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HYDROLOGIC REGIME AND HERBIVORY STABILIZE AN ALTERNATIVE STATE IN YELLOWSTONE NATIONAL PARK

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Abstract. A decline in the stature and abundance of willows during the 20th century occurred throughout the northern range of Yellowstone National Park, where riparian woody-plant communities are key components in multiple-trophic-level interactions. The potential causes of willow decline include climate change, increased elk browsing coincident with the loss of an apex predator, the gray wolf, and an absence of habitat engineering by beavers. The goal of this study was to determine the spatial and temporal patterns of willow establishment through the 20th century and to identify causal processes. Sampled willows established from 1917 to 1999 and contained far fewer young individuals than was predicted from a modeled stable willow population, indicating reduced establishment during recent decades. Two hydrologically distinct willow establishment environments were identified: fine-grained beaver pond sediments and coarse-grained alluvium. Willows established on beaver pond sediment earlier in time, higher on floodplain surfaces, and farther from the current stream channel than did willows on alluvial sediment. Significant linear declines from the 1940s to the 1990s in alluvial willow establishment elevation and lateral distance from the stream channel resulted in a much reduced area of alluvial willow establishment. Willow establishment was not well correlated with climate-driven hydrologic variables, but the trends were consistent with the effects of stream channel incision initiated in ca. 1950, 20–30 years after beaver dam abandonment. Radiocarbon dates and floodplain stratigraphy indicate that stream incision of the present magnitude may be unprecedented in the past two millennia. We propose that hydrologic changes, stemming from competitive exclusion of beaver by elk overbrowsing, caused the landscape to transition from a historical beaver-pond and willow-mosaic state to its current alternative stable state where active beaver dams and many willow stands are absent. Because of hydrologic changes in streams, a rapid return to the historical state may not occur by reduction of elk browsing alone. Management intervention to restore the historical hydrologic regime may be necessary to recover willows and beavers across the landscape.

Key words: Canis lupus; Castor canadensis; Cervus elaphus; *dendrochronology; ecological threshold; ecosystem engineer; fluvial geomorphology; hysteresis; resilience; restoration;* Salix; *trophic cascade.*

INTRODUCTION

Woody plants are critical structural components of riparian ecosystems throughout the world (Hughes 1997). Their sturdy upright stems and strong perennial roots stabilize stream banks, enhance sediment deposition during floods, maintain stream water quality, contribute coarse woody debris and fine organic matter to streams, and provide habitat for a wide range of plants and animals (Naiman and Decamps 1997). In many boreal, mountain, and semiarid regions of North America, willows (*Salix* spp.) are the dominant woody riparian plants (Chadde and Kay 1991, Knight 1994). Willows are tied in all life history phases to the hydrologic regimes (Gage and Cooper 2004, Woods and Cooper 2005) and geomorphic processes of streams (Cooper et al. 2006). For example, willows do not form a soil seed bank but require the periodic creation of bare and moist substrates created by fluvial processes for seed germination and seedling establishment (Read 1958, Naiman and Decamps 1997). Mature willows are flood tolerant and dependent on the relatively shallow water table occurring in river corridors (Amlin and Rood 2001).

Willows also provide critical food and building material for beavers (*Castor canadensis* Kuhl; Baker and Hill 2003), whose dams fundamentally alter hydrologic and geomorphic processes in riparian areas (Westbrook et al. 2006). Beaver dams can be long-term or ephemeral geomorphic features of a stream valley (Woo and Waddington 1990) that typically span the entire channel and are maintained year round on streams with low power (Warren 1926, Johnston and

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Naiman 1990, Burns and Mcdonnell 1998, Albert and Trimble 2000). Beaver dams raise local water tables and allow deposition of fine-grained sediment (Meentemeyer and Butler 1999), producing suitable conditions for willow establishment (Bigler et al. 2001). Even after a beaver dam is abandoned, it may impound water for years to decades, and continue to influence site geomorphic processes (Naiman et al. 1988, Woo and Waddington 1990). Once a beaver pond drains, bare and moist mineral sediment is exposed providing ideal habitat for willow establishment (Read 1958). Thus, the presence of willows and beaver create mutually beneficial feedbacks (Baker et al. 2005) that maintain a regional abundance of willow and beavers along streams.

There is accumulating evidence that disruption of these feedbacks on the northern range of Yellowstone National Park has caused a transition in ecosystem states on the landscape. Historically, the landscape of the northern range was dissected by riparian zones dominated by willow communities extending up to 40 m laterally from stream margins (Warren 1926, Houston 1982). Dams created by beaver punctuated the stream network, flooding areas of the landscape, and creating hydrologic and soil conditions particularly well suited to the life history requirements of willows. We refer to this historical condition as the beaver–willow state (Fig. 1A). Demographic studies and comparisons of modern and historical photographs illustrate that striking reductions in the abundance and stature of willows (Kay 1990), cottonwoods (*Populus angustifolia* James; Keigley 1997, Beschta 2003), and aspen (*Populus tremuloides* Michaux; Ripple and Larsen 2000) occurred during the 20th century, particularly on the northern range. These riparian woodlands have been replaced by grasslands in many areas (Houston 1982, Engstrom et al. 1991, Singer et al. 1994) leading to an alternative state that we refer to as the elk–grassland state (Fig. 1B). In this state, willow communities are limited to small, isolated fragments and active beaver dams are absent.

The causes of these landscape-scale changes are poorly understood, although three factors are hypothesized to have played critical roles: (1) an increasingly dry climate that reduced streamflow (Houston 1982, Singer et al. 1998), (2) intense herbivory from abundant and increasing elk (*Cervus elaphus* L.) populations following the elimination of gray wolves (*Canis lupus* L.) from Yellowstone ca. 1920 (Kay 1990, Keigley 1998, 2000, Beschta and Ripple 2006), and (3) a change in stream and riparian hydrologic characteristics due to a reduction in beaver populations and beaver dams (Singer et al. 1994). Understanding the relative importance of these potential causes of landscape changes has emerged as a high priority for research (National Research Council 2002).

Following their extirpation in ca.1920, gray wolves were reintroduced to Yellowstone beginning in 1995. Wolf reintroduction represents a potentially strong disturbance to the elk–grassland state. Recent research suggests that wolf reintroduction has triggered a trophic cascade by reducing elk numbers and exposing elk to predation risk in riparian corridors (Ripple and Larsen 2000, Ripple et al. 2001, Beschta 2003, 2005, Ripple and Beschta 2003, 2004, 2006, Gude et al. 2006), which, in turn, has reduced browsing intensity and allowed woody plants to recover from decades of heavy browsing (Ripple and Beschta 2003, Creel et al. 2005, White and Garrott 2005). The disturbance triggered by wolf reintroduction may cause a recovery from the elk–grassland to the beaver–willow state by allowing the return of tall willows and re-creating conditions suitable for stream engineering by beavers (Ripple and Beschta 2004).

However, decades of overbrowsing may have triggered hydrologic changes in riparian ecosystems that could prevent recovery through reduction of elk browsing alone. The ecosystems may be in a state of hysteresis, where a return to the previous condition requires a different pathway or set of processes than those that caused the initial transition. Lewontin (1969) and later Holling (1973) developed the idea that communities and ecosystems exist in one of several potential states that can shift abruptly in response to physical or biotic stresses. This idea and its subsequent elaborations (reviewed by Beisner et al. 2003, Briske et al. 2003, 2005, Shurin et al. 2004, Suding et al. 2004) expanded on the historical view that internal feedbacks cause ecological systems to return to a single equilibrium following disturbance. Rapid shifts in ecosystems to novel states create unpredictable, sometimes catastrophic outcomes for natural and managed systems (see reviews of Scheffer et al. 2001, Folke et al. 2004, Gunderson and Folke 2004, Mayer and Rietkerk 2004, Peters et al. 2004, Rietkerk et al. 2004).

In this study we quantify the influence of hydrologic regimes, as controlled by climate variation, beaver damming, and landscape changes, on the patterns and processes of willow establishment along small streams on Yellowstone's northern range. Our objectives were to (1) reconstruct the timing of willow establishment during the 20th century, (2) relate the timing and spatial extent of willow establishment to climate factors (rainfall and streamflow) and beaver influence (areas and periods of beaver pond deposits), (3) determine the relative influences of climate, beaver, and elk herbivory on willow establishment during the 20th century, and (4) identify specific hydrologic, geomorphic, and ecological processes that were affected by the loss of willows, and determine which of these processes can be recovered.

