of both narrowleaf and black cottonwoods (Fig. 4). This situation is even more surprising given that seedling establishment is apparently unimpeded on alluvial substrates throughout the Lamar Valley, as currently demonstrated by the high densities and widespread occurrence of cottonwood seedlings in September 2001 (Table 1) and a 1992 field study (Keigley 1998) of young cottonwoods near the Soda Butte Creek confluence.

The temporal pattern of narrowleaf cottonwood recruitment (Fig. 6) suggests at least two important results. First, cottonwoods of 100–200 years of age, or greater, occur along the Lamar River in the northern range of YNP. Merigliano (1996) similarly found narrowleaf cottonwoods 100–200 years old and >200 years old comprising $\sim 40\%$ and 5% , respectively, of a riparian forest along the South Fork of the Snake River. Thus, cottonwoods can provide an important long-term perspective from which to view the role of environmental factors affecting their growth and recruitment. A 200-yr time frame is considerably longer than that of aspen, a species on which much of the debate regarding the effects of elk herbivory and other factors has been focused (Shepperd et al. 2001, National Research Council 2002a).

Second, and perhaps most importantly, reduced cottonwood frequencies occur in the early 1900s, become more evident in the 1920s, 1930s, and 1940s, and cease entirely from the late 1940s to the present (Fig. 6). Projecting the pre-1900 trends in tree frequencies toward the present (dashed lines in Fig. 6) provides an approximation of the number of small and intermediate sized cottonwoods in the younger age classes needed to sustain the numbers of larger cottonwoods shown for the 1800s. The hiatus in narrowleaf cottonwood recruitment represented in Fig. 6 represents an enormous departure from natural stand dynamics and seems to have occurred independently of fire history, flow

disturbance regime, or landform (meander vs. floodplain). The frequency distribution of diameter classes for black cottonwood (Fig. 4) indicates a similar scarcity of young trees.

While factors such as frost, blowdown, insect attack, and disease could represent important causes of cottonwood mortality for some species, for some groves and age cohorts, or for some years (Fowells 1965), it seems highly improbable that such effects would persist year after year, decade after decade, and be similar for both narrowleaf and black cottonwood. Thus, there seems to be no apparent physiological or physical environment factor that explains why cottonwood recruitment in northeastern YNP has been unsuccessful over the last 60 years.

Ungulate herbivory

A large number of studies have shown that grazing by domestic ungulates can be a major factor in the decline of riparian plant communities and their capability to function (Kauffman et al. 1983, Platts 1991, Fleischner 1994, Case and Kauffman 1997, Belski et al. 1999). Herbivory, by either domestic or wild ungulates, is particularly damaging to cottonwood establishment since seedlings and saplings are highly palatable and thus vulnerable (Braatne et al. 1996, Clayton 1996, Heilman 1996, Whitham et al. 1996). In western Montana, Clayton (1996) suggested that the lack of cottonwoods 10–50 yr of age along the upper Clarks Fork River could be related to the high elk populations of the 1970s and 1980s, as well as to historical grazing practices by livestock. Although wild ungulates often have different grazing/browsing patterns relative to those of managed livestock, when they have unlimited access to young woody species, the effects can be pronounced (Kay and Bartos 2000). Furthermore, the stripping of bark and girdling by elk may cause the mortality of tall saplings and young trees.

During the 1870s and early 1880s, the market hunting of elk common on many western rangelands also occurred within YNP. Many thousands of elk were killed for their hides and their carcasses poisoned to help exterminate predator and scavenger populations. Thus, by 1883, when public hunting became illegal within the park, elk populations had been greatly reduced and wolves temporarily exterminated (Yellowstone National Park 1997). With the arrival of the U.S. Army in 1886 to administer the newly designated park, wildlife management consisted primarily of protecting wild ungulates from hunters, predators, and winter mortality. Elk populations increased during the period of army administration and by the late 1920s and 1930s comprised approximately 10 000 animals in the northern range. From the 1920s to the late 1960s, elk were trapped and shipped to game ranges across North America, partially in an attempt to reduce their browsing impacts. During the 1950s and 1960s, many elk within the Park were simply shot to help reduce pop-

ulations and by the late 1960s, elk numbers had been reduced to ~3000–5000 animals. However, all culling of elk within the Park stopped in 1968 and elk have been fully protected from hunting or capture since that time. By the 1980s and early 1990s, annual elk counts on the northern winter range ranged from 10 000–19 000 animals (Yellowstone National Park 1997).

