THESIS

BARRIERS TO ESTABLISHMENT AND GROWTH OF COTTONWOODS IN YELLOWSTONE NATIONAL PARK'S NORTHERN RANGE

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ABSTRACT

BARRIERS TO ESTABLISHMENT AND GROWTH OF COTTONWOODS IN YELLOWSTONE NATIONAL PARK'S NORTHERN RANGE

Riparian ecosystems play a vital role in water storage, sediment retention, nutrient and contaminant removal, and wildlife habitat in western North American landscapes. Cottonwood (*Populus* spp.) trees form the principle riparian forest type in the semi-arid western United States and therefore understanding their abundance and processes affecting establishment and survival are critical. Within Yellowstone National Park (YNP) herbivory by ungulates shapes ecosystem structure and function of riparian forests. However, our understanding of the interactions between herbivores and cottonwoods is largely from studies of domestic livestock grazing and may not reflect free ranging herds of wild ungulates.

In this study I quantify the influence of stream hydrologic regime and herbivory on cottonwood establishment and growth along three rivers in Yellowstone's northern range. My research addresses three questions: 1) What is the current distribution and composition of cottonwood communities? 2) What is the relative influence of ungulates and hydrologic regime on cottonwood establishment? 3) Does herbivory by ungulates limit cottonwood height?

Approximately 500,000 of the 1.9 million cottonwoods in Yellowstone established between 1996 and 1998, the years immediately following wolf (*Canis lupus*) reintroduction to YNP. Recruitment was driven by the largest sequence of peak stream flows in the 20th century. The flows caused large scale channel changes, and provided suitable habitat for cottonwood seedling establishment and survival. The Lamar River cottonwood forest appears to regenerate following infrequent to rare large peak flow events as occur on many streams in western North America. However, Soda Butte Creek and the Gardner River cottonwoods exhibited nearly annual recruitment similar to other low-order montane streams. For the three rivers studied, over 92% of cottonwoods occur along the Lamar River. After the 1997 flood, establishment has been nearly continuous on the Lamar River with the resulting cottonwood biomass exceeding herbivore demand. However, even with their relatively low consumption rates bison are able to remove a significant proportion of total cottonwood production in the study areas and limit plant height and forage available to wintering elk.

In the absence of human perturbation of bison populations, either in pre-history or today, bison and other ungulates shape their environment. Future investigation of how these species shape the structure of their environment will serve to inform management decisions and educate park visitors on habitat dynamics in a multi-herbivore system.

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1. INTRODUCTION

Riparian ecosystems play a vital role in water storage, sediment retention, nutrient and contaminant removal, and wildlife habitat in western North American landscapes (NRC 1995, 2002). The importance of riparian ecosystems to wildlife is evident in their disproportionate use of these habitats (Thomas 1979). Specifically, riparian forests provide essential sources of food and cover to many species of birds and mammals (Hunter et al. 1987, Naiman et al. 1993, Knopf and Samson 1994, Martinsen and Whitham 1994, Clements et al. 2011).

Cottonwood (*Populus* spp.) trees form the principle riparian forest type in the semi-arid western United States and therefore understanding their abundance and processes affecting establishment and survival are critical. Extensive research has focused on seedling establishment (Baker 1990, Scott et al. 1997, Kranjcec et al. 1998, Cooper et al. 1999, Roberts 1999, Friedman and Lee 2002, Lytle and Merritt 2004). Cottonwoods are prolific seed producers although seed viability may be as short as a few weeks (Moss 1937, Schweitzer et al. 2002). Establishment occurs over 3-7 years (Willms et al. 2006) when several hydrologic factors are critical: 1) the peak discharge magnitude must be sufficient to create bare and wet mineral soils for seed germination, and a 1 in 10-year peak discharge is generally sufficient to provide the needed disturbance, 2) for several years the summer water table must support seedling growth, 3) the timing of peak flow must occur prior to seed dispersal, 4) peak flows in the years following germination must be large enough to wet floodplain soils but not cause seedling mortality through physical removal or burial of seedlings (Baker 1990, Scott et al. 1996, Scott et al. 1997, Mahoney and Rood 1998, Cooper et al. 1999, Cooper et al. 2003).

Asexual reproduction is an important recruitment process for some cottonwood species (Rood et al. 1994, Schweitzer et al. 2002). Herbivory and disturbance by large floods can induce root sprouting (Kalischuk et al. 2001). Transport of branches by beaver (*Castor canadensis*) and physical removal of branches or whole stems during large floods can also result in asexual reproduction through branch propagation (Kalischuk et al. 2001, Rood et al. 2003). Asexual reproduction allows individual trees to extend their influence in space and time until conditions occur that are suitable for sexual reproduction (Eriksson 1992, Gardner and Mangel 1997, Schweitzer et al. 2002). Although hydrologic factors play an important role in determining whether a seedling establishes, herbivores can significantly influence the post-establishment structure of riparian ecosystems (Case and Kauffman 1997, Andersen and Cooper 2000, Andersen 2005).

Herbivory by ungulates shapes ecosystem structure and function in Yellowstone National Park (YNP). Competitive interactions between beaver and elk (*Cervus elaphus*) have converted landscapes with a beaver-pond and willow mosaic to one where beaver dams and tall willow communities are largely absent (Wolf et al. 2007). Recovery of these ecosystems is uncertain due to changes in stream channels (Wolf et al. 2007). The effect of wildlife on cottonwood communities is evident across Yellowstone's northern winter range. Browsing by wild ungulates in the Lamar Valley and Soda Butte Creek drainages has resulted in short stature and hedged cottonwoods (Keigley 1997). However, our understanding of the interactions between herbivores and cottonwoods is largely due to studies of domestic livestock grazing (Auble and Scott 1998, Lucas et al. 2004, Samuelson and Rood 2004) and may not reflect free ranging herds of wild ungulates (Wisdom et al. 2006).

Within YNP three large herbivores heavily utilize cottonwoods: beaver, elk, and bison (*Bison bison*). Beaver are widely distributed but uncommon in YNP and only one colony was known to be associated with cottonwoods in recent years (Smith 1998). Elk populations and cottonwood abundance have been the focus of most previous studies (Keigley 1997, 1998, Ripple and Beschta 2003, 2004, Beschta 2005). The importance of herbivory and multiple hydrologic factors on cottonwood establishment and growth has not been previously studied.

In this study I quantify the influence of stream hydrologic regime and herbivory on cottonwood establishment and growth along three rivers in Yellowstone's northern range. My research addresses three questions: 1) What is the current distribution and composition of cottonwood communities? 2) What is the relative influence of ungulates and hydrologic regime on cottonwood establishment? 3) Does herbivory by ungulates limit cottonwood height?

2. SITE DESCRIPTION

The study was conducted along three rivers in YNP, the Lamar River, Gardner River, and Soda Butte Creek (Figure 1). The Lamar River (Lamar) study area extended from 2km downstream of Opal Creek to the western edge of the Lamar Valley. The reach was divided into an upper (1), middle (2), and lower (3) sub-reach based upon channel morphological characteristics and cottonwood presence. The upper reach began at 2,018 m elevation and extends to its confluence with Soda Butte Creek at 2,013 m elevation. This floodplain reach is entrenched, approximately 400 m wide, with medium sized cobbles and a ground surface largely of bare mineral soil with small stands of cottonwoods and willows (*Salix* spp). The middle reach extends from the upper reach to just above the Lamar Ranger Station at 1,992 m elevation. The channel is highly entrenched and slightly braided with little or no floodplain. Small patches of cottonwood occur on river margins and bars and one mature stand is present. Sagebrush (*Artemisia tridentate* Nutt.) and bunch grasses are the primary species on bank edges, with smooth brome (*Bromus inermis* Leyss) in low-lying areas. The lower reach is nearly double the length of the middle and upper reaches and extends to the valley exit at 1,971 m elevation. It is characterized by an approximately 600 m wide floodplain with a braided channel. Small stands of cottonwood and willow occur on the floodplain, smooth brome in low-lying areas, and sagebrush and bunch grasses in drier areas.

The Soda Butte Creek (Soda Butte) study area extended from below Round Prairie at 2,039 m elevation to the confluence with the Lamar River at 2,013 m elevation. The upper portion of the study area is highly entrenched and cottonwoods and willows occur on the channel margin, lodgepole pine with mixed shrub and bunch grass understory on the banks, and an island just below the start of this reach supports cottonwood, willow, and pine with a mixed shrub and sparse bunch grass understory. Much of the island is bare mineral soil. Approximately 700 m downstream from the beginning of the study area to its terminus at the Lamar River has a braided channel with a low gradient floodplain approximately 250 m wide. Cottonwoods and willows dominate the floodplain vegetation, although large areas lack woody plants.

The Gardner River (Gardner) study area extended from the highway bridge southeast of Mammoth Hot Springs at 1,787 m elevation to the confluence with the Yellowstone River at 1,608 m elevation. The Gardner River is entrenched into tuff parent material. A single thread channel occupies most of the reach and floodplain development is limited in some reaches. Cottonwoods dominate floodplain vegetation with few willows or grasses.

3. METHODS

3.1 Current and Historic Cottonwood Establishment

3.1.1 Peak Flow Modeling and Flood Frequency

Stream discharge records were obtained from the United States Geological Survey gauging network for the Yellowstone River at Corwin Springs (USGS No. 06191500), Gardner River near Mammoth YNP (USGS No. 06191000), Lamar River near Tower Ranger Station YNP (USGS No. 06188000), and Soda Butte Creek near Lamar Ranger Station YNP (USGS No. 06187950). Daily discharge records exist for the Yellowstone River from 1911 to 2010 and periodic peak and daily discharge data are available for Lamar, Gardner and Soda Butte. The annual peak discharge of the Yellowstone River was significantly correlated to that of Lamar ($N = 71$, $r = 0.92$, $P < 0.001$), Gardner ($N = 61$, $r = 0.88$, $P < 0.001$), and Soda Butte ($N = 19$, $r = 0.82$, $P < 0.001$), allowing models based on Yellowstone River discharges to fill gaps in these records. Models were selected that minimized the residuals across available records resulting in the selection of the following parameters:

X_d) Yellowstone River peak discharge in cubic meters per second (m^3/s) for that year

X_r) Wiebull rank of Yellowstone River discharge from 1911 to 2010 for that year

Regression analysis resulted in the following equations for the study rivers:

$$Lamar\ peak\ discharge\ (\mathrm{m^3/s}) = 0.7227x_d + 0.7018x_r - 135.2826$$

$$Gardner\ peak\ discharge\ (\mathrm{m^3/s}) = 0.02610x_d - 0.26181x_r + 35.20317$$

$$Soda\ Butte\ discharge\ (\mathrm{m^3/s}) = 0.01609x_d - 0.28435x_r + 46.18509$$

Flood-frequency analysis was performed utilizing USGS software PeakFQ 5.2, with Pearson Type III frequency distribution to identify years that had an exceedance probability < 0.1 (Flynn 2006).

3.1.2 Hydrogeomorphic Disturbance

Aerial photos obtained from Yellowstone National Park, USGS Earth Explorer, National Geo-spatial Intelligence Agency (NGA) and the Yellowstone Ecological Research Center (YERC) (Table 1) were geo-referenced using ArcGIS®, the channel digitized, and flow lines developed (Robertson-Rintoul 1993). The last year of the photo period was used to identify each period (e.g. 1999 for photo period 1994 to 1999).

Total sinuosity was used to quantify channel change between photos for each river. Total sinuosity was calculated as:

$$P = \frac{\sum L}{R}$$

where P = *total sinuosity*, L = *channel length*, and R = *reach length* (Hong 1979).

Although total sinuosity was used to analyze long-term patterns of channel change, it could not be used to quantify channel avulsion. I measured new channel length formed in a given photo period by removing flow lines where previous and current year channels overlapped (Figure 2). The flow lines that remained were channel that formed between the photo dates.

All statistical analyses and modeling were performed in R version 2.13.0 with the “stats” package (R Development Core Team 2011) unless otherwise referenced. Analysis of Variance (ANOVA) and Tukey multiple comparison adjustments were utilized to compare river, year, and reach (Lamar only) for total sinuosity and new channel length. To ensure comparison between approximately equal time periods the analysis of interactions with river were performed for years with photos available for the Gardner. If photo years did not match, comparisons were performed with the next closest photo year of Lamar and Soda Butte. Regression analysis was performed using the new channel lengths and mean peak discharge over each photo period.