STUDY AREA

We worked along four streams (Elk Creek, Lost Creek, and the West and East Forks of Blacktail Deer Creek) on the northern range of Yellowstone National Park, USA at elevations from 1923 to 2076 m (Fig. 2). The study streams are 1–3 m wide, up to 1 m deep, with

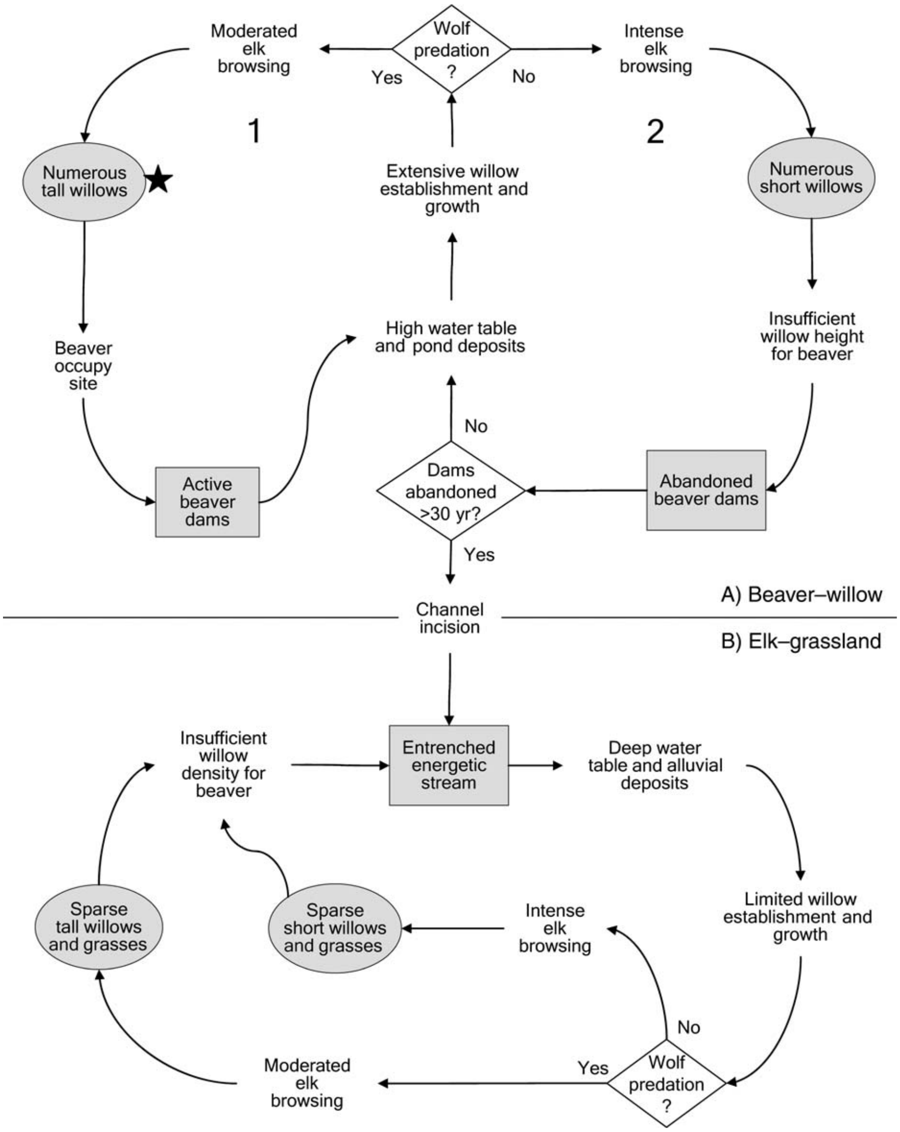

FIG. 1. Conceptual model of the shift in small-stream riparian ecosystems from (A) an initially stable beaver–willow state supporting dense willow populations, to (B) an alternate stable elk–grassland state where willows are sparse. Gray ovals represent states of the willow plant community, gray rectangles describe the fluvial geomorphic state, diamonds are decision points based on a specific condition, and plain text describes causal processes that lead from one state to another. The black star indicates the historical reference condition. The numbers identify two loops within the beaver–willow system: (1) the stable beaver–willow feedback, and (2) destabilized beaver–willow ecosystem where elk browsing excludes beaver. Channel incision is identified as the primary cause of the shift from (A) stable state to (B) the alternative stable state.

banks 0.5–1.0 m high, except at unstable cutbanks, where bank height may exceed 2 m. The vertical banks create two distinct riparian environments: (1) narrow, deeply incised channels, and (2) broad, flat, terraces above the banks. Ground surfaces within incised channels are near the stream water table level; however, terrace ground surfaces are 1 to >2 m above the water table (Bilyeu et al., *in press*). The streams we studied have low-sinuosity, meandering single channels with low to moderate gradient, and cobble, gravel, and sand beds.

The study watersheds were glaciated during the Pleistocene, and contain surficial deposits of poorly sorted till overlying volcanic bedrock (Knight 1994). Mean annual precipitation is 410 mm, with 44% falling as snow, mostly between mid-October and mid-April, and the rest as summer rain (National Climatic Data Center 2004). All study sites were within the 1988 fire burned-area perimeter, and charred logs at the Elk Creek site indicate that its floodplain vegetation burned.

Douglas-fir (*Pseudotsuga menziesii* Mirbel) and lodgepole pine (*Pinus contorta* Loudon) dominate upland forests throughout the study watersheds. At lower elevations sagebrush and grasses dominate. Small aspen clones are scattered along the valley slopes of the study

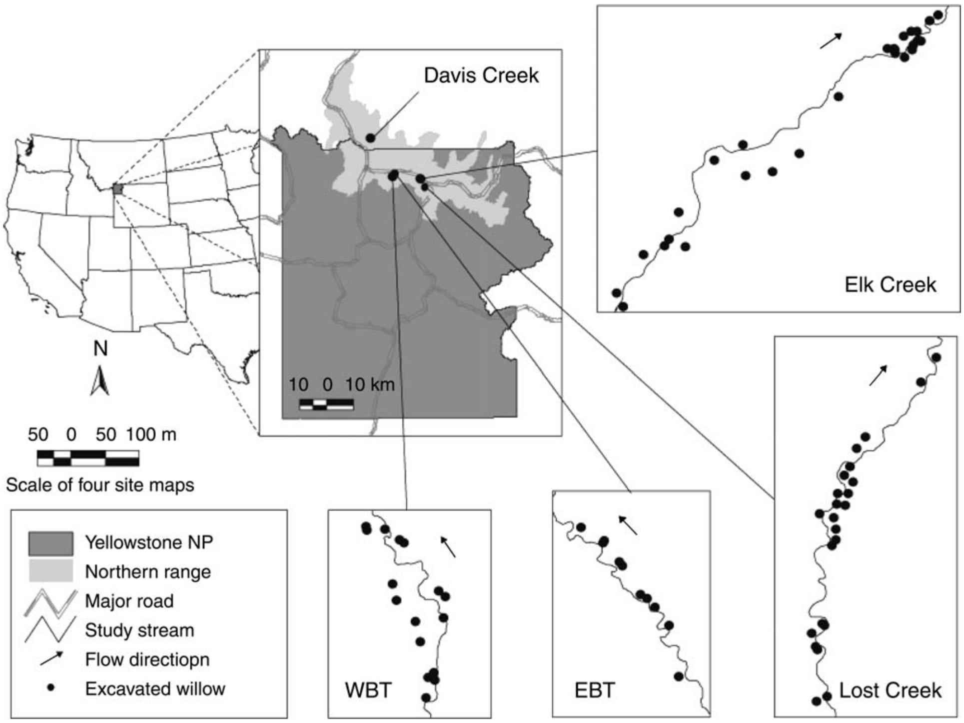

FIG. 2. Map showing the location of the study sites in Yellowstone National Park, USA. The positions of excavated willows are shown within the site insets. The West Fork of Blacktail Deer Creek is abbreviated as WBT, and the East Fork as EBT.

reaches. Sedges (*Carex* spp.), grasses, and herbaceous dicots dominate the understory of riparian communities. Willow and lodgepole pine are the dominant woody riparian plants, with some scattered occurrences of alder (*Alnus incana* (L.) Moench var. *occidentalis* (Dippel) Hitchcock). Of the 20 species of *Salix* in Yellowstone (Dorn 2001), *S. bebbiana* Sarg., *S. geyeriana* Anderss., *S. drummondiana* Barratt ex Hook., *S. boothii* Dorn, and *S. pseudomonticola* Ball are most common in the study area. These species do not reproduce by cloning and, although they normally reach 3–5 m in height, most individuals were <1 m tall. Clonal willow species such as *Salix exigua* and *S. planifolia* are uncommon at our sites, and are not a significant component of the riparian community.