Observations by Smith et al. (1915), that the willows and shrubs (including mountain maple, service berry, wild rose, snowberry, fly honeysuckle, and others) were showing “evidence of much browsing during past winters,” represent some of the earliest written statements indicating that ungulates were beginning to impact woody species. Park administrators in the 1920s recognized the “bad condition” of the winter range and, in 1928, inaugurated an extensive study of the situation (Grimm 1939). Even though the Park Service undertook a program to control animals over a period of several decades, ungulate browsing of woody species continued and likely became more severe after herd reduction efforts were curtailed in the late 1960s. Various assessments of deciduous woody species, such as aspen, willows, berry-producing shrubs, and others in the northern range, have consistently indicated the effects of elk browsing on these species to be long-term and severe (Grimm 1939, Houston 1982, Chadde 1989, Kay 1990, 2001, Chadde and Kay 1996, Ripple and Larsen 2000, Larsen and Ripple 2003), with additional browsing impacts on sagebrush and conifers. Similarly, based on long-term photo comparisons within YNP, >75% of the sites originally photographed with riparian plant communities (principally willows) have shown a decline during the last century (Meagher and Houston 1998).

There has been little mention of cottonwood in most vegetation assessments of the northern range with the notable exception of Keigley's (1997, 1998) research in the Lamar Valley, which reported that cottonwood reproduction had experienced sustained and severe impacts from elk browsing. The results of this study fully support a hypothesis that elk herbivory throughout much of the 20th century has had a persistent and substantial impact on cottonwood recruitment in northeastern YNP, effectively creating a “recruitment gap.” This long-term recruitment gap is now strongly reflected in the stand structure of Lamar Valley cottonwoods.

The role of wolves

Little historical information is available regarding predator (wolf) and prey (elk) relationships prior to the establishment of YNP. However, in 1881, Superintendent Norris reported (Schullery and Whittlesey 1992) that “the large, ferocious gray or buffalo wolf. . . were once exceedingly numerous in all portions of the Park, but the value of their hides and their easy slaughter with strychnine-poisoned carcasses of animals have nearly led to their extermination.” The killing of wolves that occurred in YNP during the 1870s was

symptomatic of what was happening throughout the northern Rockies.

There were few reported sightings of wolves in YNP between 1881 and 1908 (Weaver 1978). From 1904 to 1925, however, ~130 wolves and numerous other predators were removed from the Park (Skinner 1926). Finally, in 1926, the last known wolves were killed. Thus, the “notorious wolf-killing era” of 1914–1926 essentially finished what had been nearly accomplished by 1880 (Schullery and Whittlesey 1992). It is important to note that there was a major ecological difference between the two eradications (Ripple and Larsen 2000). In the late 1800s, predators (i.e., wolves, mountain lions, and coyotes) and wild ungulates alike were heavily hunted, whereas efforts since the early 1900s were undertaken to exterminate only the predators. Between 1926, when wolves had been eradicated, and the winter of 1995–1996, when they were reintroduced, the park experienced a 70-yr period when it was entirely free of this apex predator. It is this exact period that stands out as being so remarkably different regarding the lack of cottonwood recruitment in the Lamar Valley. By the fall of 2001 ~220 wolves were present within YNP and the greater Yellowstone ecosystem.

White et al. (1998) have proposed a multi-level “trophic cascades” model involving humans, wolves, elk, and aspen for Rocky Mountain national parks that highlights the potential effects of wolves on elk densities. Subsequently, a predation risk component has been suggested for this model (Ripple and Larsen 2000, Ripple et al. 2001, White and Feller 2001). If one accepts the working hypothesis that a “top-down” trophic cascades model (involving humans, wolves, elk, and deciduous woody plants) is appropriate for YNP, then the park history can be viewed as a sequence of several long-term experiments. Based on this hypothesis, and for purposes of discussion and comparison, I have separated the historical record of Yellowstone National Park into a chronosequence of four “experimental” periods: I (pre-1870), II (1870–1925), III (1926–1995), and IV (1996–present).

The era prior to 1870 (Period I) is obviously of interest for understanding trophic interactions in a naturally functioning ecosystem. Although little quantitative information is available for this period, Fig. 6 indicates that cottonwood recruitment had occurred.