3.1.3 Cottonwood Establishment and Density

Cottonwood trees were collected for precision age analysis in 2007 and 2008. In 2007, 100 trees were sampled to represent the full range of tree sizes present in the study area and each size class was equally sampled. During 2008, 40 points were randomly generated on Soda Butte and Lamar, and 20 on the Gardner, in cottonwood stands. The nearest cottonwood to each point that had a basal diameter <30 cm at the ground surface and a height ≤6 m was collected. Trees selected for harvest were marked at the ground surface and the plant was excavated using hand tools to a depth sufficient to collect the root crown. Each tree was cut into 2-5 cm long sections and the point of germination was identified as the section where the pith originated (Everitt 1968, Scott et al. 1996, Cooper et al. 2003). Each section was sanded with progressively finer paper to 400 grit and annual rings counted using a binocular microscope along a minimum of two transects radiating from the pith.

Cottonwood stands rather than individual trees were mapped because of the large number of saplings and seedlings. Homogenous stands were identified using patterns of landform and estimates of tree density. In 2007, 59, 21, and 11 stands were randomly selected representing 0.40, 0.45 and 0.61 of the total stand area along Lamar, Soda Butte, and Gardner. Five points were randomly generated within each stand using ARCGIS® for quantifying tree density. Plot size varied from 4 to 100 m^2 in size where tree density was estimated to be <1 plant/m^2 and was determined by the largest plot that could fit within the stand boundaries. Where plant densities exceeded 1/m^2 a 1 m^2 plot was used. Height and crown diameter were measured for each plant in each plot. Population estimates were generated for each river by multiplying the total stand area by the areal weighted mean density to minimize the effects of small stands with high tree density.

Analysis of a randomly sampled population was ensured by using tree samples collected in 2008. Tree density and establishment year data were not normally distributed. Therefore, means were compared using a Kruskal-Wallis test, and 95% confidence intervals about the mean were developed via a non-parametric bootstrap with 10,000 iterations. Comparison of distributions was performed with a Komorogov-Smirnov test with bootstrapping in R and the "Matching" package (Sekhon 2011). Within each study river plants were separated into two groups, those <20 and >150, and those 20 – 150 cm tall. Regression analysis was utilized to identify relationships between plant age and height.

3.1.4 Mature Cottonwood Stand Characterization

Trees with a bole diameter >10 cm at the ground surface were mapped using a hand held Trimble® GPS unit in 2007. Tree diameter was the mean of two perpendicular bole measurements. Trees were placed into one of five size classes < 30, 31 - 50, 51 - 70, 71 - 100, and > 100 cm and identified to species and sex. Species were determined using leaf and bole morphology, crown diameter, and plant structures and sex by the presence or absence of female catkins (Brayshaw 1996, Dorn 2001, Hardin 2001). The species present were *Populus trichocarpa* Torr. & A. Gray ex. Hook and *Populus angustifolia* James, as well as intersectional hybrids.

Size class, sex and species count data were analyzed by comparing the proportion of individuals in each class by sample (river) (Ott and Longnecker 2001). To identify significant differences in proportions between rivers, contingency tables and Fisher's exact test for count data were utilized. Analysis was performed in R with the "gmodels" package (Warnes 2011).

3.1.5 Factors Influencing Cottonwood Establishment

I modeled tree establishment for the period 1984 through 2004 to investigate the relative importance of hydrologic factors and ungulate populations on cottonwood establishment. This period was selected because it includes periods of limited and extensive establishment on all three rivers and excludes the most recent establishment years where mass mortality is likely (Anderson and Cooper 2000, Polzin and Rood 2006). A bootstrapped Komorogov-Smirnov test (Sekhon 2011) was used to assess the validity of pooling 2007 and 2008 age data with a p-value ≈ 1 for all three rivers. Logistic regression was performed on pooled count and presence/absence data using negative binomial and binomial distributions in the "pscl" package (Jackman 2011). The Poisson distribution was not used because the sample variance exceeded the mean for count data. Correlation of each variable with patterns of cottonwood establishment was analyzed separately. Goodness of fit for each model was assessed using deviance (Dev) over degrees of freedom (df), with $Dev/df = 1$ indicating a good fit. The significance of each variable and the variation it explained was assessed using ANOVA with a chi-squared test and Mcfadden's Pseudo-R^2. The relative importance of each variable was assessed by calculating AIC_C scores and Akaike weights for each model (Burnham and Anderson 2002). Significant establishment of cottonwoods occurred along all three rivers during the decade of the 1990's. Comparisons of hydrologic factors and ungulate populations from years prior to and following 1990 were performed using ANOVA. Missing values in population count data for elk (E) and bison (B) were linearly interpolated for regression analysis; however, years with missing population counts were not used in comparisons of ungulates pre and post 1990.

The magnitude of disturbance is represented by peak discharge for the current (X_t) and following two years (X_{t+1}, X_{t+2}) from reconstructed peak discharges. The date of annual peak discharge (P_t) for each study river was converted to days after April 30th. The date of annual peak discharge on the Yellowstone River was substituted for missing values on the study rivers. Mean discharge on August 1st of each year was used as a proxy for late summer water table depth (*D)*. I assumed that increasing discharge resulted in higher water table and a positive relationship between count data and discharge. August 1st mean daily discharge on the Yellowstone River was used to reconstruct Lamar (N = 20, r = 0.88, $P < 0.05$) and Lamar recorded and reconstructed values were used to reconstruct Soda Butte (N = 20, r = 0.94, $P < 0.05$).

3.2 Barriers to Cottonwood Growth

3.2.1 Production and Herbivory Estimates

Biomass estimates of current annual growth (CAG) were developed from 5 plants of varying heights and crown diameters. All CAG was removed, oven dried, and stem and leaf material were weighed separately. The sum of plant height and crown diameter was significantly correlated with the log of total (N = 5, r = 0.996, $P < 0.001$), stem (N = 5, r = 0.984, $P < 0.01$), and leaf biomass (N = 5, r = 0.983, $P < 0.01$). Regression equations of CAG vs. biomass are;

Total Biomass (g) $y_t = e^{2.017+0.0167x_{ch}}$

Stem Biomass (g) $y_s = e^{1.042+0.0168x_{ch}}$

Where y_t is the dry-matter weight of total CAG, y_s is the dry-matter weight of stem CAG, and x_{ch} is the sum of plant height and crown diameter in cm.

Production estimates were developed for two groups of stands, those with mean height < 20 cm, and > 20 cm. Height classification for production estimates was used to account for cottonwoods < 20 cm that represented small land areas but a large number of plants. Within each height class regression equations were applied to each stand's mean crown and height. Production estimates for total and stem biomass along each river are areally weighted biomass per plant multiplied by the population estimate for each height class.

To develop estimates of large mammal herbivory on cottonwoods, plots were exclosed in eight locations: two each along Gardner and Soda Butte, and four along Lamar (Figure 3). Plots represented the full range of spatial distribution and floodplain elevation occupied by cottonwood. Two plots per location were designated for summer or winter herbivory measures, 110 x 110 cm were established around 1 to 5 individual plants located approximately 5 m apart. Seasonality of exposure to herbivory was controlled by moving exclosures from the summer to winter plot. Five plants or basal branches were tagged and measurements of basal diameter, tip diameter, and length were measured in fall 2008 and spring 2009 within each exclosure using methods of Bilyeu et al. (2007).

Stems 2 to 90 cm long were selected on the 5 plants used for production estimates. Basal diameter (cm) was significantly correlated to the square root of stem weight (g) (N = 100, r = 0.96, $P < 0.05$) and the following equation was used to estimate biomass production and removal at each plot.

$$y_{st} = (-0.4649767 + 4.5244836x_s)^2$$

Where x_s is the stem diameter in cm and y_{st} is the stem weight in grams. Biomass removed was the mass estimated from the basal diameter minus mass estimated for the tip diameter. Individual stem estimates were summed for each plant to estimate total production and biomass removed per plant.

Data were not normally distributed. Therefore, means were compared using a Kruskal-Wallis test, and 95% confidence intervals about the mean were developed via a non-parametric bootstrap with 10,000 iterations.

3.2.2 Cottonwood Production versus Consumption

The impact of bison and elk herbivory on cottonwoods was assessed using three models, one for theoretical populations of 0-2000 animals, one for population count data acquired from YNP for 1970-2007, and one representing a diet composed of 1% cottonwoods over several months against cumulative production of cottonwoods from 1970-2007. Elk and bison distributions from the Lamar Valley were used because the majority of cottonwoods are along Lamar. Winter distribution of collared elk between 1963 and 2007 resulted in 0 to 21% of the animals residing in the Lamar Valley with a mean of 7.75% (White et al. 2010). Although no specific distribution estimates were identified, bison are present throughout the year (Meagher 1973, Olexa and Gogan 2007) and congregate in the valley during the rut (Olexa and Gogan 2007, Wallen 2011). It was assumed that no more than 10% of the northern range elk or 70% of bison utilized the study cottonwood stands in a given month. The proportion of browse consumed by elk and bison varies by season, population, and forage type (Reynolds et al. 2003, Christianson and Creel 2007). A linear relationship was assumed between animal numbers and cottonwood in the animal's diet and ranged from 1-20% of total monthly consumption. A continuous record of elk population was developed by linearly interpolating elk counts between years. Northern range bison counts were utilized and missing values were linearly interpolated. Total production estimates from 2007 and 2008 were used as the biomass of cottonwood available to ungulate populations. The proportion of this production that could be utilized was not quantified in this study and it was assumed that all stem biomass produced was available as forage for both species.

Data on the mean body mass, age and sex ratios were used to develop a weighted mean body mass for elk (Quimby and Johnson 1951, Wyman 2010, Montana Fish Wildlife and Parks unpublished data) and bison (Reynolds et al. 2003, Wallen 2011). Bison were observed browsing on cottonwoods primarily during the summer months, while elk occupy these low elevation portions of the northern range in the winter from November through April or May (Craighead et al. 1972, White et al. 2010). Forage intake rates were set at 3% and 2.5% of mean body mass for bison and elk to reflect the seasonal effect on maximal intake rate (Coughenour 2005). Calf bison consumption rates during summer are assumed to be zero. During the summer bison consume leaves and stems while wintering elk only have stems available as forage. To facilitate comparisons of consumption rate of elk and bison, total consumption rates for bison were standardized by weighting total consumption by the ratio of stem weight to total production (0.38).

4. RESULTS

4.1 Current and Historic Cottonwood Establishment

4.1.1 Peak Flow Modeling and Flood Frequency

Peak flow models and recorded means were nearly equal for the three rivers and standard deviations were within 4% of their means (Table 2). Models underestimated the large discharge events of 1996 and 1997 and for Lamar and Gardner underestimates occurred during low discharge years including those in the 1940’s (Figure 4).

The historical recorded and reconstructed 10-year exceedance discharges were similar (Table 1). Flood-frequency analysis revealed that few flows exceeding the 10-year discharge occurred between the 1930's and the mid 1950's on all three study rivers (Figure 5). In particular Lamar had only 1 year that exceeded the 10-year discharge between 1919 and 1994 in the available and reconstructed records. Thus 67% of the 10-year exceedance discharges occurred after 1995 for Lamar and 30% after 1995 on Gardner and Soda Butte.

4.1.2 Hydrogeomorphic Disturbance

New channel lengths differed among reaches (Table 3) and year for Lamar (Table 4) with the period 1994-99 having significantly greater channel formation than all periods except 2006-09. New channel averaged ~26% in reach one, ~7% in reach two, and 40% in reach three over the period of record. The mean percentage of new channel formed was significantly greater ($P < 0.05$) after 1999 with reach one increasing nearly 3.5 times above pre-1994 and nearly double the 1954-2009 average (Table 5).

Total sinuosity and new channel length differed significantly by river ($P < 0.05$). Only new channel length varied by year ($P < 0.05$) and 1991-94 vs. 1994-99 was the only significant comparison ($P < 0.05$). New channel formed on Lamar in 1994-99 was outside the 95% confidence intervals across all rivers (Figure 6). The correlation between new channel length and mean peak discharge for each photo period was significant for Lamar (N=12, r = 0.85, $P < 0.001$) and Gardner (N = 9, r = 0.76, $P < 0.5$) but not Soda Butte (N = 11, r = 0.24, $P > 0.1$).

4.1.3 Cottonwood Establishment and Density

Cottonwood age distribution for Lamar and Gardner indicated that little establishment occurred during most of the 20th century, while relatively continuous establishment occurred on Soda Butte (Figure 7). Mean plant age in Lamar was 6.4 years, which was significantly lower than Soda Butte (16.9 years) and Gardner (10.9 years) ($P < 0.001$). There was no significant difference in the cottonwood age structure of Soda Butte and Gardner ($P > 0.05$), however, Lamar was significantly different from both rivers ($P < 0.05$). The relationship between plant height and age varied by river. Soda Butte had a significant correlation between height and age for plants 20-150 cm tall (N = 62, r = 0.34, $P < 0.01$) but not for plants < 20 or > 150 cm tall (N = 4, r = -0.49, $P > 0.1$). Height and age were significantly correlated for Lamar and Gardner plants that were < 20 and > 150 cm tall (N = 41, r = 0.70, $P < 0.0001$, N = 5, r = .85, $P < 0.1$) but not for plants 20-150 cm tall (N = 35, r = -0.04, $P > 0.1$, N = 24, r = 0.18, $P > 0.1$).