The four study streams were selected because they (1) are located within the northern range, (2) support relatively large willow populations, (3) have riparian zones where groundwater is supported by streamflows, and (4) lack significant hillslope groundwater inflows. Moreover, all study streams were dammed by beaver as evidenced by relict beaver dams and historical records (Warren 1926, Jonas 1955). As a reference for sediment accumulation in natural beaver ponds, we also worked at Davis Creek, a small stream on the northern range outside of Yellowstone National Park that supports an active beaver colony of animals reintroduced to the area in 1995 (D. Tyers, *personal communication*). Davis Creek is located at a similar elevation, in the same geologic setting, and supports similar riparian vegetation to the other study sites, but has a steeper channel and valley profile.

METHODS

Overview of research approach

We sought to determine the spatial and temporal patterns of willow establishment through the 20th century and to correlate these patterns with causal processes. Temporal establishment data were collected by aging individual willow plants, and spatial data were gathered using a topographic survey. Willow establishment data were compared to 20th century streamflow and precipitation data to detect climatic influences on the timing of establishment. We examined shifts in spatial establishment patterns through time by correlating the location of willow establishment points relative to the channel with plant age. The historical role of beaver in affecting willow establishment was described by identifying beaver pond deposits and determining whether sampled willows established on fine-grained beaver pond deposits or on coarse-grained alluvium.

Hydrology

To determine the historical hydrologic regime of our study sites, we reconstructed annual peak and annual average discharge for the 20th century. Mean daily stream discharge data are available from the U.S. Geological Survey gauge on the Yellowstone River at Corwin Springs (gauge 06191500) from 1911 to 2002.

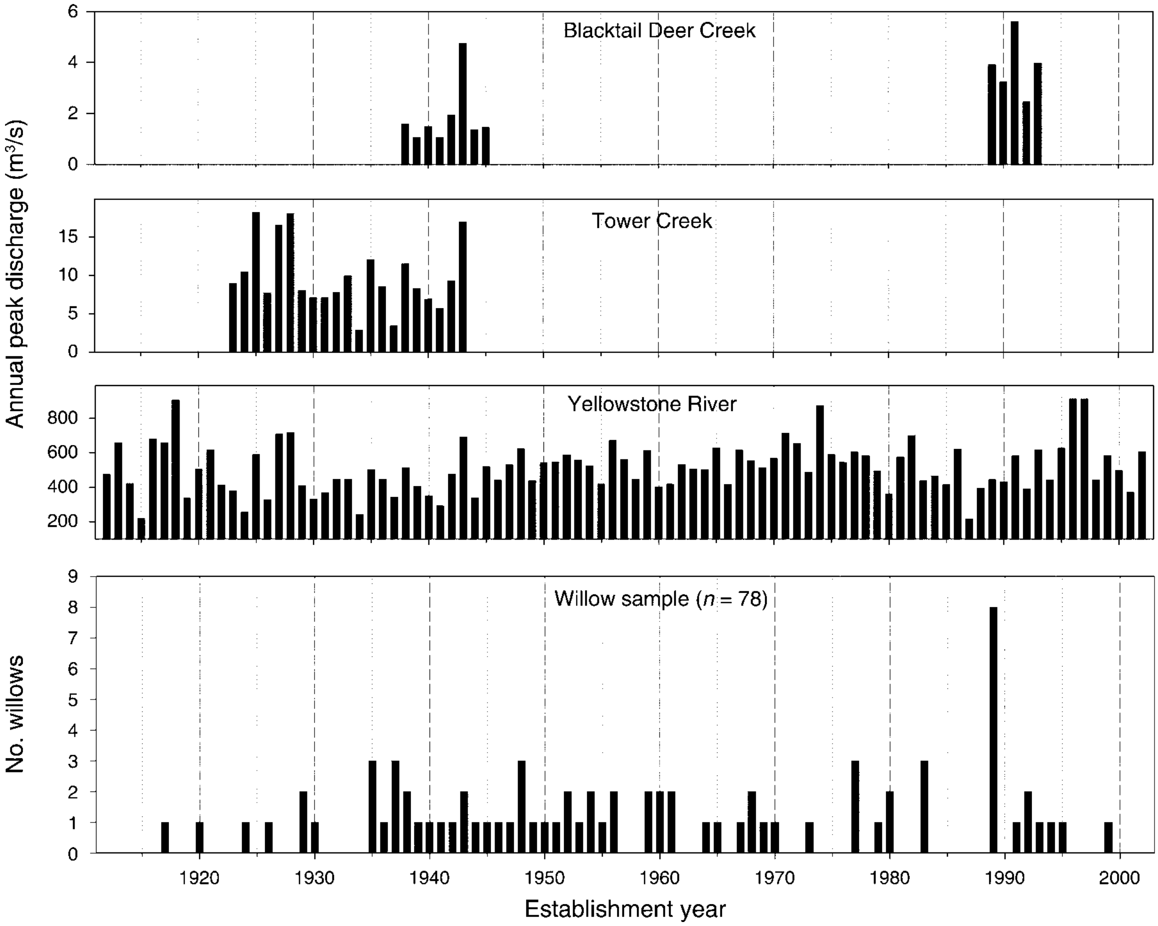

FIG. 3. Streamflow records of annual peak discharge for Blacktail Deer Creek near Mammoth, Tower Creek at Tower Falls, and the Yellowstone River at Corwin Springs, and distribution of establishment years in the sample of 78 willows.

Periodic streamflow data are available for two other streams in the study area, Blacktail Deer Creek (gauge 06189000), and Tower Creek (gauge 06187500) (Fig. 3). We correlated annual peak and annual average discharge on West Blacktail Deer and Tower Creeks with the Yellowstone River using bivariate correlation analyses (SPSS 2001).

Annual peak discharge of the Yellowstone River at Corwin Springs was significantly correlated with the annual peak discharge of both Blacktail Deer ($N = 13$ years, $r^2 = 0.72$, $P = 0.006$) and Tower Creeks ($N = 21$, $r^2 = 0.89$, $P < 0.001$). In addition, the mean annual discharge of the Yellowstone River at Corwin Springs was significantly correlated with Blacktail Deer ($N = 11$, $r^2 = 0.87$, $P = 0.001$) and Tower Creeks ($N = 19$, $r^2 = 0.97$, $P < 0.001$). The strong correlations between the Yellowstone River and the two smaller streams allowed us to use Yellowstone River discharge to estimate annual peak and mean annual discharge for the study streams from 1911 to 2002.

Long-term precipitation data is available from the two weather stations nearest the sites, Mammoth and Tower (National Climatic Data Center 2004). The Mammoth station is at 1900 m elevation and 10 km west of the study areas, and Tower is at 2050 m elevation and 1 km east. Because these stations are positioned at opposite ends of the elevation and west–east gradients across the study sites, we averaged their data to obtain estimates of total annual precipitation in the study area, which is used as a hydrologic variable in willow establishment models.

Willow establishment

We aged a spatially stratified random sample of willows selected within each study site to determine the timing and periodicity of willow establishment. We stratified willows by patch, as delineated by geomorphic position along streams. For conservation reasons, we never excavated >20% of the willows from one patch. Selected willows were identified to species, the ground surface position was marked on the main stem, and soil was removed from around the roots using hand shovels. The root structure and sediment layers exposed by the excavation were sketched and photographed in situ. A sample from each distinct sediment layer was collected for organic matter and grain-size analysis. The root mass was carefully excavated and the main large roots collected. All sampled plants were individuals and not part of a larger willow clone.