Period II (1870–1925) represents a time when elk and wolves were known to be present in YNP, but their numbers and interactions were being heavily influenced by hunting and poisoning efforts. Results from this study indicate Period II was also a time during which cottonwood recruitment occurred within the Lamar Valley (Fig. 6). However, narrowleaf cottonwood recruitment appears to be somewhat less frequent during the first two decades of the 1900s than for decades in the late 1800s. Since the narrowleaf and black cottonwood diameter distributions are similar (Fig. 3), this would suggest that black cottonwood recruitment was

also beginning to be suppressed toward the end of this period.

For Period III (1926–1995), wolves were absent in YNP. As a consequence, any predation effects wolves might have exerted upon wild ungulates were also absent. During this period, cottonwood recruitment throughout the study area departed from what would normally be expected. Throughout the study area, relatively few trees recruited from the 1920s through the 1940s and cottonwood recruitment was effectively terminated since the 1960s (Fig. 6). White et al. (1998) have suggested that the extirpation of wolves early in the 20th century probably was a major factor contributing to the high elk densities that followed and to the relatively high levels of herbivory on aspen and other woody species within the YNP. Similarly, Ripple and Larsen (2000) found that aspen recruitment ceased during the years that wolves were absent from YNP.

The years following cessation of elk culling efforts (i.e., after 1968) represent a period of “natural regulation” by the park service (Yellowstone National Park 1997). However, this was also a period when the recruitment of narrowleaf and black cottonwood was at its lowest. A natural regulation management approach, without wolves, apparently provided the opportunity for ungulate herds to expand in numbers and, more importantly, to forage without hindrance across the northern winter range. The consequences for cottonwoods (see *Results*), other riparian plant communities (e.g., Chadde and Kay 1996, Meagher and Houston 1998), and aspen (Ripple and Larsen 2000, Kay 2001, Larsen and Ripple 2003) have been significant. In Rocky Mountain National Park, Baker et al. (1997) also quantified the effect of elk on aspen in the winter range of that park, with particular emphasis on the period following the adoption of a natural regulation policy in 1968. Results indicated that excessive elk browsing (without the presence of wolves) rather than fire suppression, beavers, or climatic fluctuations, significantly limited aspen regeneration in the park’s elk winter range.

In Yellowstone much of the controversy regarding the potential effects of elk herbivory on aspen has focused on the numbers of elk that use the northern range during winter. Interestingly, the cottonwood recruitment data in this study suggest that elk numbers might not necessarily be the most important variable of concern. For example, even when elk populations were reduced to relatively low levels in the late 1950s and 1960s, recruitment of cottonwoods did not improve (Fig. 6). Keigley (1997, 1998) similarly found that browsing effects continued during the period of intensive elk control; these effects became even more severe after the culling operations ceased.

Ripple and Larsen (2000) indicate that wolves may positively influence aspen recruitment through modifying elk movement and herbivory patterns via a spatially variable mechanism of predation risk. White and

TABLE 3. A four-level trophic cascade model linking humans, wolves, elk, and riparian vegetation (modified from White et al. 1998) in the northern range of Yellowstone National Park during two periods.

Trophic level	Period III, 1926–1995	Period IV, 1996–present
Humans	extirpation of wolves from Yellowstone National Park	reintroduction of wolves into Yellowstone National Park
Wolves	totally absent; elk numbers vary due to forage availability, weather patterns, and Park Service culling efforts	wolf numbers increasing; elk numbers slightly lower in recent years
Elk	lack of wolf predation allows elk populations to heavily browse terrestrial deciduous vegetation (e.g., aspen) and woody riparian species (e.g., cottonwoods, willows, berry-producing shrubs)	predation risk begins to alter patterns of ungulate herbivory (?) upon woody riparian species
Plants	cottonwood seedlings common and widely distributed in the study area; heavy browsing of cottonwood seedlings (and other woody riparian species); complete loss of intermediate-sized cottonwoods; riparian functions negatively affected	cottonwood seedlings common and widely distributed in the study area; increased likelihood (?) of cottonwoods attaining tall sapling and tree stature; initial recovery (?) of willows underway; possible recovery (?) of riparian functions

Note: Period III (1926–1995) represents multiple decades of ungulate protection from predation by wolves, and Period IV (1996–present) represents less than a decade following wolf reintroduction and the restoration of predation effects upon wild ungulates.