A total of 279 cottonwood stands were mapped, including 161 along Lamar, 89 along Soda Butte, and 20 along Gardner. Sampled stands occur along the entire length of Lamar and Soda Butte, but were of limited distribution along Gardner (Figure 8). Approximately 1.9 million cottonwoods occur in the study area, 92% on Lamar (Table 6). Mean stand density, height, and crown diameter differed significantly by river ($P < 0.05$) (Table 7) and Lamar stands were significantly different from the other rivers ($P < 0.05$) (Table 8). Weighted mean stand densities for Lamar, Soda Butte, and Gardner were 7.6, 0.97, and 2.7 plants/m^2.

4.1.4 Mature Cottonwood Stand Characterization

A total of 1,052 trees larger than 10 cm basal diameter were identified in the study areas, including 590 along Lamar, 111 along Soda Butte, and 351 along Gardner. Trees were distributed along the entire length of Gardner, scattered patches on Lamar, and one stand along Soda Butte (Figure 9). Lamar trees were significantly larger than those on other rivers ($P < 0.05$) but no size difference occurred between Soda Butte and Gardner trees ($P > 0.05$). 70% of Lamar trees had diameters exceeding 50 cm while Soda Butte and Gardner populations were primarily less than 50 cm (Table 9).

The mean female:male ratio for all trees was 1:1.2 with no significant differences between rivers ($P > 0.05$) (Table 10). Species differed between rivers ($P < 0.05$) with Lamar having the greatest proportion of hybrids (0.73) and the only population of *P. trichocarpa*. Soda Butte had the greatest proportion of *P. angustifolia* (0.97), and Gardner included *P. angustifolia* (0.43) and hybrids (0.57).

4.1.5 Factors Influencing Cottonwood Establishment

Variation in ungulate population size explained up to 8% of the variability in cottonwood count and presence/absence data on any river (Table 11 and Table 12). Pre/post 1990 population counts were significantly different for both elk and bison. X_t (Peak discharge) and D (August 1st discharge) were significantly better predictors of cottonwood presence/absence than the null model ($P < 0.05$) on Lamar, explaining 43 and 16% of the variance. D was the only variable not significantly different ($P > 0.05$) in the comparison of pre/post 1990 (Table 13). Bison population was the best predictor of the number of cottonwood that established in a given year but explained little of the variance (pseudo-$R^2 = 0.06$). D and P_t (Timing of peak discharge) were the best models for Gardner ($P < 0.05$) explaining 28 and 18% of the variability. In the pre/post 1990 analysis only P_t was significantly different ($P < 0.05$). Along Soda Butte no model performed better than the null model ($P > 0.1$) but P_t was the best. There were no differences in any of the environmental variables along Soda Butte in pre/post 1990 analysis ($P > 0.05$). For both Gardner and Soda Butte, D and X_t were significantly better predictors than the null model for cottonwood count data ($P < 0.05$) but explain little variation (Table 12).

4.2 Barriers to Cottonwood Growth

4.2.1 Production and Herbivory Estimates

Total above ground cottonwood production in the study area was approximately 66,741 kg/yr, with 84% occurring along the Lamar River (Table 15). Stems accounted for approximately 38% and leaves 62% of total production.

In five of eight plots the number of stems browsed and biomass removed was greatest in summer (Figure 10). Plots along Soda Butte had no biomass removal during the summer of 2008 even though bison were observed browsing near the exclosures. The mean proportion of biomass removed, 0.07 and 0.12, and stems browsed, 0.12 and 0.29, for winter and summer were not significantly different between seasons ($P > 0.1$). Although there was no detectable difference in stems browsed or biomass removed by river, biomass removed along Lamar was more than double that of Gardner for both summer and winter (Table 14). Along Lamar browsing removed an estimated 4,300 kg of stem biomass during the summer and 2,350 kg during winter.

4.2.2 Cottonwood Production versus Consumption

Weighted mean body mass for elk was 226 kg and for bison was 377 kg resulting in body-mass based estimates of dry matter intake of 169 kg/month per elk and 311 kg/month per bison. Standardized bison total consumption rates resulted in a consumption rate of 118 kg/month. If bison and elk diets included 1% cottonwood in 2007-2008 all available cottonwood forage on Soda Butte and Gardner would be consumed in one month by less than 2,000 elk or just over 2,100 bison (Figure 11). For Lamar the proportion of cottonwood in diets would need to exceed 9.5% for bison or 6.5% for elk to consume all production. If 10% of ungulate diet consisted of cottonwood approximately 2,100 bison or 1,500 elk would consume all available forage in the study sites in one month (Figure 11). One month consumption models for YNP ungulates resulted in elk herbivory alone consuming more than the total annual cottonwood production along Soda Butte and over 20% of the production along Lamar at the lowest population levels and 5% consumption (Figure 12). Beginning in approximately 1985 bison populations had grown enough to consume all of the production along Soda Butte at a 5% diet of cottonwood (Figure 12). Only consumption levels of 1% or less resulted in consumption rates that did not exceed production on Soda Butte and 5% or less on Lamar.

A hypothetical model using the 1% consumption rate at 3 months for bison and 2 months for elk resulted in bison consuming nearly all annual production along Soda Butte and Lamar until 1997 (Figure 13). Estimated 3 month consumption from the model was similar to summer removal estimates from plots at 3,650 and 4,300 kg.

5. DISCUSSION

Approximately 500,000 of the 1.9 million cottonwoods in Yellowstone established between 1996 and 1998, the years immediately following wolf (*Canis lupus*) reintroduction to YNP. Recruitment was driven by the largest sequence of peak stream flows in the 20th century. The flows caused large scale channel changes, and provided suitable habitat for cottonwood seedling establishment and survival. The Lamar River cottonwood forest appears to regenerate following infrequent to rare large peak flow events as occur on many streams in western North America (Auble and Scott 1998, Mahoney and Rood 1998, Zamora-Arroyo et al. 2001, Friedman and Lee 2002, Merigliano and Polzin 2003, Lytle and Merritt 2004, Samuelson and Rood 2004, Stromberg et al. 2010). However, Soda Butte Creek and the Gardner River cottonwoods exhibited nearly annual recruitment similar to other low-order montane streams (Samuelson and

Rood 2004, Charron et al. 2011). For the three rivers studied, over 92% of cottonwoods occur along the Lamar River. After the 1997 flood, establishment has been nearly continuous on the Lamar River with the resulting cottonwood biomass exceeding herbivore demand. However, even with their relatively low consumption rates bison are able to remove a significant proportion of total cottonwood production in the study areas and limit plant height and forage available to wintering elk.

5.1 Status of Cottonwood in YNP

The current spatial distribution of cottonwoods along the rivers is consistent with photography from as far back as 1871. Meagher and Houston (1998) present two photo series each along Lamar and Soda Butte to show that few trees occurred in either valley just before and shortly after the establishment of the park. While these photos do not depict the entire northern range, there is no evidence to suggest an expansive cottonwood forest existed in either valley. Meager and Houston (1998) presented photos that included Gardner from differing angles, however only one from 1912 provided a clear view of the river and included a road suggesting that anthropogenic disturbance is evident and cottonwood distribution could not be determined.

Species of cottonwood varied by river, however it is likely that most YNP cottonwoods are a composite of F_1 hybrids and backcrosses of *P. angustifolia*, *P. balsamifera*, and *P. trichocarpa*. Although *Populus* exhibits heterophylly (Critchfield 1960, Eckenwalder 1980) the selection of mature leaves can limit the effect of leaf dimorphism on identification (Eckenwalder 1984, Rood et al. 1986) and studies have demonstrated confident identification of hybrids using leaf morphology (Gom and Rood 1999, Floate 2004). Every female tree inspected had catkins with both bi- and tri-valve capsules and expressed leaf blade and petiole traits inconsistent with single species descriptions (Brayshaw 1996, Dorn 2001, Hardin 2001). The prevalence of F_1 and backcross cottonwood is consistent with hybrids being at least as fit in sexual reproduction and 2-4 times greater in asexual reproduction than parent taxa (Schweitzer et al. 2002). Additionally, increased growth in intersectional hybrids over *P. angustifolia* has been demonstrated (Kranjcec et al. 1998, Willms et al. 2006), reducing the time a plant is susceptible to herbivory. The tendency of hybrids to be intermediate between parent taxa is evident in the size class distributions by river. Along Lamar leaf morphology of cottonwood is intermediate between *P. angustifolia* and *P. trichocarpa* and 70% of the trees are > 50 cm in diameter while along Soda Butte trees are primarily *P. angustifolia* and 70% of the trees are < 50 cm in diameter for the same age trees (Beschta 2005).

5.2 Hydrology and Cottonwood Establishment:

Cottonwood establishment along Lamar follows the general-replenishment model where recruitment results from episodic hydrologic and climatic conditions (Braatne et al. 1996). The relationship between peak discharge and cottonwood establishment is relatively well known (Baker 1990, Scott et al. 1996, Scott et al. 1997, Mahoney and Rood 1998, Cooper et al. 1999, Cooper et al. 2003). In addition, after long periods lacking fluvial disturbance channels can become stable. Large episodic floods cause geomorphic disturbances that create habitat for recruitment of cottonwood for several subsequent years (Friedman et al. 1996, Mahoney and Rood 1998, Stromberg 1998, Polzin and Rood 2006). The floods of 1996 and 1997 had a 100-year recurrence interval and created larger areas of potential seedling habitat than occurred in any previous period in the air photo record. These floods fundamentally reshaped large portions of the river channel and floodplain. More than 58% of the Lamar channel was in a new flow path in the 1994-99 photo period. More than 40% of aged cottonwood plants were from the 1994-99 period. Prior to this period the highest channel migration occurred in 1971-76 when 33% of the area was new channel, and 1% of the sample plants were collected from the 1971-76 period. The concept of episodic disturbance and recruitment in YNP is also supported by previous research in Yellowstone. For example, Beschta (2005), used data from increment cores from cottonwoods along Lamar and Soda Butte to illustrate three clustered age classes from 1950-1970, 1860-1900 and 1780-1815. There is ~80 years between the centroids of these three periods, which is similar to the recurrence interval of large flood events on the plains of eastern Colorado identified by Friedman and Lee (2002). Meyer (2001) reconstructed large flood events along Soda Butte which dated to the years 1918, 1873 and 1790, and the two older floods are in similar periods to those identified by Beschta (2005).

Graumlich et al. (2004) reconstructed annual discharge volume for the Yellowstone River from 1706-1977 using data on Pacific Decadal Oscillation (PDO) and tree rings collected in YNP. This reconstruction indicated that above average annual discharges occurred during the periods from 1770-1780, 1860-1890, 1905-1920, 1945-1955, 1965-1975 and 1995 to 2003. These high annual discharges overlap two of the three cottonwood recruitment periods (Beschta 2005) indicating a correlation between climate and tree establishment. Only two periods of the PDO reconstruction (Graumlich et al. 2004) do not align with the establishment dates,1770-1780 and 1905-1920. Field observations along cut banks revealed that some YNP cottonwood stands have accumulated ~2m of fine sediment over the cobble stream bed that was the likely establishment surface. This may have resulted in collection of increment cores 2-3 m above the germination point and an unknown underestimate of tree age for any establishment event. The lack of establishment from 1905-1920 is indicates a single large flood followed by drought of unprecedented magnitude in the previous 300 years during the 1930's (Graumlich et al. 2004).

Although the flood would have initiated a period of establishment the drought likely induced significant mortality of sapling cottonwoods.

Establishment along Soda Butte and Gardner followed an incremental-recruitment model (Braatne et al. 1996) where small floods (≤ 5 yr return interval) allow recruitment on mid-channel and point bars. Recruitment along Gardner and Soda Butte was not strongly correlated with large peak flow events, supporting the incremental-recruitment model. The braided channel pattern and low bar and floodplain heights relative to base flow allow for frequent overbank floods (Charron et al. 2011) and shallow water tables late in the summer along Soda Butte. Along Gardner similar processes occurred in upper portion of the study area but significant asexual reproduction was occurring within mature stands throughout the entire reach. The nearly continuous recruitment along these streams varies significantly from Lamar; however, continuous recruitment is known to occur along other streams, especially those with fine-grained sediments (Cooper et al. 2003, Samuelson and Rood 2004, Charron et al. 2011).