The root mass of each plant was cross-sectioned by sawing perpendicular to the direction of extensional growth, and the depth below ground surface was calculated for each cross section. Plant shoot material contains pith, while root material does not, and the root crown is contained within the cross section with pith on its top, but not its bottom (Scott et al. 1996). By successive cuts we isolated the root crown in a section no thicker than 2 cm and determined its depth below the ground surface. The root crown identifies the location of germination, and the soil layer at that depth is the establishment surface (Cooper et al. 2003, 2006, Friedman et al. 2005).

The upper and lower surfaces of cross sections containing the root crown were sanded with successively finer sand paper, finishing with 5-μm grit, and annual growth rings were counted from the center to cambium on both surfaces (Cooper et al. 2006). At least three people independently verified ring counts on each plant. Missing or false rings rarely occur in riparian plants with perennial water sources (Fritts 1976); however, partial rings were common because willow root crowns often exhibit a lobate growth form. All ring counts were made along radii of the sections where active growth occurred throughout each year of the plant's life.

The position of each sampled willow was surveyed using a total station (Spectra Precision Geodimeter, Westminster, Colorado, USA) and GPS unit (Trimble, Sunnyvale, California, USA). The position of the thalweg (the deepest active stream channel) was also surveyed at each site. For each willow, a distance above and away from the nearest point along the thalweg was calculated.

We tested the validity of pooling establishment year and elevation data for all willow species and among all sites using ANOVA and Tukey's pairwise multiple comparison (SPSS 2001). All data were pooled, with the exception of those from the 1989 willow cohort. The only major 20th century fire in northern Yellowstone occurred in 1988 (Romme and Despain 1989) and created an on-site disturbance that uniquely affected the site by triggering soil erosion and scorching, and the formation of bare mineral soils from processes other than fluvial action.

We used nonlinear Poisson regression to model willow establishment through time as a function of annual peak discharge and mean annual discharge of the Yellowstone River, and total annual precipitation. We related the number of willows established in a given year (W_t) to each of the three hydrologic variables for the current (X_t), previous (X_{t-1}), and following years (X_{t+1}). To test the possibility that the climatic variables may have a cumulative or lag effect across years (e.g., extended droughts or wet periods), we generated four hydrologic variables each from the mean annual discharge data set and total annual precipitation data set. These variables were calculated as the sum of the current year's value plus the preceding 1, 2, 3, and 4 years' values:

$$X_t + X_{t-1}, X_t + X_{t-1} + X_{t-2}, \ldots, \sum_{i=0}^{4} X_{t-i}.$$

Willow establishment data were analyzed with each hydrologic variable separately. Deviance (D) divided by the degrees of freedom (df) was used to assess the goodness of fit of each model, with $D/\text{df} = 1$ indicating an excellent model fit, and $D/\text{df} > 1$ indicating overdispersion. The significance of each variable was assessed by chi-square tests of likelihood ratio statistics in type III analyses. Pseudo-R^2, the proportion of variation explained that exceeds the variation explained by a model using only an intercept term, was used to assess the predictive strength of the model (SAS Institute 2001, Merritt and Wohl 2002, Birken and Cooper 2006).

To determine if the Yellowstone willow population was stable, increasing, or diminishing over time we used a matrix projection model (Appendix) to generate a static age distribution of a stable willow population for comparison. Fecundity and mortality rates were balanced to result in one willow from each cohort surviving to 86 years, the age of the oldest willow we sampled.

History of beaver activity and sediment analyses

Historical records, including photographs and written reports, were used to identify previous beaver activity at the study sites. Floodplain sediment stratigraphy on study reach cut-banks was analyzed to identify soil texture and indicators of anoxic depositional environments, such as gleyed or low chroma soil colors (Munsell Soil Color Chart) and oxidized root channels in major soil layers. Soil texture was quantified by measuring the grain-size distribution using sieve and hydrometer methods (Gee and Bauder 1986). Radiometric ^{14}C ages for six wood and charcoal samples from floodplain sediments were used to constrain the timing of sediment deposition. Radiocarbon analyses were performed by Beta Analytic (Beta Analytic 2003).

Beaver pond grain-size distributions were determined by collecting sediment from both natural and experimentally constructed beaver ponds. Experimental ponds were created by installing dams on study streams in October 2001 using timbers, fence posts, and pond liner (Bilyeu et al., *in press*). One year after pond construction, five 10 cm diameter and 20 cm long vertical cores were collected from each of the seven experimental ponds and the natural pond at Davis Creek by pushing a PVC pipe through the sediment. Grain-size distributions were calculated for the natural and experimental ponds to create beaver pond-sediment signatures.

The sediment grain-size distribution of floodplain soils and willow establishment surfaces were compared to experimental beaver pond signatures using a chi-square test. Samples were classified as pond deposits if

TABLE 1. Results of nonlinear Poisson regression relating willow establishment in Yellowstone National Park, USA, in year t to models including the hydrologic parameters listed for the year of establishment (t), the year before establishment ($t - 1$), the year following establishment ($t + 1$), and so on.

Parameter	df	D	D/df	Pseudo-R^2	P
Annual peak discharge (yellpk)					
t	82	89.18	1.09	0.010	0.357
$t - 1$	82	89.16	1.09	0.010	0.352
$t + 1$	82	90.10	1.10	0.000	0.961
Average annual discharge (yellave)					
t	82	88.45	1.08	0.018	0.157
$t - 1$	82	89.42	1.09	0.008	0.407
$t + 1$	81	88.36	1.09	0.000	0.841
$\Sigma\ t$ and $t - 1$	82	87.71	1.07	0.027	0.134
$\Sigma\ t$ to $t - 2$	82	87.34	1.07	0.031	0.107
$\Sigma\ t$ to $t - 3$	82	87.13	1.06	0.033	0.094
$\Sigma\ t$ to $t - 4$	82	84.63	1.03	0.061	0.021*
Total annual precipitation (precip)					
t	78	83.06	1.06	0.001	0.741
$t - 1$	78	81.59	1.05	0.002	0.706
$t + 1$	77	76.22	0.99	0.054	0.036*
$\Sigma\ t$ and $t - 1$	76	78.08	1.03	0.003	0.643
$\Sigma\ t$ to $t - 2$	75	76.36	1.02	0.002	0.672
$\Sigma\ t$ to $t - 3$	74	74.71	1.01	0.001	0.822
$\Sigma\ t$ to $t - 4$	73	72.69	1.00	0.004	0.600
precip$_{t+1}$ × yellave$_{\Sigma t \text{ to } t-4}$	77	80.42	1.04	0.002	0.676
precip$_{t+1}$ and yellave$_{\Sigma t \text{ to } t-4}$	76	71.92	0.95	0.108	0.033*

Notes: Deviance divided by the degrees of freedom (D/df) = 1 indicates an excellent model fit. Pseudo-R^2 is the proportion of variation explained by the given model that exceeds the variation explained by a model fit using only an intercept term. The P value is calculated from the likelihood ratio statistic in type III analysis.

* $P < 0.05$.

they were statistically similar to, or finer than, the pond sediment signature. Sediment samples more coarse-textured than the pond sediments were considered to be deposited in a flowing water environment and were classified as alluvial sediments. Willows with a pond establishment surface are hereafter referred to as pond willows, and those with an alluvial-sediment surface, as alluvial willows.

RESULTS

Timing and habitat for willow establishment

Willows in our sample (n = 78 plants) established during 49 of the 86 years between the establishment of the oldest plant, in 1917, and our excavation in 2002 (Fig. 3). At least one willow established in each year from 1935 to 1956. The two longest periods lacking establishment were 1931–1934 and 1984–1988. The first establishment gap, in the 1930s, was during the longest period of below-average Yellowstone River annual flow in the past 300 years, and the second, in the 1980s, occurred in the 11th driest decade in the last three centuries (Graumlich et al. 2003).