Feller (2001) similarly suggest that foraging behavior can be an important issue in efforts to understand the effects of ungulate populations upon various plant communities. If elk foraging behavior in the Lamar Valley had been altered by the predation risk associated with hunting and other methods of herd reduction (such as was undertaken by the Park Service in the 1950s and 1960s), increased cottonwood recruitment would have been expected. Even though the Park Service was hunting and trapping elk over a period of many years, these activities apparently did not prevent elk from browsing along river bottoms at night or at other times of the year when hunting crews were not active; thus, cottonwood seedlings/suckers were unable to grow beyond browsing levels.

A notable exception to the general lack of cottonwood recruitment in the Lamar Valley occurs at the Lamar Ranger Station. Various human activities and operations associated with hunting, herding, and trapping of elk during the decades leading up to 1968 were undertaken from these facilities. Based on the comparison of a 1933 photograph showing a section of stream near the ranger station with conditions that existed in 2001, it is clear that the recruitment of small cottonwood trees occurred sometime after 1933. The fact that small cottonwoods 5–30 cm in dbh have been able to successfully recruit along streams adjacent to the ranger station is in stark contrast to the total absence of comparable size classes (Fig. 4) across floodplains and on point bars throughout the Lamar Valley study area (Figs. 1 and 2). While weather patterns have sometimes been proposed as a major factor limiting the establishment and growth of deciduous woody species in the northern range (e.g., Houston 1982, Singer et al. 1998), such patterns obviously did not prevent the recruitment of small cottonwood trees near the ranger

station (where elk were at direct risk from humans from the 1920s to 1968).

The years from 1996 to the present characterize the initial phase of Period IV in the temporal sequence of northern range “experiments” (Table 3). In this case, the experiment is one of ecological restoration (Kauffman et al. 1997, National Research Council 2002b) where a key ecosystem component (i.e., wolves) has been restored. Should existing or future cottonwood seedlings/suckers (and those of tall willows and other deciduous woody riparian plants) eventually attain heights above the browse level of elk (due to changes in elk numbers, migration patterns, foraging behavior, or some other factor) there could be a concurrent recovery in the capability of these plant species to again provide a wide range of ecological functions (e.g., root strength, allochthonous inputs, shade and microclimate moderation, large wood recruitment, food web support, habitat) associated with riparian systems in the Lamar Valley.

While the early years of Period IV represent a time of transition, they obviously provide a rare opportunity to characterize and evaluate the role of wolves as a keystone predator (Mills et al. 1993) in the potential recovery and sustainability of riparian ecosystems. It is not yet known whether a general period of cottonwood regeneration is underway or likely to occur in the coming years. However, if the recruitment of cottonwood and other riparian plants was to begin, monitoring during this critical phase could chronicle what might become a preeminent example of ecological restoration. Such results might not only be relevant for understanding trophic cascades of predator/prey/vegetation associated with the riparian systems of northeastern YNP but also for other riparian areas in the American West where the recovery of wolves is underway or being contemplated.

CONCLUSIONS

Based on the results of this study, a nearly complete collapse in narrowleaf and black cottonwood recruitment has occurred over an extended period encompassing approximately the last six decades. This long-term gap in recruitment represents a huge divergence from normal cottonwood age class distributions for a gallery forest composed of multiple spatially distributed groves, such as is the case in the study area. The current scarcity of small diameter trees of both narrowleaf and black cottonwood, from which future large trees will be derived, cannot be replaced even if cottonwood recruitment was to immediately recover. Thus, large cottonwoods in the Lamar Valley are destined to become increasingly uncommon in forthcoming decades.

Multiple lines of evidence and information were evaluated in an attempt to understand the role, or lack thereof, that various factors might play in causing the loss of cottonwood recruitment. After considering several major environmental factors affecting cottonwood seedling establishment and growth, the conclusion seems inescapable that unimpeded browsing over a period of many years has been the primary cause in the decline and loss of cottonwood recruitment in the northern range. The absence of wolves, a keystone predator in the Yellowstone ecosystem (Period III, Table 3), coincides remarkably with the multiple decades of little or no cottonwood recruitment. When viewed from the perspective of a top-down trophic cascades model of ecosystem response involving humans, wolves, elk, and plants, the critical linkage between wolves and elk during this period was severed (by humans).