Sapling densities on all three study rivers were similar to unbrowsed sites outside of Yellowstone (Auble and Scott 1998, Lucas et al. 2004, Samuelson and Rood 2004) indicating that herbivore populations have had little effect on the establishment or survival of cottonwoods. Along the Yampa and Green Rivers Andersen (2005) found that wild ungulates significantly reduced cottonwood survival in some river reaches while having little impact in others. Bison populations in YNP explained only 6% of the variability in the count data in the cottonwood establishment model for Lamar. This suggests that bison likely play a small role in long-term sapling survival. Furthermore, the relative importance of ungulate induced cottonwood mortality in YNP is uncertain when considering that few seedlings survive three years even in the absence of herbivory (Cooper et al. 1999, Polzin and Rood 2006).

5.3 Herbivory and cottonwood growth:

Cottonwood height along the study rivers appears to be controlled primarily by bison herbivory. Reynolds et al. (Reynolds et al. 2003) presented bison diet composition from eight locations across North America and more than 60% of the populations browsed woody plants. Consumption rates of woody plants are reported to be above 20%, and as high as 95% during the summer months in interior Alaska (Waggoner and Hinkes 1986). Bison diets may be highly variable between years (Larter 1988), however Painter and Ripple (2012) found only a slightly greater percentage of stems browsed in the Lamar Valley indicating bison diets in YNP may be relatively stable.

Along Lamar and Gardner biomass removed during the summer was nearly double the biomass removed during the winter indicating lower winter browsing. In addition, more than double the biomass was removed during the summer along Lamar than Gardner indicating that bison consume more cottonwood than elk. In a review of 72 elk winter diet studies Christianson and Creel (2007) found that browse comprised a mean of 29% of elk winter diet, but that graminoids were always more common than expected based upon availability. In central YNP, White et al. (2008) found the proportion of shrubs in elk diet varied during the winter and averaged 2.3%, with a range of 0 - 11%. Cottonwoods cover approximately 2% of the Lamar and Soda Butte valley floors. Elk reside along Gardner all year, and only 14% of total cottonwood biomass was removed. 22% of Gardner trees were in the 10-30 cm dbh size class, with 20 individuals over 4 m tall in the areas of heaviest herbivory, however, all 20 were removed by beaver during the first winter of my study. The minimal availability of cottonwood along Lamar and Soda Butte and their growth along Gardner is consistent with cottonwood being a relatively small proportion of elk diet.

My results show that relatively low consumption rates by ungulates can result in a significant portion of total cottonwood biomass being removed annually. Although these models simplify herbivore-plant interactions they provide valuable insight into how low levels of consumption by herbivores can retard height increase in trees. Herbivory models resulted in removal estimates of ~17% of the 2008 total biomass in three months at a 1% consumption rate for bison alone. Singer and Zeigenfuss (2002) found that elk diets were composed of 11.7% willows yet they removed ~27% of annual growth and browsed ~39% of the leaders in Rocky Mountain National Park. Elk can consume a large proportion of the annual growth of woody plants; however, in YNP they have little opportunity to do so. In the hypothetical consumption model bison would have consumed all production until 1995. During and after the 1996 and 1997 floods substantial cottonwood establishment along Lamar produced an increasing total cottonwood biomass that exceeded the low levels of consumption. Reduced bison and elk populations have likely had little effect. During a period of low population counts for both species, such as 1970, a much higher cottonwood biomass would have been needed to meet the forage demand.

Removal of apical dominance during the growing season can result in sylleptic branching (Zeleznik 2007) and a 40% increase in branch biomass (Coyle et al. 2008). Timing of apical meristem removal can have a significant effect on the number of sylleptic branches. Removal of apical meristems early in the growing season can increase the number of branches by 2-6 times over non-browsed plants while removal late in the season has little impact (Zeleznik 2007). If removal of the apical meristem is not recurrent the plant can recover to pre-browse height (Zeleznik 2007), however recurrent apical meristem removal reduces plant height but does not limit above ground biomass production in plants of similar age and height (Zeleznik 2007, Coyle et al. 2008). In two consecutive years bison were observed browsing throughout the summer along Lamar and Soda Butte while no herbivory was detected along Gardner until August when elk were observed actively foraging. Differences in foraging habit were also observed. Bison consumed entire stems while elk primarily stripped leaves leaving stems mostly intact. The implications at the plant level to the timing and intensity of herbivory are changes in the level of sylleptic branching, reduced height resulting in extended or indefinite period when apical meristems are available to herbivores, and energy diversion to many apical meristems.

Bison can significantly affect the structure and biodiversity of their surrounding habitat (Campbell et al. 1994, Knapp et al. 1999, Trager et al. 2004, Joern 2005). In YNP the prevalence of summer herbivory, lack of height increase even though elk populations have declined, and an absence of young cottonwoods in historical photographs (Meagher and Houston 1998, Wagner 2006) indicates that bison may control the structure of cottonwood forests. Where free ranging herbivores are able to remove greater than 40% of apical meristems at low consumption rates, such as in YNP, it is unlikely that many individuals are able to grow to maturity except in situations where significant herbivore decline occurs in combination with substantial plant recruitment, or in locations where plants are protected from herbivores by log jams and other physical constraints.

6. MANAGEMENT IMPLICATIONS

Cottonwood recruitment in YNP is driven by hydrologic factors that vary among stream types. On higher order rivers recruitment events are rare, because they require peak discharges with return intervals of 50-100 years to create large areas of seedling habitat. Pulses of establishment result in increases in biomass production that exceed the forage demand of native ungulates allowing some cottonwoods to grow to maturity. During the intervening period between establishment events saplings along these rivers are subject to season long herbivory. Although smaller order streams maintain continuous recruitment of cottonwood, in areas of high ungulate use the release from herbivory pressure is the result of episodic mass establishment along larger rivers.

Herbivory during the summer has significant implications at the plant level. The repeated season long browsing by bison shapes the cottonwood forests along Lamar River and Soda Butte Creek. The type of browsing results in lateral plant growth limiting the ability of cottonwood saplings to escape herbivory. The migration of elk into the valley and subsequent browsing of cottonwoods is additive in these valleys. Along the Gardner River herbivory by elk during the summer allows some individual cottonwoods to escape herbivory. The few plants that escape ungulate herbivory are still subject to removal by beaver further limiting the number of plants that are able to attain a mature height. In the absence of human perturbation of bison populations, either in pre-history or today, bison and other ungulates shape their environment. Future investigation of how these species shape the structure of their environment will serve to inform management decisions and educate park visitors on habitat dynamics in a multi-herbivore system.

Table 1: The year air photographs were taken for the disturbance anlaysis by river. X indicates the use of photographs in analysis.

Year	Lamar	Soda Butte	Gardner
1954	**X**	**X**	**X**
1962	**X**	**X**	
1969			**X**
1971	**X**	**X**	
1976	**X**		
1979	**X**	**X**	**X**
1982	**X**	**X**	
1988	**X**	**X**	
1989			**X**
1991	**X**	**X**	**X**
1994	**X**	**X**	**X**
1998			**X**
1999	**X**	**X**	
2001	**X**	**X**	**X**
2006	**X**	**X**	**X**
2009	**X**	**X**	**X**

Table 2: 10-year peak discharge recorded and modeled for each river with 95% confidence intervals, mean discharge with standard deviation for the available record and estimates, and correlation coefficient for the available record and estimates.

	Record	Model
Lamar		
10-yr peak	377	390
10-yr 95%	350-413	365-423
mean	267.06	266.73
st.dev	84.48	77.01
r		0.93
Gardner		
10-yr peak	52	52
10-yr 95%	48-57	48-57
mean	36.15	36.16
st.dev	11.55	10.33
r		0.90
Soda Butte		
10-yr peak	58	55
10-yr 95%	54-71	52-59
mean	41.12	41.20
st.dev	12.83	10.81
r		0.84

Table 3: Tukey's multiple comparisons of mean new channel formed between reaches with 95% family-wise confidence levels and adjusted p-values for the upper, middle, and lower reaches on the Lamar River.

Reach	Diff	lwr	upr	p adj
three-one	344.6667	151.4813	537.852	0.0005251
two-one	-359.5833	-552.7687	-166.398	0.0003286
two-three	-704.25	-897.4353	-511.0647	< 0.000001

Table 4: Tukey's multiple comparisons of mean new channel formed between years with 95% family-wise confidence levels and adjusted p-values on the Lamar River. Bold type represents years with a p-value ≤ 0.05.

Year	Lower 95% CL	Upper 95% CL	Adjusted p-value
eightythree-eightyeight	-597.483	521.482998	1
nine-eightyeight	-207.8163	911.149665	0.5123269
ninetyfour-eightyeight	-540.1497	578.816332	1
ninetynine-eightyeight	**225.517**	**1344.482998**	**0.0018919**
ninetyone-eightyeight	-428.483	690.482998	0.9990136
one-eightyeight	-534.8163	584.149665	1
seventynine-eightyeight	-664.483	454.482998	0.9998744
seventyone-eightyeight	-619.1497	499.816332	0.9999996
seventysix-eightyeight	-344.1497	774.816332	0.9514307
six-eightyeight	-336.8163	782.149665	0.9399084
sixtytwo-eightyeight	-338.1497	780.816332	0.9421277
nine-eightythree	-169.8163	949.149665	0.3702855
ninetyfour-eightythree	-502.1497	616.816332	0.9999997
ninetynine-eightythree	**263.517**	**1382.482998**	**0.0010729**
ninetyone-eightythree	-390.483	728.482998	0.9915122
one-eightythree	-496.8163	622.149665	0.9999993
seventynine-eightythree	-626.483	492.482998	0.9999986
seventyone-eightythree	-581.1497	537.816332	1
seventysix-eightythree	-306.1497	812.816332	0.8730095
six-eightythree	-298.8163	820.149665	0.852549
sixtytwo-eightythree	-300.1497	818.816332	0.8563913
ninetyfour-nine	-891.8163	227.149665	0.5900554
ninetynine-nine	-126.1497	992.816332	0.2383343
ninetyone-nine	-780.1497	338.816332	0.9432164
one-nine	-886.483	232.482998	0.6116446
seventynine-nine	-1016.1497	102.816332	0.1836733
seventyone-nine	-970.8163	148.149665	0.3000332
seventysix-nine	-695.8163	423.149665	0.9985934
six-nine	-688.483	430.482998	0.999141
sixtytwo-nine	-689.8163	429.149665	0.9990577
ninetynine-ninetyfour	**206.1837**	**1325.149665**	**0.0025248**
ninetyone-ninetyfour	-447.8163	671.149665	0.999774
one-ninetyfour	-554.1497	564.816332	1
seventynine-ninetyfour	-683.8163	435.149665	0.9993853
seventyone-ninetyfour	-638.483	480.482998	0.9999926
seventysix-ninetyfour	-363.483	755.482998	0.9742984
six-ninetyfour	-356.1497	762.816332	0.9668308
sixtytwo-ninetyfour	-357.483	761.482998	0.9682928
ninetyone-ninetynine	**-1213.483**	**-94.517002**	**0.0131562**
one-ninetynine	**-1319.8163**	**-200.850335**	**0.0027339**
seventynine-ninetynine	**-1449.483**	**-330.517002**	**0.0003963**
seventyone-ninetynine	**-1404.1497**	**-285.183668**	**0.0007768**
seventysix-ninetynine	**-1129.1497**	**-10.183668**	**0.0435068**
six-ninetynine	**-1121.8163**	**-2.850335**	**0.0480976**
sixtytwo-ninetynine	**-1123.1497**	**-4.183668**	**0.0472309**
one-ninetyone	-665.8163	453.149665	0.9998582
seventynine-ninetyone	-795.483	323.482998	0.9145806
seventyone-ninetyone	-750.1497	368.816332	0.9788917
seventysix-ninetyone	-475.1497	643.816332	0.9999856
six-ninetyone	-467.8163	651.149665	0.9999668
sixtytwo-ninetyone	-469.1497	649.816332	0.9999713
seventynine-one	-689.1497	429.816332	0.9991002
seventyone-one	-643.8163	475.149665	0.9999856
seventysix-one	-368.8163	750.149665	0.9788917
six-one	-361.483	757.482998	0.9723985
sixtytwo-one	-362.8163	756.149665	0.9736762
seventyone-seventynine	-514.1497	604.816332	1
seventysix-seventynine	-239.1497	879.816332	0.638537
six-seventynine	-231.8163	887.149665	0.6089479
sixtytwo-seventynine	-233.1497	885.816332	0.6143404
seventysix-seventyone	-284.483	834.482998	0.8080196
six-seventyone	-277.1497	841.816332	0.7831459
sixtytwo-seventyone	-278.483	840.482998	0.7877641
six-seventysix	-552.1497	566.816332	1
sixtytwo-seventysix	-553.483	565.482998	1
sixtytwo-six	-560.8163	558.149665	1

Table 5: Mean percentage of the channel that was new in pre-1994, across all years, and post-1994 photo periods for reaches of the Lamar River.

	Pre-1994	1962-2009	Post-1994
one	14.8	25.9	48.3
two	4.4	7.4	13.3
three	36.6	41.6	51.5

Table 6: Total stand area (m^2), stand area represented by density sampling (m^2), weighted mean density, and estimate of seedling and sapling totals by river.