The largest cohort in our sample contained eight plants that established in 1989, the year after the 1988 fires. This cohort established up to 2.2 m above and 42 m away from the current channels of the study streams. Because this fire disturbance was unique in the 20th century, and produced establishment opportunities that were unrelated to fluvial processes, these eight plants were treated separately, leaving 70 willows for the primary analyses.

Two hydrologic variables were significant predictors of willow establishment (W_t) based on the Poisson regression likelihood ratio tests: (1) total precipitation in the year following establishment, precip$_{t+1}$, and (2) mean annual Yellowstone River discharge in the establishment year plus the previous four years' discharge, yellave$_{\Sigma t-4}$ (Table 1). The positive parameter value associated with the variable precip$_{t+1}$ in the Poisson model, W_t = exp(−1.84 + 3.97precip$_{t+1}$ (P = 0.036 and pseudo-R^2 = 0.05), indicates that willow establishment is positively influenced by precipitation in the year following establishment. The negative parameter value for yellave$_{\Sigma t-4}$ in the Poisson model, W_t = exp(2.08–5.18yellave)$_{\Sigma t-4}$ (P = 0.021 and pseudo-R^2 = 0.06), indicates that willow establishment is inversely related to current and antecedent average annual streamflow. The interaction term of the two significant variables, precip$_{t+1}$ × yellave$_{\Sigma t-4}$, was not significant. A model including both variables, W_t = exp(0.36 + 3.88precip$_{t+1}$ − 4.99yellave)$_{\Sigma t-4}$, was statistically significant (P = 0.033 and pseudo-R^2 = 0.11), and explained 11% of the variability in willow establishment. It is likely that most of the explanatory power of this model is in describing willow establishment that occurs in the last year of a drought, followed by an above average precipitation year. All of the Poisson models fit the data well with little or no overdispersion (D/df ≈ 1).

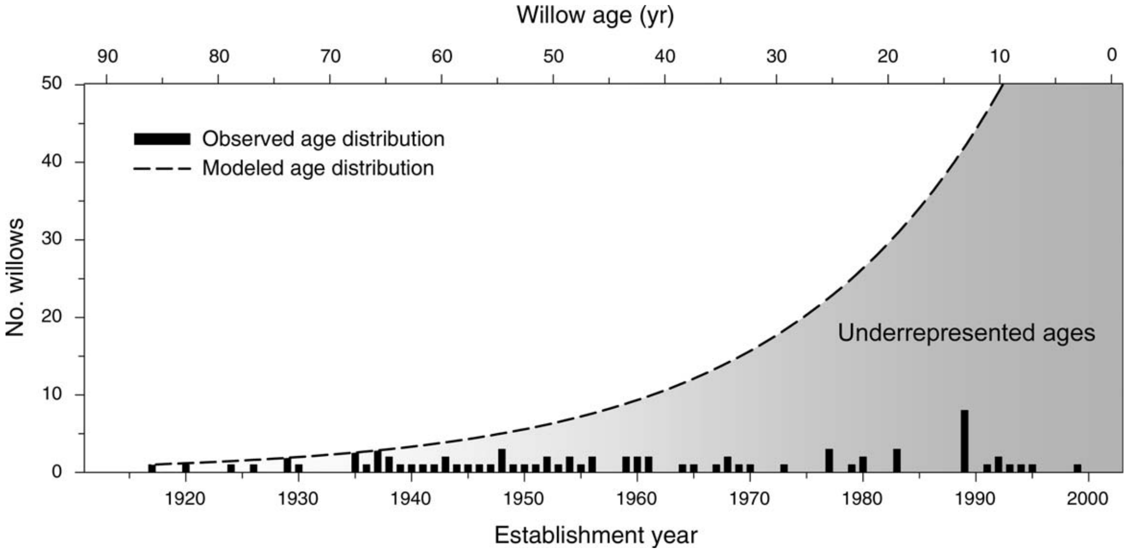

FIG. 4. Age distribution of 78 sample willows compared to a modeled age distribution. The modeled distribution shows the number of individuals expected in a stable population that contains a single 86-year-old individual (see Appendix). The shaded region represents a deficit between the observed and modeled age distributions.

We did not detect interactions between establishment elevation and willow species ($F_{5,64} = 1.03$, $P = 0.401$), elevation and site ($F_{4,65} = 1.52$, $P = 0.218$), or establishment year and species ($F_{5,64} = 1.92$, $P = 0.118$). However, establishment year was related to site ($F_{4,65} = 4.37$, $P = 0.007$). We found that willow establishment years at Lost Creek are significantly later in time than at East Blacktail Creek using Tukey's multiple comparison procedure (mean difference = 24.98, $W = 19.94$, $P = 0.008$). This may be due to bank collapse along East Blacktail Creek, where we observed blocks of soil containing live willows slumping from their original establishment terraces onto channel bottoms, significantly altering their apparent establishment elevation. For this reason we only sampled willows from terraces along East Blacktail Creek, likely skewing our sample toward older willows. Because the one detected age difference between sites was the likely result of a necessary change in sampling protocol and not a functional difference in establishment processes between sites, we determined that pooling all the data was appropriate.

A model of willow population growth (Appendix) showed that hundreds of seedlings are necessary to maintain a stable population containing one 86-year-old plant. The calculated fecundity for adult willows ages 7 through 86 was 11.0 seedlings per adult per year. In comparing the observed willow population to the model, all but the oldest age classes are underrepresented in the Yellowstone willow population (Fig. 4).

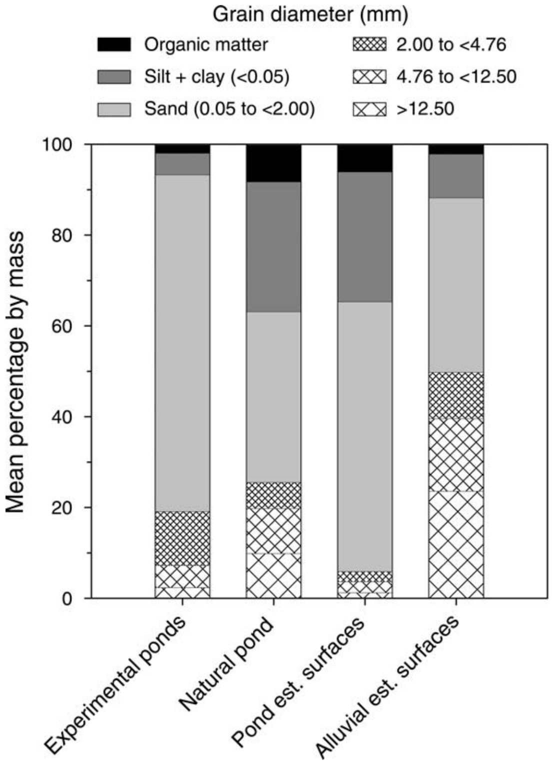

FIG. 5. Grain-size distribution of willow establishment (est.) surface sediments in relation to natural and experimental beaver pond sediments. Establishment surfaces classified as pond deposits are statistically similar to or finer than the site-specific experimental beaver pond sediments.

Sediment analyses

Sand-sized grains (0.05 to <2 mm) comprised 76% ± 4.3% (mean ± SE) of experimental beaver pond sediment, with grains 2 to <4.76 mm comprising 12%

TABLE 2. Comparison of the mean, variance (in parentheses), and variance in residuals after linear regression (italics) for three willow establishment parameters between the two establishment surface groups (pond and alluvium).

Willow establishment parameter	Pond	Alluvium	*P*
Year	1945.3 (196.2)	1969.3 (376.4)	<0.001* (0.052)
Elevation above stream (m)	1.22 (0.264)	0.88 (0.494, *0.241*)	0.027* (0.005,† *0.983*)
Distance from stream (m)	12.95 (81.90)	8.15 (45.76, *18.87*)	0.014* (0.262, *0.003*†)

Note: Italics in the *P* value column indicate the comparison of pond variance with the residuals of alluvium variance after linear regression.

* Significantly different means between pond and alluvium groups for the given parameter ($P < 0.05$, *t* test).

† Significantly different variances between pond and alluvium groups for the given parameter ($P < 0.05$, Levene test).