Considering the period from 1996 to the present (Period IV), conclusions are perhaps more appropriately framed as a series of linked hypotheses. Wolves obviously can reduce prey numbers by direct predation, which in turn could reduce browsing pressure on riparian plant communities. The increasing numbers of wolves may also influence elk herbivory through displacement, habituation, and risk-sensitive foraging behavior. Such indirect effects may be contributing to the generally widespread occurrence of cottonwood seedlings observed in 2001 or the initial "recovery" of willows (Ripple and Beschta, *in press*) that seems to be occurring in portions of the Lamar Valley. Although cottonwood seedlings are common along the Lamar River, indicating a potential for cottonwood recruitment into the future, which of these seedlings (if any) might eventually grow above elk browse levels into tall saplings and finally into trees represent important restoration questions that are largely unanswerable at this time. Even the return of a long missing keystone predator might not guarantee that cottonwood seedlings/suckers will successfully recruit into tall saplings and trees across the Lamar Valley in the coming years.

Only the passage of time will allow the ongoing "experiment" to generate the rightful conclusions regarding our understanding of trophic cascades, predation risk, wolves and elk, and cottonwood recruitment in the northern Yellowstone. Regardless of the outcome, the reintroduction of the North American gray wolf, a keystone predator, must certainly be viewed as the return of a critical element of the pre-Euro-American ecosystem that previously existed within and outside of Yellowstone National Park—an element that had been missing for nearly three-quarters of a century.

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LITERATURE CITED

- Avery, T. E., AND H. E. Burkhart. 2002. Forest measurement, Fifth edition. McGraw Hill, New York, New York, USA.
- Baker, W. L. 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. *Journal of Biogeography* 17:59–73.
- Baker, W. L., J. A. Munroe, and A. E. Hessler. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. *Ecography* 20:155–165.
- Belski, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. *Journal of Soil and Water Conservation* 54:419–431.
- Berg, N. H., technical coordinator. 1989. Proceedings of the symposium on fire and watershed management, October 26–28, 1988, Sacramento, California. USDA Forest Service General Technical Report PSW-GTR-109.
- 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. University of Washington, Institute of Forest Resources, Contribution 57. 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: symposium on fire in wilderness and park management. USDA Forest Service General Technical Report INT-GTR-320.
- Case, R. L., and J. B. Kauffman. 1997. Wild ungulate influences on the recovery of willows, black cottonwood and thin-leaf alder following cessation of cattle grazing in northeastern Oregon. *Northwest Science* 71:115–126.
- 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, May 8–12, 1989, Billings, Montana. U.S. Bureau of Land Management, BLM-MT-PT-89-001-4359.
- 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. Technical Report NPS/NRYELL/NRTR/96-01, National Park Service, 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.
- Dykaar, B. B., and P. J. Wigington. 2000. Floodplain formation and cottonwood colonization patterns on the Willamette River, Oregon, USA. *Environmental Management* **25**:87–104.
- Farnes, P., C. Heydon, and K. Hansen. 1999. Snowpack distribution across Yellowstone National Park. Final Report, Cooperative Agreement Number CA 1268-1-9017, Montana State University, Bozeman, Montana, USA.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* **8**:629–644.
- Fowells, H. S. 1965. Silvics of forest trees of the United States. USDA Forest Service, Agricultural Handbook **271**.
- 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.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Pages 133–302 in A. Macfadyen and E. D. Ford, editors. *Advances in ecological research*, volume 15. Academic Press, Orlando, Florida, USA.
- 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.
- Johnson, R. R., C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, technical coordinators. 1985. Riparian ecosystems and their management: reconciling conflicting uses—first North American riparian conference. USDA Forest Service General Technical Report RM-GTR-120.
- Kauffman, J. B., R. L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the Western United States. *Fisheries* **22**(5): 12–24.
- Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications: a review. *Journal of Range Management* **37**:430–438.
- Kauffman, J. B., W. C. Krueger, and M. Vavra. 1983. Effects of late season cattle grazing on riparian plant communities. *Journal of Range Management* **36**:685–691.
- 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. 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, June 13–15, 2000, Grand Junction, Colorado. USDA Forest Service RMRS-P-18.
- Kay, C. E., and D. L. Bartos. 2000. Ungulate herbivory on Utah aspen: assessment of long-term exclosures. *Journal of Range Management* **53**:145–153.
- 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**(3/4):57–67.
- Knutson, K. L., and V. L. Naef. 1997. Management recommendations for Washington's priority habitats: riparian. Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- Koehler, D. A., and A. E. Thomas, compilers. 2000. Managing for enhancement of riparian and wetland areas of the western United States: an annotated bibliography. USDA Forest Service General Technical Report RMRS-GTR-54.
- Krammes, J. S., technical coordinator. 1990. Effects of fire management of southwestern natural resources. USDA Forest Service General Technical Report RM-GTR-191.
- Larsen, E. J., and W. J. Ripple. 2003. Aspen age structure in the northern Yellowstone ecosystem: USA. *Forest Ecology and Management* **179**:469–482.
- Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. *Wetlands* **18**:634–645.
- Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin, technical editors. 1988. From the forest to the sea: a story of fallen trees. USDA Forest Service General Technical Report PNW-GTR-229.
- 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. Technical Bulletin 96-9, USDI Bureau of Land Management, Boise, Idaho, USA.
- Michener, W. K., and R. A. Haeuber. 1998. Flooding: natural and managed disturbances. *BioScience* **48**:677–680.
- Mills, L. S., M. E. Soule, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* **43**:219–223.
- National Research Council. 2002a. Ecological dynamics on Yellowstone's northern range. National Academy Press, Washington, D.C., USA.
- 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.
- Patten, D. T. 2000. Riparian ecosystems of North America's intermountain west and adjacent plains. Pages 245–250 in P. J. Wigington and R. L. Beschta, editors. *Riparian ecology and management in multi-land use watersheds*. TPS-00-2, American Water Resources Association, Middleburg, Virginia, USA.
- Platts, W. S. 1991. Livestock grazing. Pages 389–423 in W. R. Meehan, editor. *Influences of forest and rangeland man-*