	Total area	sampled area	weighted density	est. # of plants
Lamar	230144	91077	7.62	1752775
Soda Butte	102580	45744	0.97	99553
Gardner	15662	9555	2.73	42765

Table 7: Comparison of mean plant density, height, and crown diameter between rivers utilizing a Kruskal-Wallis test.

Data type	Chi-squared	df	p-value
Density	14.0196	2	0.000903
Height	43.0342	2	4.52E-10
Crown	30.2351	2	2.72E-07

Table 8: Comparison of plant density, height, and crown diameter distributions between rivers utilizing a bootstrapped Kolmogorov-Smirnov test.

River	Density p-value	Height p-value	Crown p-value
Lamar to Gardner	0.031	0.0666	0.0001
Soda Butte to Gardner	0.196	0.3373	0.875
Soda Butte to Lamar	0.0001	0.0001	0.0001

Table 9: Number and proportion of cottonwoods in each size class by river.

Size Class (cm)	Lamar River	Soda Butte Creek	Gardner River	Total
10-30	31(0.05)	16(0.14)	76(0.22)	123
30-50	145(0.25)	62(0.56)	173(0.49)	380
50-70	201(0.34)	28(0.25)	73(0.21)	302
70-100	128(0.22)	4(0.04)	15(0.04)	147
100+	85(0.14)	1(0.01)	14(0.04)	100
Total	590	111	351	1052

Table 10: Number and proportion of female to male cottonwoods by river.

Sex	Lamar River	Soda Butte Creek	Gardner River	Total
Female	279(0.47)	48(0.43)	145(0.41)	472
Male	311(0.53)	63(0.57)	206(0.59)	580
Total	590	111	351	1052

Table 11: Values of dispersion factor, Mcfadden's psuedo-R^2, p-value for chi-squared test, and Akaike weights from logistic regression of presence/absence of cottonwoods on each river. Bold indicates significance $P < 0.05$ for chi-squared test.

River	Variable	*Dev/df*	Pseudo-R^2	chi^2 (*P*)	Akaike wt
Lamar	X_t	**0.83**	**0.43**	**0.001**	**0.95**
	D	**1.02**	**0.16**	**0.04**	**0.02**
	B	1.08	0.08	0.13	0.01
	P_t	1.11	0.03	0.41	0.00
	X_{t+1}	1.11	0.01	0.63	0.00
	X_{t+2}	1.11	0.01	0.65	0.00
	E	1.11	0.01	0.71	0.00
Gardner	D	**0.90**	**0.28**	**0.01**	**0.66**
	P_t	**1.02**	**0.18**	**0.03**	**0.17**
	X_{t+2}	1.09	0.09	0.12	0.05
	X_t	1.11	0.07	0.17	0.04
	X_{t+1}	1.11	0.06	0.20	0.04
	B	1.10	0.02	0.46	0.02
	E	1.11	0.01	0.59	0.02
Soda Butte	P_t	1.08	0.08	0.19	0.25
	X_{t+1}	1.07	0.04	0.34	0.16
	X_{t+2}	1.13	0.03	0.39	0.15
	X_t	1.10	0.01	0.61	0.12
	D	1.11	0.01	0.73	0.11
	B	1.10	0.01	0.74	0.11
	E	1.12	0.00	0.76	0.11

Table 12: Values of dispersion factor, Mcfadden's psuedo-R^2, p-value for chi-squared test, and Akaike weights from logistic regression of cottonwoods counts on each river. Bold indicates significance $P < 0.05$ for chi-squared test.

River	Variable	*Dev/df*	psuedo-R^2	chi^2 (*P*)	Akaike wt
Lamar	B	**0.84**	**0.06**	**0.01**	**0.58**
	X_t	0.90	0.03	0.11	0.13
	E	0.65	0.02	0.22	0.08
	D	0.68	0.01	0.36	0.06
	X_{t+2}	0.70	0.01	0.44	0.05
	P_t	0.68	0.00	0.67	0.04
	X_{t+1}	0.63	0.00	0.88	0.04
Gardner	D	**0.98**	**0.08**	**0.01**	**0.52**
	X_t	**0.91**	**0.05**	**0.05**	**0.21**
	X_{t+1}	1.23	0.02	0.24	0.07
	B	1.10	0.02	0.28	0.06
	E	1.08	0.01	0.42	0.05
	P_t	1.27	0.01	0.46	0.05
	X_{t+2}	1.08	0.00	0.92	0.04
Soda Butte	D	**0.91**	**0.14**	**< 0.0001**	**0.95**
	X_t	**1.14**	**0.05**	**0.04**	**0.03**
	B	1.12	0.02	0.24	0.01
	X_{t+1}	1.67	0.01	0.52	0.00
	P_t	1.46	0.00	0.76	0.00
	E	1.46	0.00	0.79	0.00
	X_{t+2}	1.45	0.00	0.94	0.00

Table 13: P-values for comparison of pre and post 1990 for the independent variables used in logistic regression by river. Bold indicates $P < 0.05$.

River	X_t	D	X_{t+1}	X_{t+2}	P_t	E	B
Lamar	**0.045**	0.378	**0.018**	**0.01**	**<0.0001**	**0.038**	**< 0.001**
Gardner	0.75	0.25	0.52	0.51	**< 0.01**	**0.038**	**< 0.001**
Soda Butte	0.58	0.35	0.42	0.41	0.07	**0.038**	**< 0.001**

Table 14: Mean proportion of stems measured that were browsed and proportion of biomass removed by river during summer and winter.

	Summer		Winter	
	Stems	Biomass	Stems	Biomass
Lamar	0.40	0.20	0.16	0.11
Soda Butte	0	0	0	0
Gardner	0.35	0.09	0.18	0.05

Table 15: Areally weighted mean total and mean stem weights (g) with estimate of total production and total stem production (kg) by river

River	Total production per plant (g)	Stem production per plant (g)	Total stem production (kg)	Total production (kg)
Lamar	32.12	12.25	21479	56304
Soda Butte	79.71	30.45	3031	7935
Gardner	58.49	22.33	955	2501

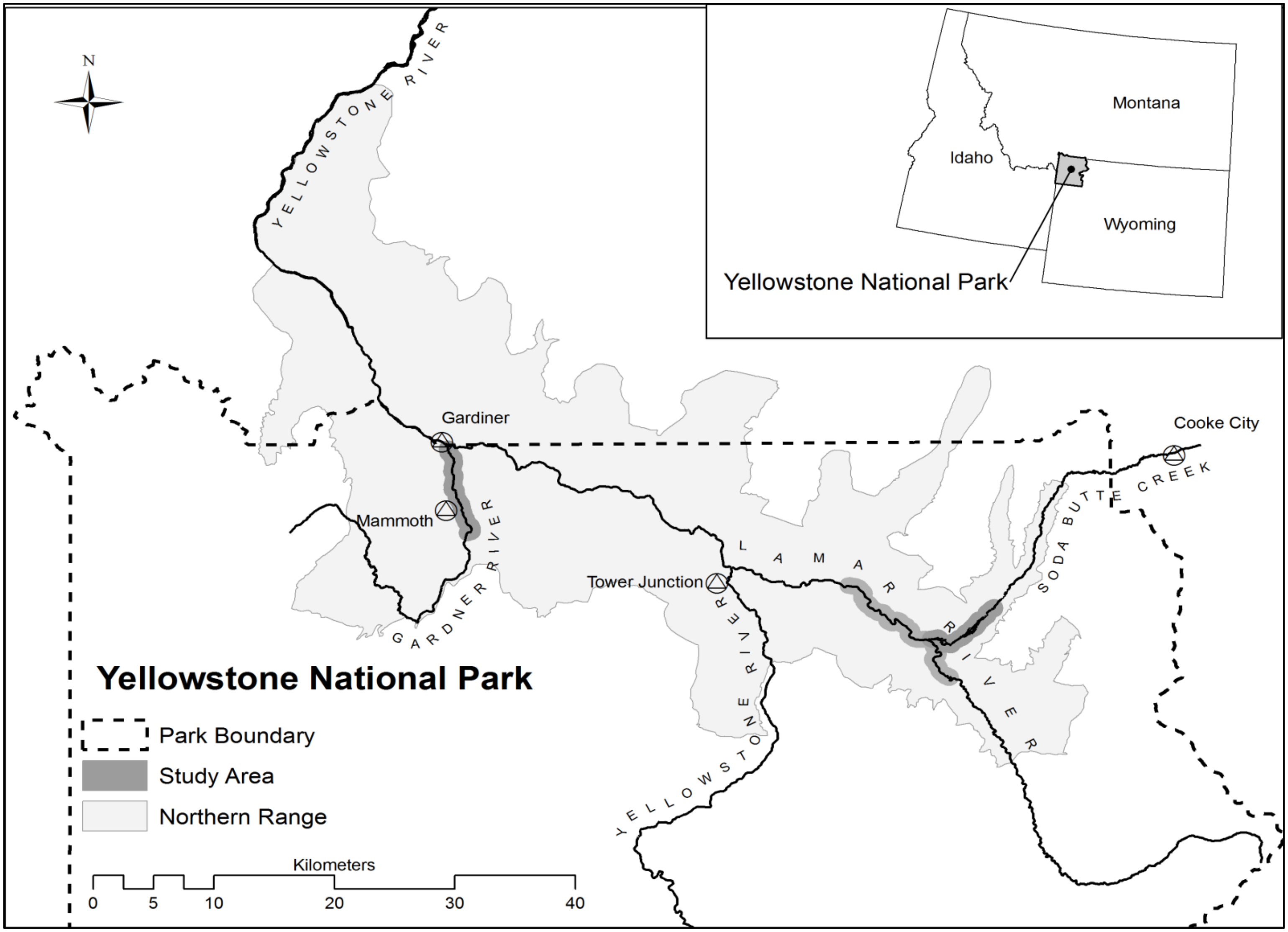

Figure 1: Location of Yellowstone National Park and the Gardner River, Lamar River and Soda Butte Creek study areas.

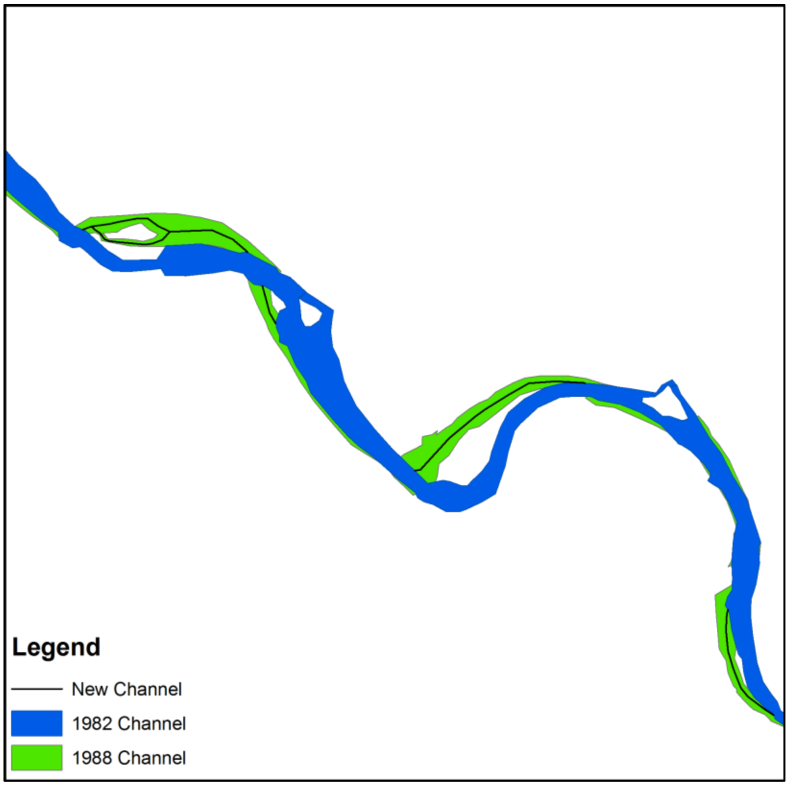

Figure 2: Example of method used to determine length of new channel. New channel was only form in areas where channel margins did not overlap. The length of new channel formed between photos in indicated by the solid black line.