± 3.4% (Fig. 5). Two coarser and one finer grain-size categories each accounted for <5% of the sediment. Thirty-eight of 70 willows established on surfaces with grain-size distributions statistically similar to ($\chi^2 < 5.991$, df = 2, $P > 0.05$), or finer than, the beaver pond sediments and are classified as pond willows, while 32 established on surfaces with soils more coarse than the pond sediment, and are classified as alluvial willows. Sediment from the natural beaver pond was statistically similar to the experimental beaver pond sediments, yet with higher percentage silt and organic matter. Published grain-size distributions of natural beaver pond sediment (Butler and Malanson 1995, Bigler et al. 2001) indicate that large, long-lived beaver ponds accumulate a high proportion of fine-grained sediment and organic matter, and are similar to the pond willow establishment surfaces in the study area. All 20 plants that established prior to 1943 are pond willows, with the exception of one outlier, a 1917 alluvial willow that established in an abandoned channel. All 31 other alluvial willows established between 1943 and 1999.

Pond willows established earlier in the 20th century, at higher elevations, and further from the current active stream channel than alluvial willows (Table 2). There were also significant differences in the variances of the establishment parameters between pond and alluvial willows, both before and after significant linear trends in the alluvial willow data were removed through regression analyses. No willows established on pond sediment after 1980, except 1989 post-fire cohort plants.

Alluvial willow establishment elevation declined between 1943 and 1999. Younger alluvial willows established at lower elevations relative to the current stream (Fig. 6A) as described by a significant linear trend ($y = -0.03x + 54.50$, $r^2 = 0.48$, $P < 0.001$). There was no significant linear trend in the elevation of pond willows through time. An analysis of the residuals, after linear regression removed the trend from the alluvial willow data, showed no significant difference in the variance of elevation between pond and alluvial willows (Table 2).

Alluvial willows established closer to the current stream channel from 1943 to 1999 (Fig. 6B), following a significant linear trend ($y = -0.22x + 449.8$, $r^2 = 0.46$, $P < 0.001$). There was no significant linear trend in pond willow establishment distance from the stream through time. Once the linear trend is removed by regression, the residual variance of the alluvial willow data is significantly less than that of the variance of pond willow data (Table 2).

Floodplain stratigraphy

Floodplain sediments included unconsolidated layers of fine-grained deposits interbedded with coarse, rounded alluvium. Thirty-seven of 57 strata analyzed had pond grain-size distributions ($\chi^2 < 5.991$, df = 2, $P > 0.05$), and were classified as beaver pond deposits, while the remaining 20 strata were classed as alluvium. All seven cutbanks analyzed contained pond strata ranging from 2 to 63 cm thick, and most had gleyed soil colors and/or oxidized root channels indicative of long-term anoxic soil conditions. Six ^{14}C dates from four of the floodplain stratigraphic sections (Fig. 7) indicated that pond sediments were deposited from 200 ± 90 yr BP to 2070 ± 40 yr BP (Beta Analytic sample numbers 196862, 175930, 161788, 196860, 196866, and 196867; Beta Analytic 2003).

Beaver activity

Archaeological remains (McCracken 1978), fur trapping records (Schullery 1997), and direct observations (Sawyer 1925), indicate that beaver have been present in Yellowstone for thousands of years, and were actively damming small streams on the northern range during the late 19th and early 20th centuries. Warren (1926) noted that beaver were abandoning extensive dam complexes on many small northern range streams, including the Elk Creek and Lost Creek study sites, in the 1920s. A revisit to these sites in 1954 by Jonas (1955) confirmed the patterns of abandonment, and he reported that few beaver were present at that time. In addition, Jonas (1955) noted that stream channel incision through the former beaver pond sediments at Elk Creek and Lost Creek had begun by 1954. Five aerial surveys of beaver colonies, from 1996 to 2003, found no colonies on small northern range streams (Smith 2004). A photographic time series of the Elk Creek study site shows the transition from an active

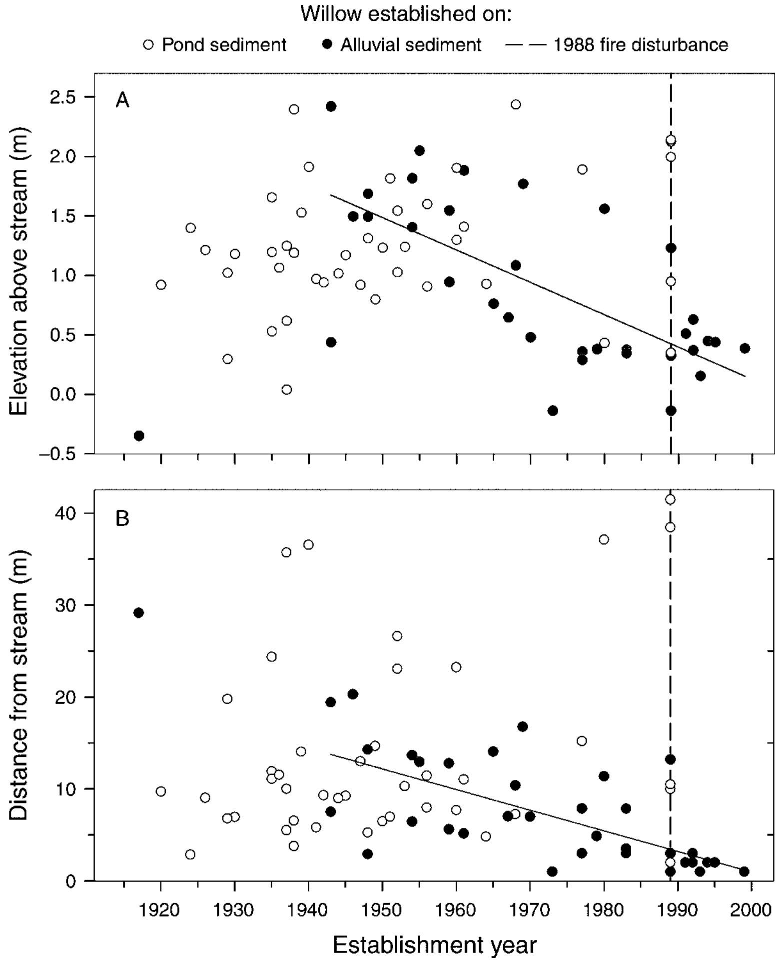

FIG. 6. Willow establishment location as (A) elevation above and (B) distance away from the stream channel through time. Solid black lines are significant linear trends in the alluvial establishment data, excluding 1989 and the 1917 outlier. The fires of 1988 created an on-site disturbance that uniquely influenced the 1989 cohort (dashed line).

beaver dam in 1923 (Warren 1926), to an abandoned dam with a channel incised through it in 1954 (Jonas 1955), to 2002 when the stream had downcut through >2 m of pond sediment (Fig. 8).

DISCUSSION

Seedling establishment and the processes that control it are critical to the long-term persistence of willow-dominated ecosystems (Gage and Cooper 2005, Cooper et al. 2006). Our analyses demonstrate that the fluvial geomorphic and hydrologic settings of small stream willow riparian ecosystems have fundamentally changed in the past century and that willow establishment is severely restricted spatially and temporally. Beaver dams were instrumental in forming and maintaining the floodplains, water table dynamics, and vegetation composition of the study sites. Because willow establishment opportunities are now limited, the potential to grow sufficient food and dam-building material for beavers is dramatically reduced. Because the physical processes of sediment deposition and scour, and water table changes are the primary controls of willow establishment opportunity, the reduction of elk browsing pressure alone is unlikely to increase willow establishment or quickly restore riparian systems to their previous ecological state.

Climate

One possible factor limiting willow establishment and growth on Yellowstone's northern range is the climate, which influences streamflow (Houston 1982). Woody riparian plant establishment is typically correlated with high annual peak and mean discharges, as well as high summer precipitation (Hereford 1984, Hughes 1997, Naiman and Decamps 1997, Cooper et al. 2003, Birken and Cooper 2006). Climate studies have shown a drying and warming trend in the Yellowstone region during the 20th century (Balling et al. 1992*a*, *b*); however Yellowstone River flows during the 20th century exceeded average flows for the 18th and 19th centuries, as reconstructed from tree rings (Graumlich et al. 2003).