- agement on salmonid fishes and their habitats. Special Publication 19, American Fisheries Society, Bethesda, Maryland, USA.
- Ripple, W. J. and R. L. Beschta. *In press*. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*.
- 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.
- Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* **102**:227–234.
- 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.
- Rutherford, I., B. Abernethy, and I. Prosser. 1999. Stream erosion. Pages 61–78 in S. Lovett and P. Price, editors. *Riparian land management technical guidelines: volume one, principles of sound management*. Land and Water Resources Research and Development Corporation, Canberra, Australia.
- 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.
- Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications* **7**: 677–690.
- Sedell, J. R., and R. L. Beschta. 1991. Bringing back the "bio" in bioengineering. *American Fisheries Society Symposium* **10**:160–175.
- Shepperd, W. D., D. Binkley, D. L. Bartos, and T. J. Stohlgren, compilers. 2001. Sustaining aspen in western landscapes: symposium proceedings, June 13–15, 2000, Grand Junction, Colorado. USDA Forest Service RMRS-P-18.
- 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.
- Skinner, M. P. 1926. Mountain goat (*Oreamnos montanus*) not found in Wyoming. *Journal of Mammalogy* **7**:334–335.
- Smith, C. L., A. A. Simpson, and V. Bailey. 1915. Report on investigations of the elk herds in the Yellowstone Region of Wyoming, Montana, and Idaho. December 14, 1915 report to the Biological Survey and Forest Service. Washington, D.C., USA.
- 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. *Natural Resources Report 14*, National Park Service, Yellowstone National Park, Mammoth Hot Springs, Wyoming, USA.
- White, C. A., and M. C. Feller. 2001. Predicting risk and elk–aspen foraging patterns. Pages 61–80 in W. D. Shepperd, D. Binkley, D. L. Bartos, and T. J. Stohlgren, compilers. *Sustaining aspen in western landscapes: symposium proceedings*, June 13–15, 2000, Grand Junction, Colorado. USDA Forest Service RMRS-P-18.
- White, C. A., C. E. Olmsted, and D. E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin* **26**:449–462.
- 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*. TPS-00-2, American Water Resources Association, Middleburg, Virginia, USA.
- Wondzell, M. 1992. Vegetation patterns along the middle fork of the Flathead River, Glacier National Park, Montana. Thesis. Colorado State University, Fort Collins, Colorado, USA.
- Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. National Park Service, Yellowstone National Park, Mammoth Hot Springs, Wyoming, USA.
- Yellowstone National Park. 2001. Yellowstone National Park fire history. National Park Service, Yellowstone National Park, Fire Management Office, Mammoth Hot Springs, Wyoming, USA.