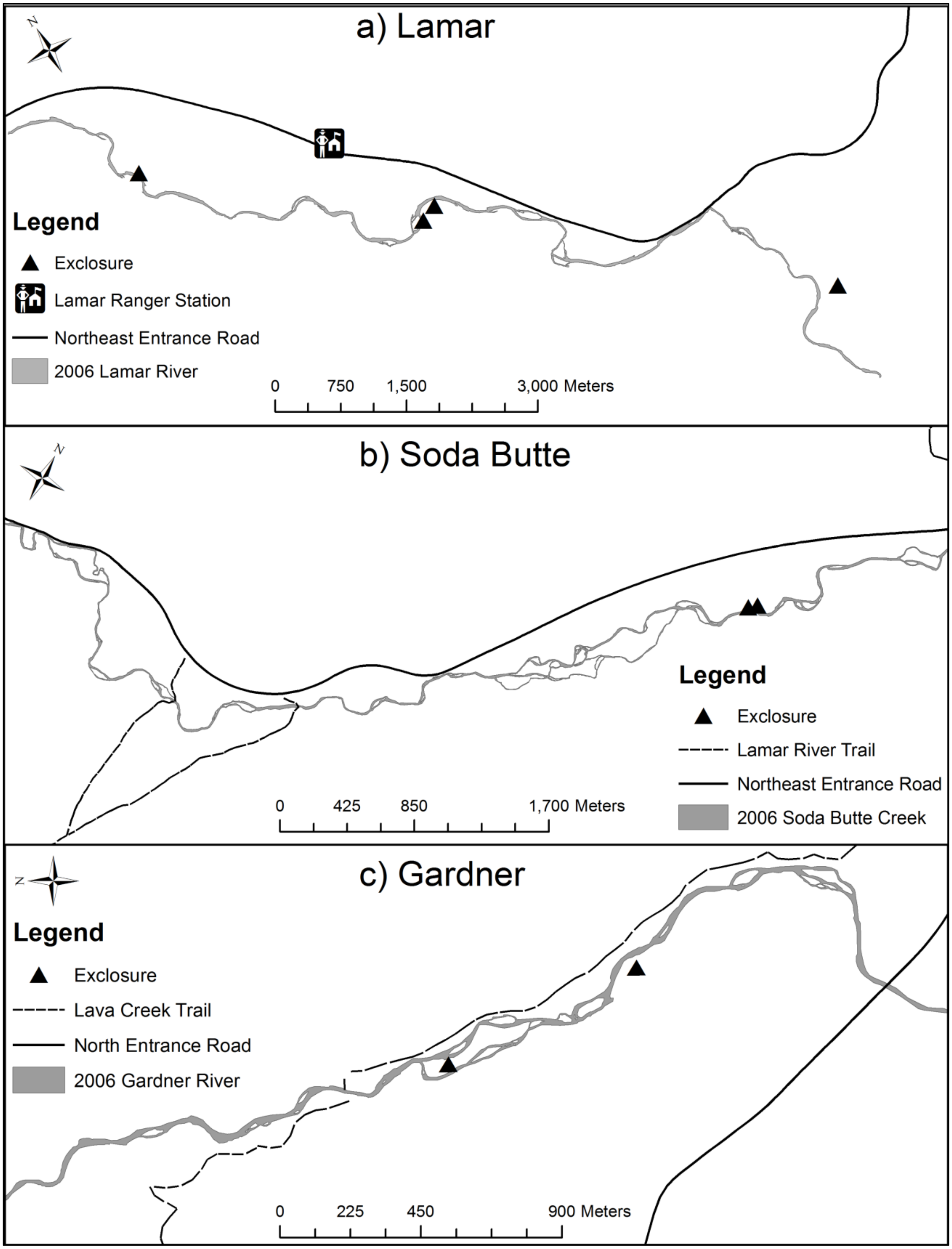

Figure 3: Location of exclosures along each study river.

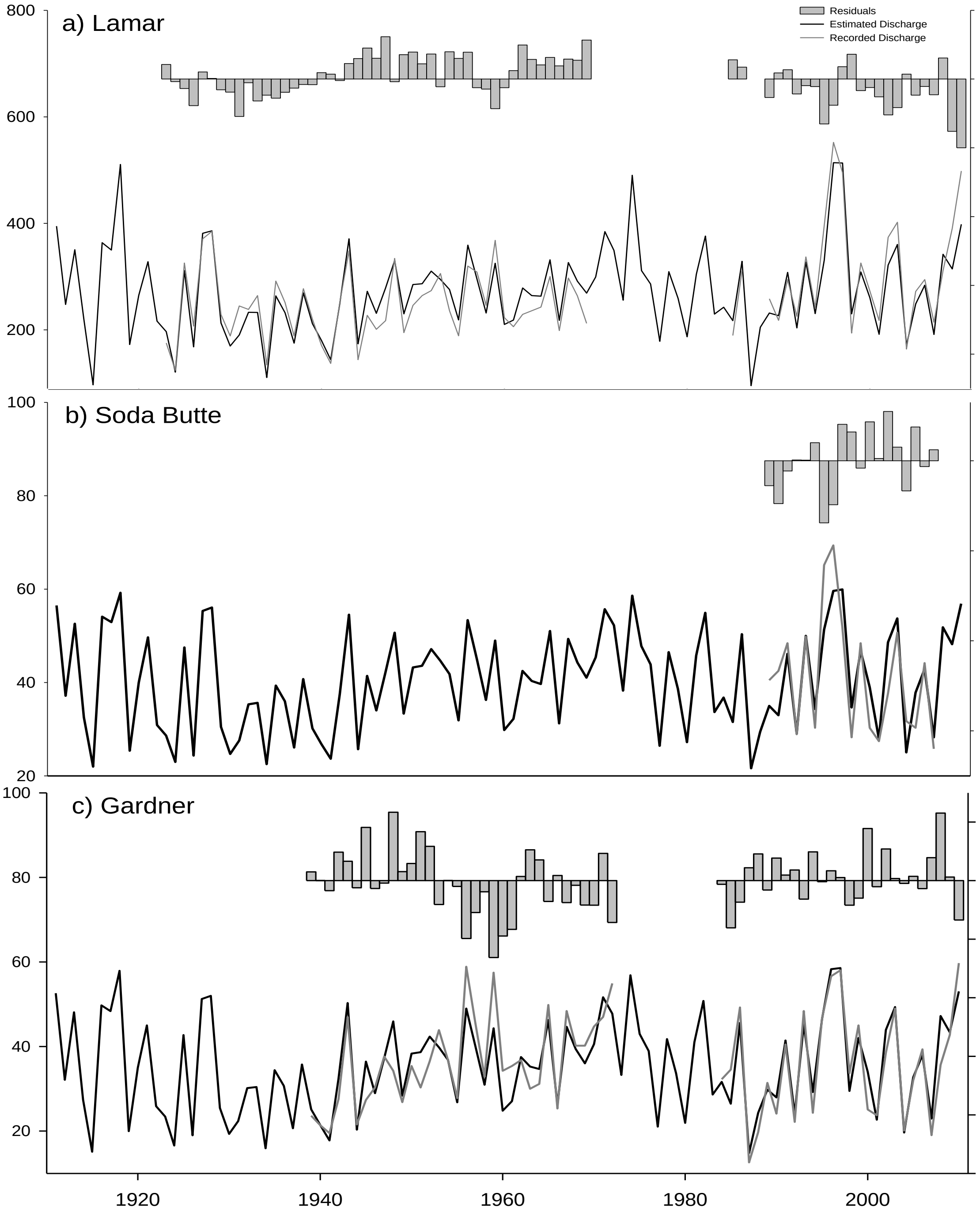

Figure 4: Comparison of peak recorded and estimated discharge for the a) Lamar River, b) Soda Butte Creek, and c) Gardner River. The black line is estimated peak stream discharge, the gray line is recorded peak stream discharge, and the gray bars are the residuals from the model and recorded peak stream discharge. The horizontal axis represents year and the left and right vertical axises are peak stream discharge and residuals in m^3/s.

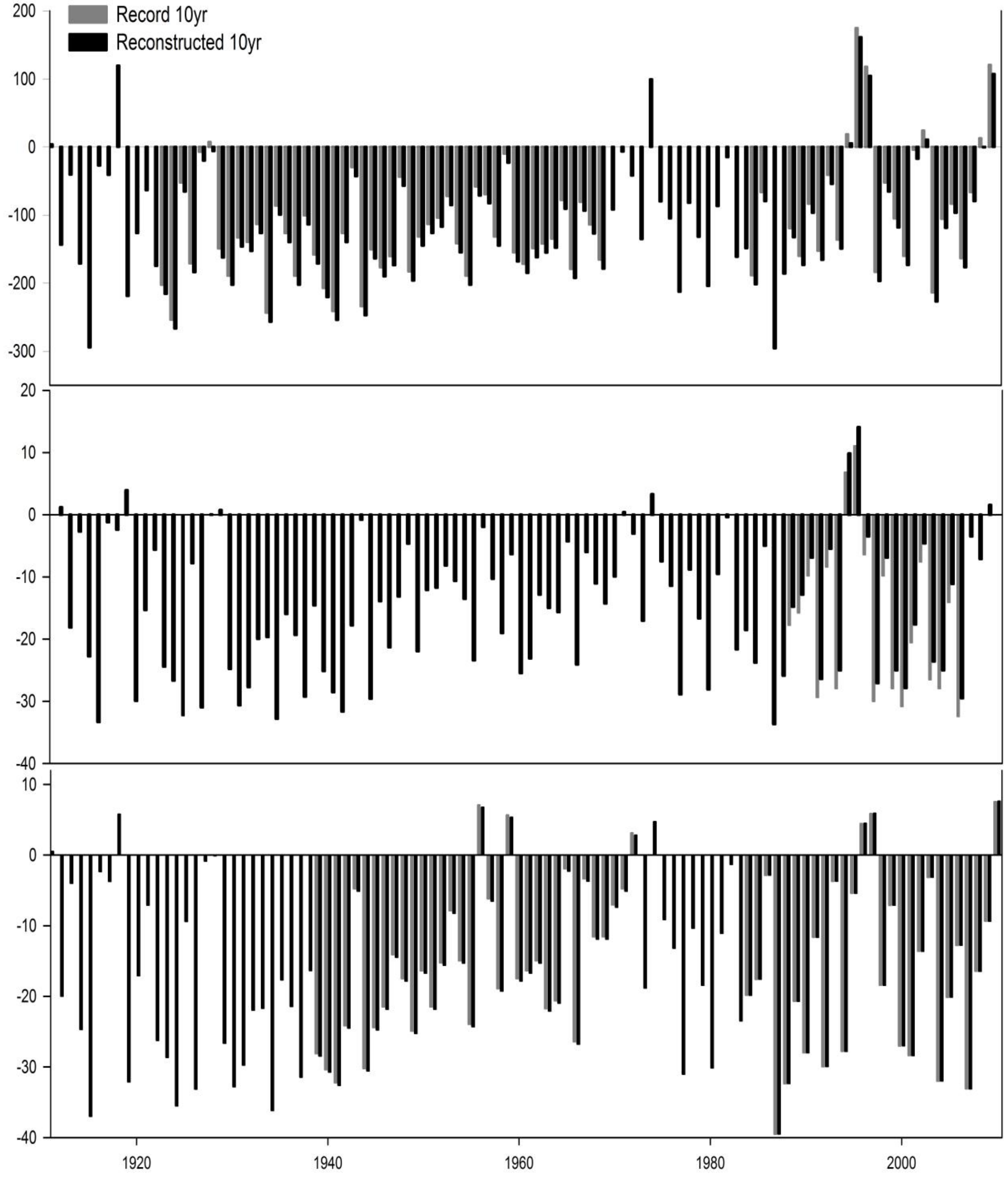

Figure 5: 10 year exceedance events at the a) Lamar River, b) Soda Butte Creek, and c) Gardner River. Black represents 10 year reconstructed hydrographs and grey represents 10 year recorded events. The horizontal axis represents year and the vertical axis is deviation from the 10 year event in m^3/s.