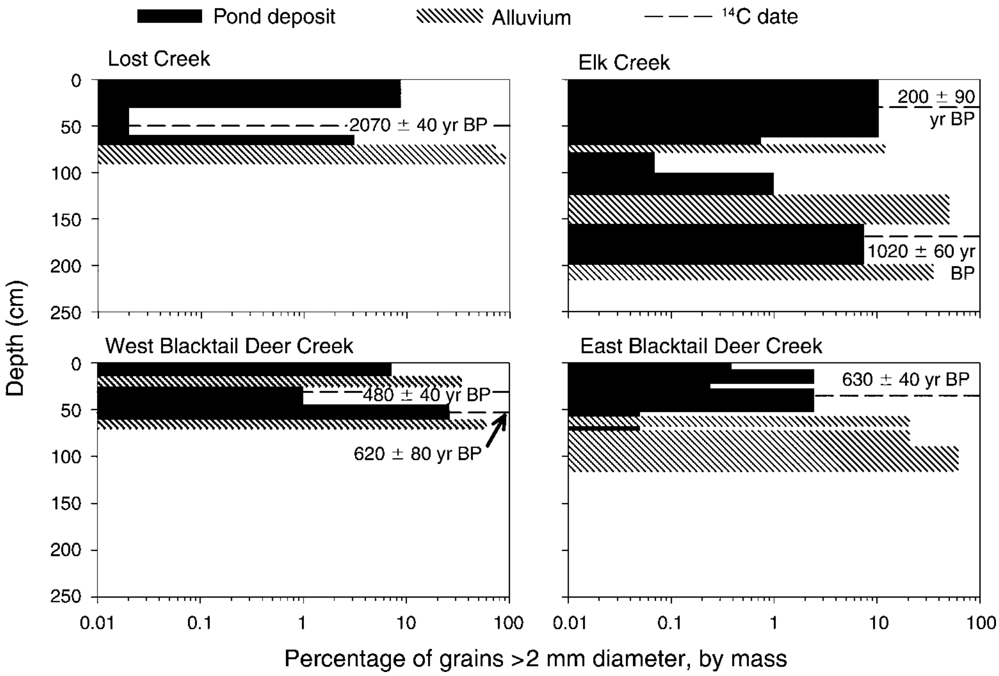

FIG. 7. Floodplain stratigraphic columns with ^{14}C dates, analyzed at cutbanks along the study streams. Depth of 0 is the ground surface at the top of the bank; the maximum depth of strata is at the current stream water level. Dashed lines with dates identify depth and age of ^{14}C samples. Note the *x*-axis log scale.

An exception was the 1930s, when the lowest streamflows of the past 300 years occurred.

Recent vegetation analyses have shown that factors other than climate are more significant drivers of the growth or establishment of willow (Chadde and Kay 1991, Kay 1997), aspen (Ripple and Larsen 2000), or narrowleaf cottonwood (Beschta 2003) in Yellowstone. Our findings indicate that climate is not limiting willow establishment in the study area. Climate-driven hydrologic variables accounted for only 11% of the variability

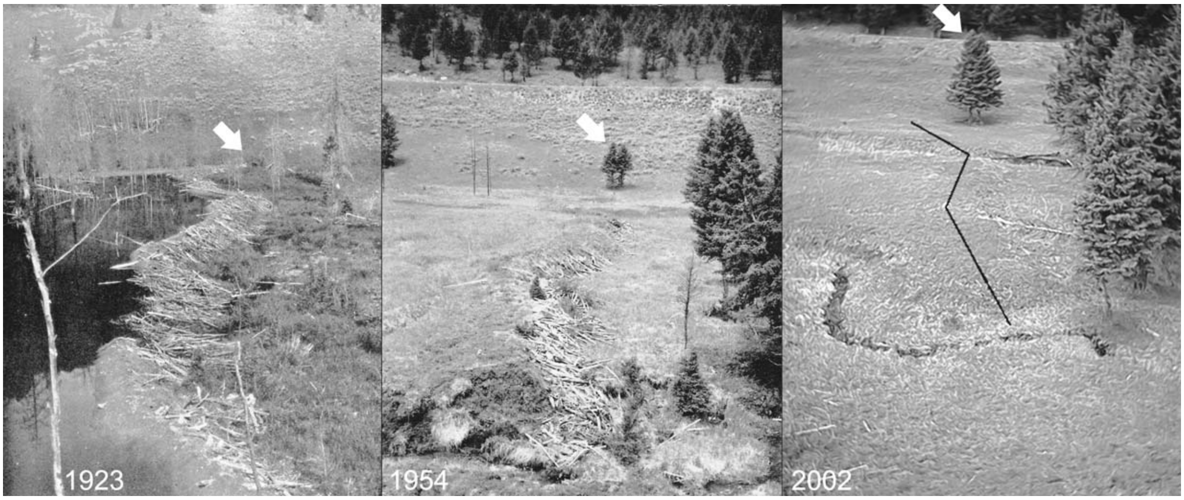

FIG. 8. Matched photos taken facing west from a hillside at Elk Creek. The photo on the left, from 1923 (Warren 1926), shows an ~107 m long dam spanning the entire valley. Warren noted thick willow growth to the right of the dam, and a small breach in the mid-foreground. The center photo, from 1954 (Jonas 1955), shows the dam with aspen logs still present but not holding surface water, the willows had died back, and a channel had cut the dam and upstream sediments, approximately where Warren noted the breach. Our photo from 2002 (right) shows a grass/sedge/lodgepole pine community in place of the willows. The old dam location is marked with a black line and is apparent in the field as a terrace abruptly dropping off to the right (downstream). The main channel in 2002 is in the mid-ground, incised over 2 m deep through the old dam and pond deposits. White arrows show the location of the same pair of lodgepole pine trees.

in our Poisson willow establishment model and were related to drought-ending events: establishment episodes were preceded by years of below average streamflow and followed by a year with higher than normal precipitation. The two largest gaps in willow recruitment occurred during the two most severe drought periods of the 20th century, indicating that water scarcity limits willow establishment, but years with higher flows apparently do not trigger establishment. The nearly continuous willow recruitment in our study areas suggests that willow establishment is not highly sensitive to annual climatic variation. This is likely due to historical willow establishment occurring along beaver pond margins, where the availability of suitable substrate for establishment was controlled by beaver dams, which dampened the effects of high and low water years (Westbrook et al. 2006).

Fire

Fire disturbance can promote the establishment of woody riparian species, including willows (Gruell 1980, MacCracken and Viereck 1990). The 1988 Yellowstone fires produced bare soil through direct burning of litter and exposed hillslope sediment to erosion, allowing establishment of the 1989 willow cohort, the largest in our sample. Some 1989-cohort willows established at elevations >2 m above and >40 m from the current channel, on surfaces isolated from flood disturbance and far above the summer water table depth. This suggests that the 1989 seedlings relied on soil water recharged by precipitation, and benefited from the abundance of bare sediment with little plant competition. Thus bare substrate, not water availability, may limit seedling establishment in most years.

Establishment response to hydrologic changes

In the early to middle 20th century willows established across the entire width of valley bottoms where fine-grained sediment was deposited in beaver ponds. After beavers abandoned the study streams in the 1920s and their dams eroded, streams incised through pond sediment, which lowered floodplain groundwater levels. In post-incision years, after ca. 1950, establishment shifted to alluvial sediments adjacent to streams. The mean and variance of establishment distance from the stream and the mean establishment elevation declined significantly. From 1981 to 2002, willow establishment occurred exclusively on alluvium at approximately one-third the valley width, and approximately one-third the elevation range as compared to earlier in the 20th century.

The presence of relatively high-elevation, coarse-textured alluvial willow establishment surfaces during the 1940s and 1950s indicates that stream channels at that time were 1–2 m above their current elevations. As alluvial willow establishment surfaces linearly declined in elevation, pond willow establishment ceased altogether, indicating a change in geomorphic environment from high elevation, fine-grained beaver pond sediments to high-energy, incising, coarse-grained stream channels. Willows preferentially establish on fine-textured sediments (McBride and Strahan 1984), which have high water-holding capacity. In addition, young willows are often uprooted by fast-flowing water (Gage and Cooper 2004). Thus, establishment has become limited by a reduction in the extent and suitability of bare sediments, due to the shift in riparian setting from beaver ponds to high-energy channel margins.

Beaver

Floodplains of the study streams contain layers of sediment deposited in ponded environments over the past 1000–2000 years, indicating that beavers have been present periodically or continuously for thousands of years. The wide, flat-bottomed valley forms of the study streams are termed "beaver meadows," and are produced by long-term beaver damming and fine-grained sediment accumulation (Ruedemann and Schoonmaker 1938, Ives 1942, Dalquest et al. 1990). Beavers can persist indefinitely within stream reaches if sufficient food is present (Hall 1960), or their activity may be dynamic as the animals shift locations to follow high density food sources (Hughes 1997). Continued or recurring beaver activity on the study streams maintained the long-term pattern of vertical sediment accretion in valley bottoms until the middle 20th century.

When beavers abandoned the study streams in the 1920s, likely due to reduced food and building material caused by increased elk browsing of willows, significant hydrologic, geomorphic, and ecological changes occurred. Although the hydrologic influence of beaver dams can last for decades following abandonment (Naiman et al. 1988), once dams breach, the pond sediments are subject to erosion (Woo and Waddington 1990). Our data, and previous observations (Jonas 1955) indicate that channel incision began in ca. 1950, 20–30 years after beaver abandoned the study streams, and fluvial geomorphic processes changed from aggrading beaver ponds (Meentemeyer and Butler 1999) to channelized flows.

During the period of beaver occupation, the floodplain water table was near the soil surface during the growing season (Warren 1926), while today the water table averages 1 to >2 m beneath the former floodplain (Bilyeu et al., *in press*). Incision of the study streams has isolated the channels from their former floodplains and allowed the invasion of upland plants, including grasses, sagebrush, herbaceous dicots, and lodgepole pine. Similar effects of incision have been seen along the larger Gallatin River, ~50 km west of our study sites (Beschta and Ripple 2006).

Elk

The reduced frequency of willow establishment during the 20th century is likely both a direct and indirect result of elk browsing. Direct results of browsing are well documented and include reduced seed production (Kay 1994, Gage and Cooper 2005) and increased plant mortality (Kay 1990). The main indirect result is the competitive exclusion of beavers (Baker et al. 2005), which can trigger dramatic changes in the hydrologic and geomorphic regimes as documented here. The increase in elk browsing after wolf extirpation in ca. 1920 coincided with the timing of beaver dam abandonment, and heavy browsing appears to contribute to the continued exclusion of beaver on these streams.

Landscape changes

Our conceptual model explains state transitions between beaver–willow and elk–grassland communities (Fig. 1). The beaver–willow state occurs when large herbivores, such as elk, are present but not overly abundant, and their browsing pressure is moderated by wolf predation (Fig. 1A). In this state, beavers share the northern range with elk. Beavers cut tall willows and use the stems to construct dams. Dams impound water, maintain wide floodplains, and accumulate fine-textured and nutrient rich sediment (Gurnell 1998, Palmer et al. 2000). The location of beaver dams varies over time because beaver foraging and willow cutting reduces the local abundance of tall willows. Because short willows are structurally inadequate for dam building and repair, beavers eventually abandon dams where tall willows are depleted, and move elsewhere to create new dams or rebuild old ones (Baker and Hill 2003). This dynamic causes ponds to form and drain, exposing bare wet sediment, which is ideal substrate for willow seedling establishment (Woods and Cooper 2005, Cooper et al. 2006). In the presence of wolf predation, which limits elk herbivory, short, beaver-utilized willows quickly recover their tall stature, and active or periodically maintained beaver ponds provide abundant willow establishment opportunities. This produces stands of tall, abundant willows that then become suitable for beaver recolonization. At the landscape scale this state is stable because beavers engineer habitat for willows, and willows provide resources exploited by beavers (Baker and Hill 2003).

The removal of wolf predation eliminated a major constraint on elk browsing, resulted in short willows, which shifted the ecosystem from loop 1 in our conceptual model, to loop 2 (Fig. 1). Without the regrowth of tall willows, beaver were unable to build and maintain dams along stream reaches. Consequently dams remained abandoned, fell into disrepair, were completely breached by streamflows within 20–30 years, and the stream channel eroded through the fine-grained pond sediment. Stream incision is the ecological threshold that transitions the riparian ecosystems from one stable state (beaver–willow) to an alternative state (elk–grassland) by creating deep water tables and a narrow and deeply incised channel, limiting willow establishment to channel margins, and eliminating the connection between the stream and its former floodplain.

In the elk–grassland state willows are marginalized and perennial grasses, upland shrubs, and herbaceous dicots dominate riparian zones. The elk–grassland state may resist reversal, even when herbivory is reduced by the reintroduction of wolves, due to the dramatic changes in stream morphology and functioning (Fig. 1B). The loss of beaver dams promoted stream channel incision, which lowered the alluvial water table (Collen and Gibson 2001), and created drier riparian zone soils, increased water stress in willows (Bilyeu et al., *in press*), and limited habitat for willow seedling establishment. Winter elk browsing removes the previous year's stems, where catkins would form the following summer, thus reducing seed rain and amplifying the effect of reduced establishment sites.

The return of the gray wolf, an apex predator, to the Greater Yellowstone Ecosystem illustrates the value in restoring critical ecological components to the region. Evidence of willow height recovery following wolf reintroduction has been documented for Yellowstone (Ripple and Beschta 2004, 2006) and Banff National Parks (Hebblewhite et al. 2005). However, height recovery of the sparse and declining willow populations may not be sufficient to restore the historical riparian ecosystem state.

Management options

The transition from the current elk–grassland state to the beaver–willow state might be facilitated by two short-term management activities, (1) the construction of artificial ponds, and (2) the fencing of riparian zones. Artificial dams could function like natural ponds, raising local water tables, and enhancing opportunities for willow establishment, while circumventing the need for large willow or aspen stems for beavers to build natural dams. Beavers are present along small streams in the study area, but not residents, and during the spring of 2003 they occupied one of our experimental beaver ponds on the East Fork of Blacktail Creek, creating bank dens and cutting willow stems. Although the pond provided an initial refuge, the site was occupied for only a short time, likely due to insufficient willow and aspen to supply their needs. Fencing riparian zones for one or more decades would eliminate ungulate herbivory and, along with the higher water tables maintained by artificial dams, maximize willow growth and opportunities for willow establishment (Bilyeu et al., *in press*).

The one major fire of the 20th century created significant establishment opportunities for willows. Maintaining the natural fire frequency along small streams with willow communities may stimulate willow establishment.

Aspen, another preferred food and dam-building material (Warren 1926), are in poor condition in the study sites. Heavily browsed short-stature aspen stems are present, but tree-sized aspen have been absent since ca. 1920 (Romme et al. 1995, Ripple and Larsen 2000, Ripple et al. 2001). Beaver colonies on small, steep-gradient streams on the northern range occurred historically in Yellowstone (Warren 1926), and occur today outside of Yellowstone National Park on the Gallatin National Forest, where aspen is a primary food and dam-building material (D. Tyers, *personal communication*). Regrowth of tree-sized aspen, along with willow recovery, may be critical to the return of beaver to their historical range.

CONCLUSIONS

Our observations provide additional evidence that the removal of an apex predator from a terrestrial food web can result in profound changes in the structure and functioning of ecosystems. The loss of wolves from the northern range of Yellowstone National Park appears strongly connected to compression of the landscape area where willows can establish and severely reduced establishment rates. These changes are associated with the loss of beaver from the ecosystem.

Can the reintroduction of predators to the food web reverse the changes that followed the loss of beaver? We offer evidence that the elk–grassland state that developed after wolf removal may resist change back to the beaver–willow state, even if browsing is reduced. Hydrologic changes in stream networks, specifically stream incision, are not rapidly reversed, particularly in the absence of beaver. If lower water tables create physiological stress in willows, their height recovery may be limited, which may prohibit the return of beaver to most stream networks.

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APPENDIX

The population model used to generate a static age distribution of a stable willow population (*Ecological Archives* A017-066-A1).