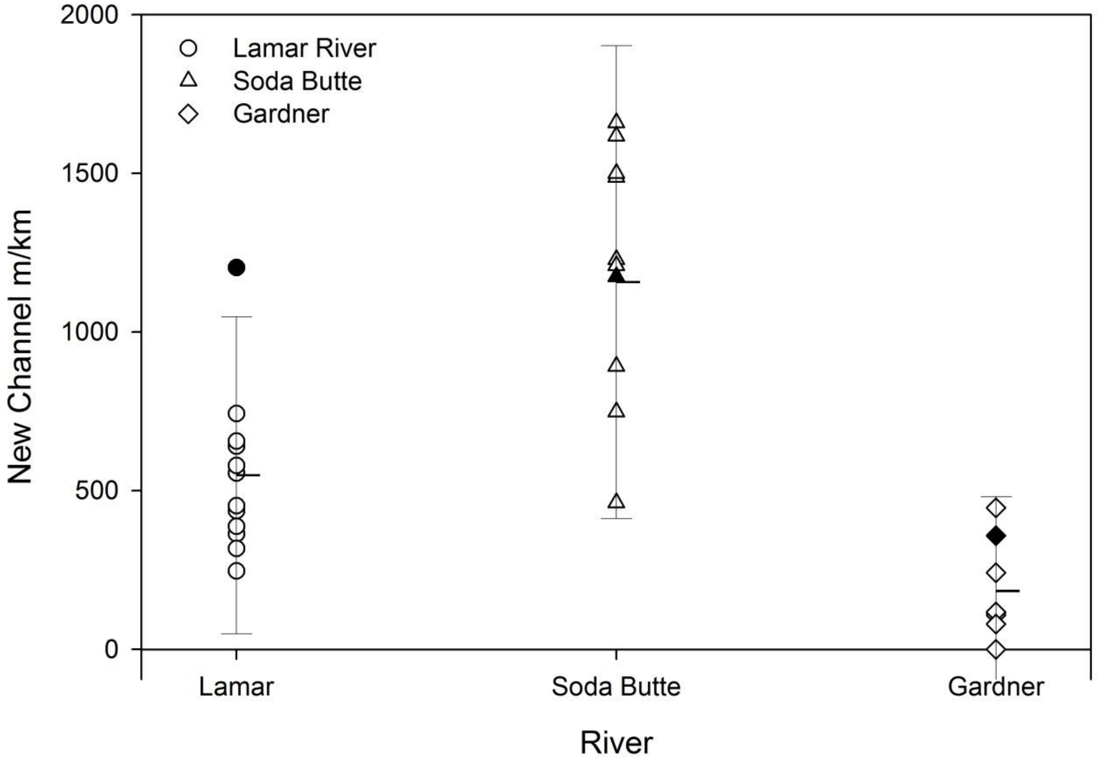

Figure 6: New channel area formed by year for the three study rivers. Bars indicate the 95% confidence interval around the mean. The mean new channel formed is identified by the horizontal bar to the right of the confidence interval and new channel formed during the photo period 1994 to 1999 is identified with a black symbol. The horizontal axis is the study river and the vertical axis is mean new channel formed in m/km.

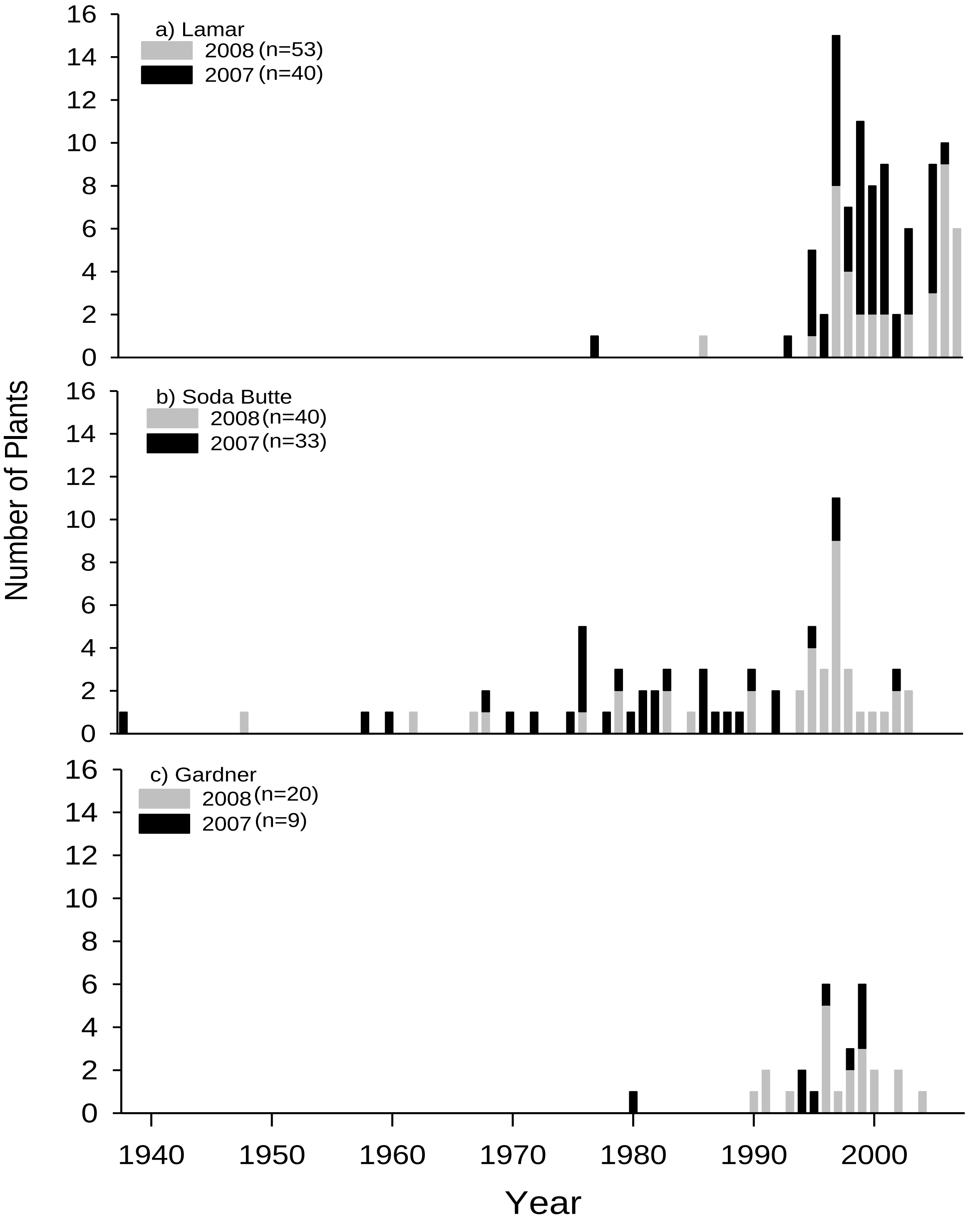

Figure 7: Number of trees established per year along the Lamar (a), Soda Butte (b) and Gardner River (c) based upon trees sampled in 2007 and 2008. The horizontal axis is the year of establishment and the vertical axis is the number of plants established in a given year.

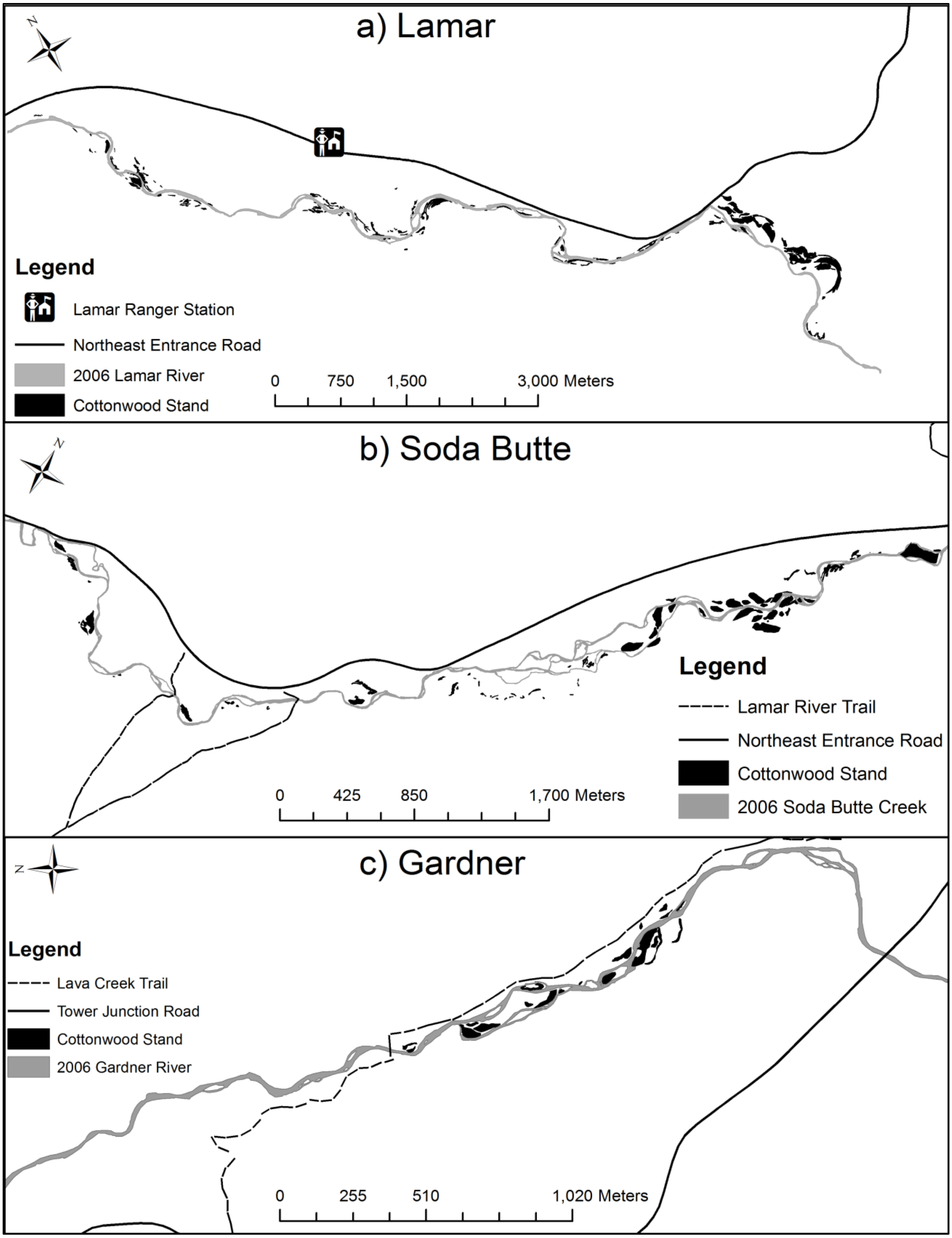

Figure 8: Location of sapling and suppressed tree stands along each study river.

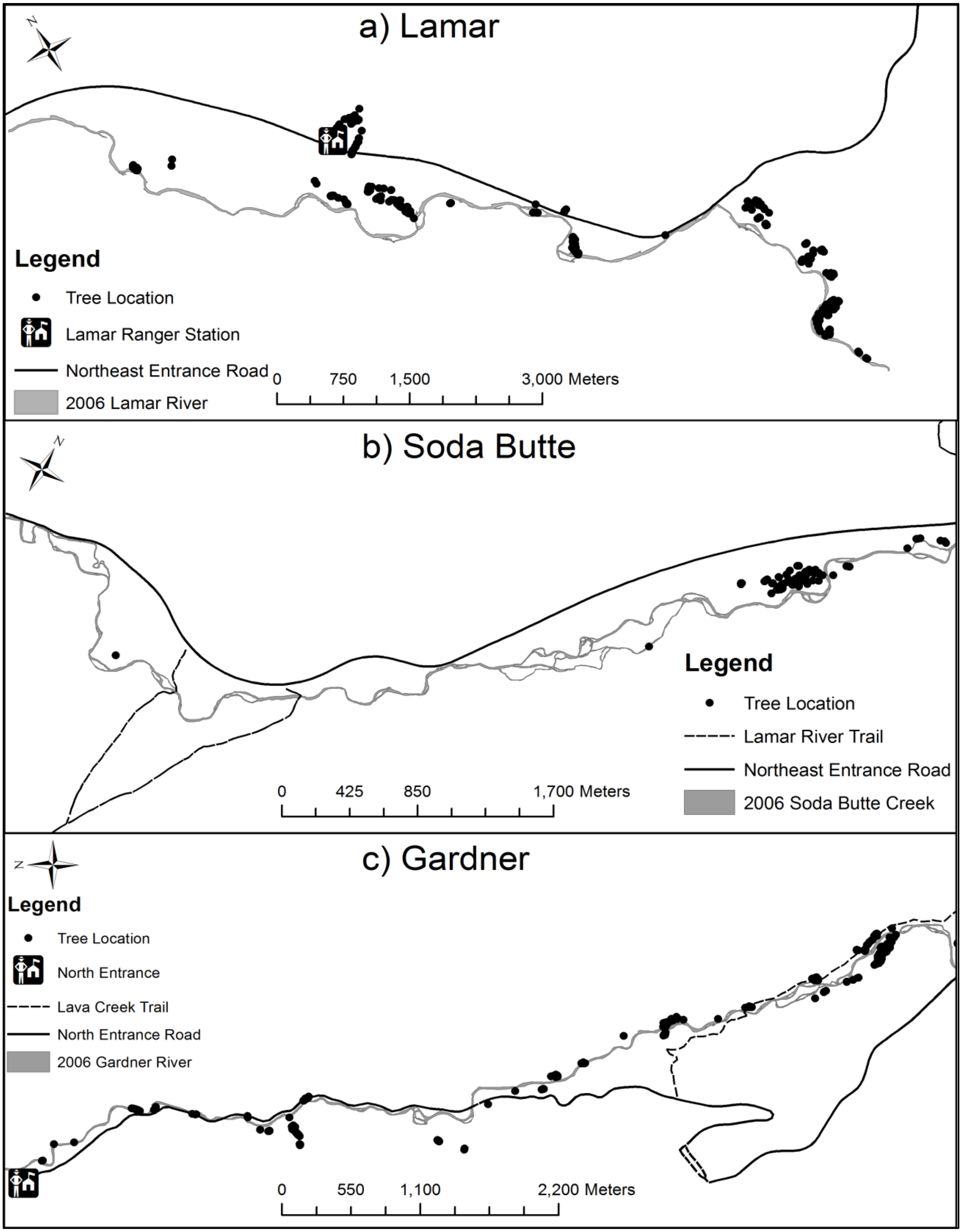

Figure 9: Location of individual cottonwood > 10 cm in diameter at ground height along each study river.

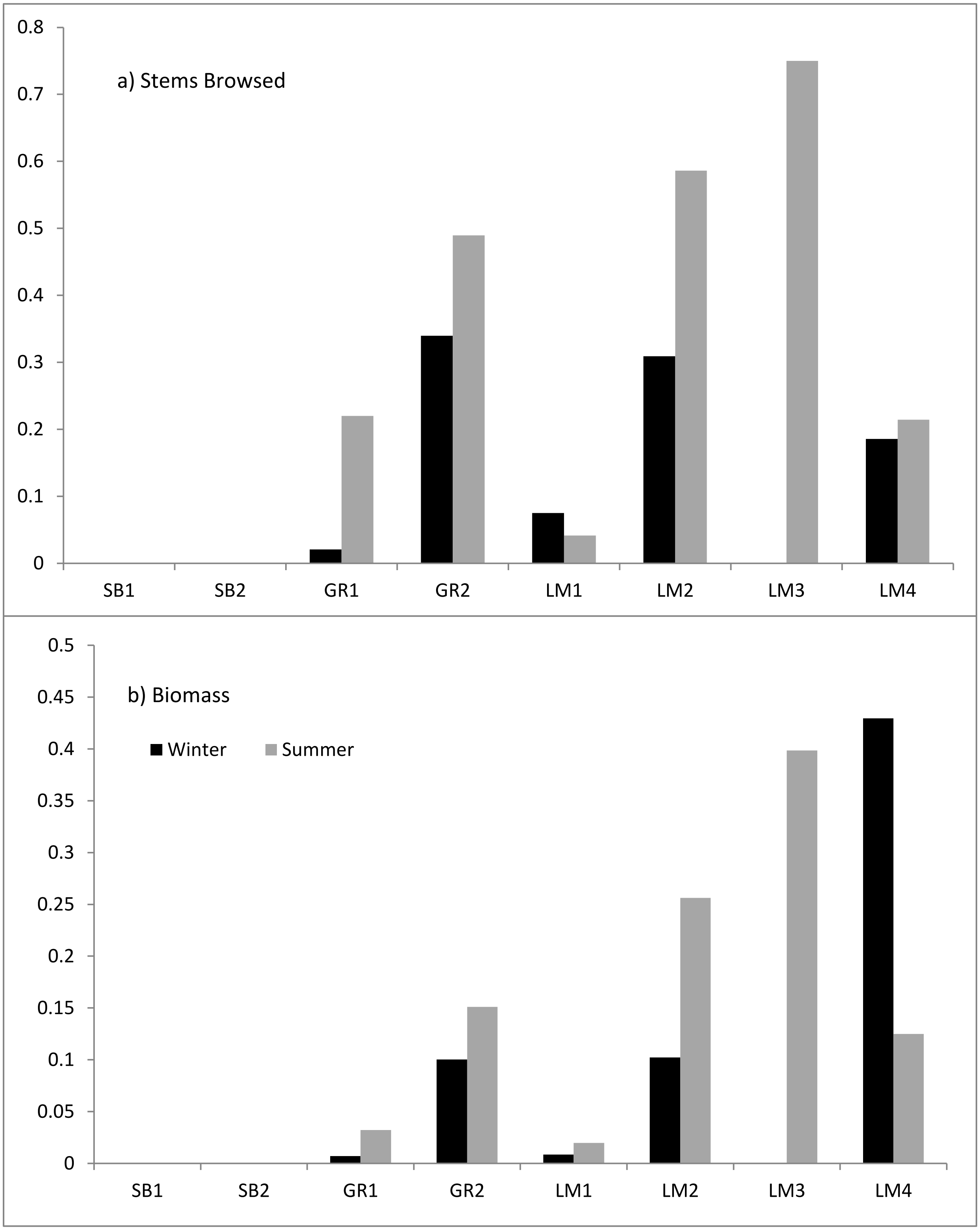

Figure 10: Proportion of stems browsed and biomass removed by season and plot. The horizontal axis is the plot identifier and the vertical axis is the a) proportion of stems browsed or b) biomass removed.

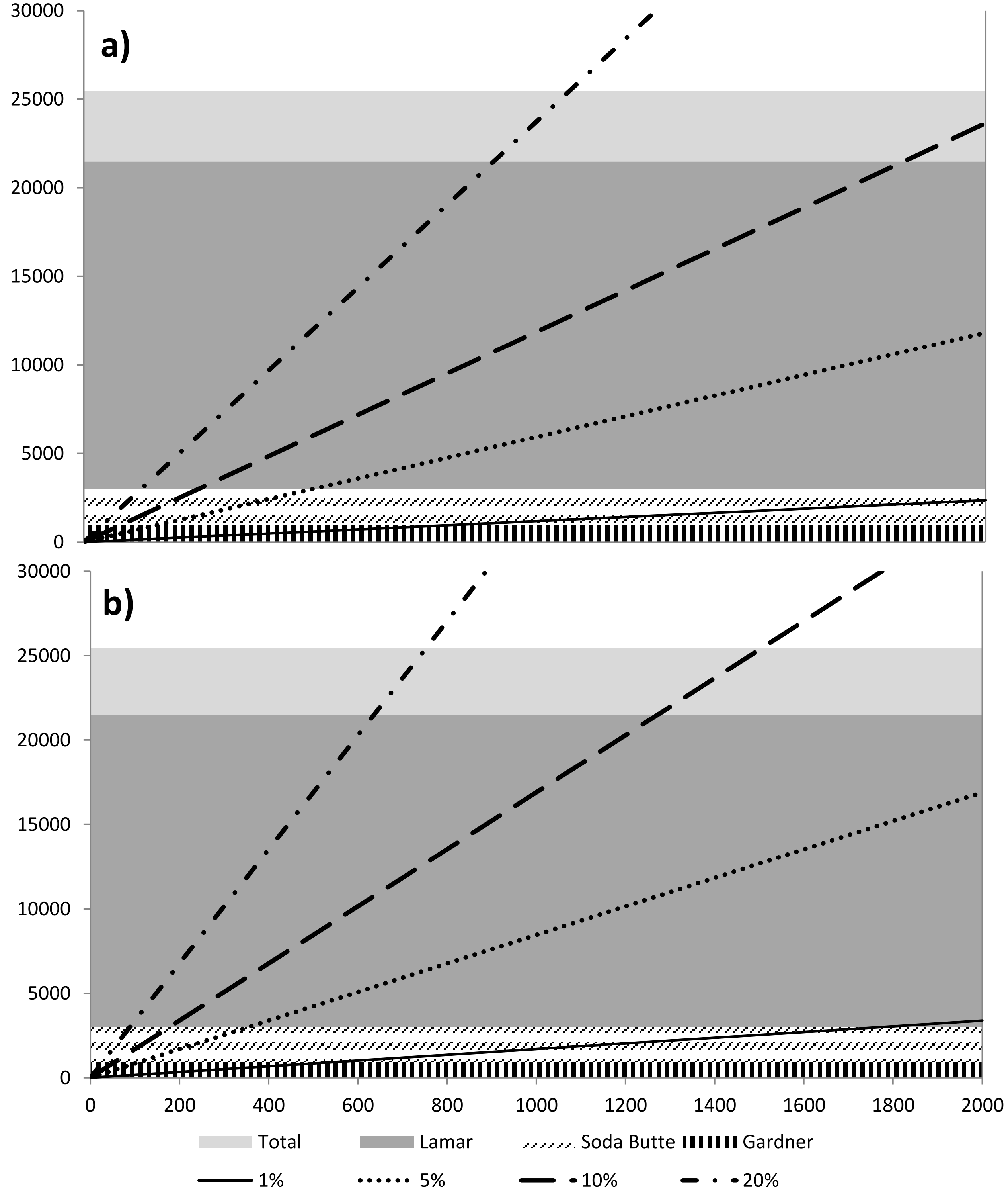

Figure 11: One month consumption for bison (a) and elk (b) at 1, 5, 10, and 20% of total monthly consumption relative to each study river and total production across the study rivers. The horizontal axis is the number of animals and the vertical axis is the total consumption and production in kilograms.

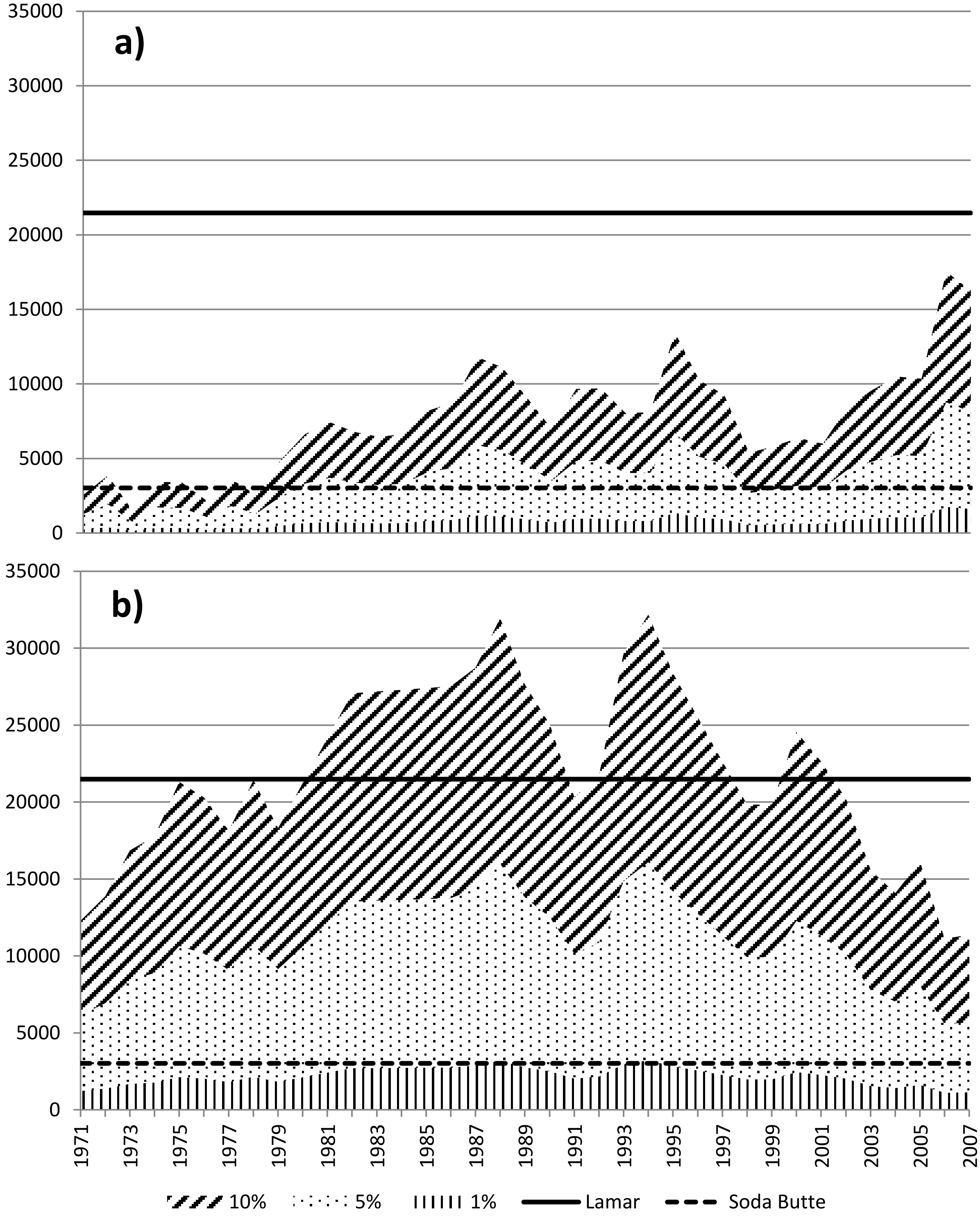

Figure 12: One month consumption for bison (a) and elk (b) at 1, 5, 10, and 20% of total monthly consumption for population estimates from 1970 through 2007. 2007-08 production estimates are plotted for reference. Consumption values are overlaid. The horizontal axis is the number of animals and the vertical axis is the total consumption and production in kilograms.

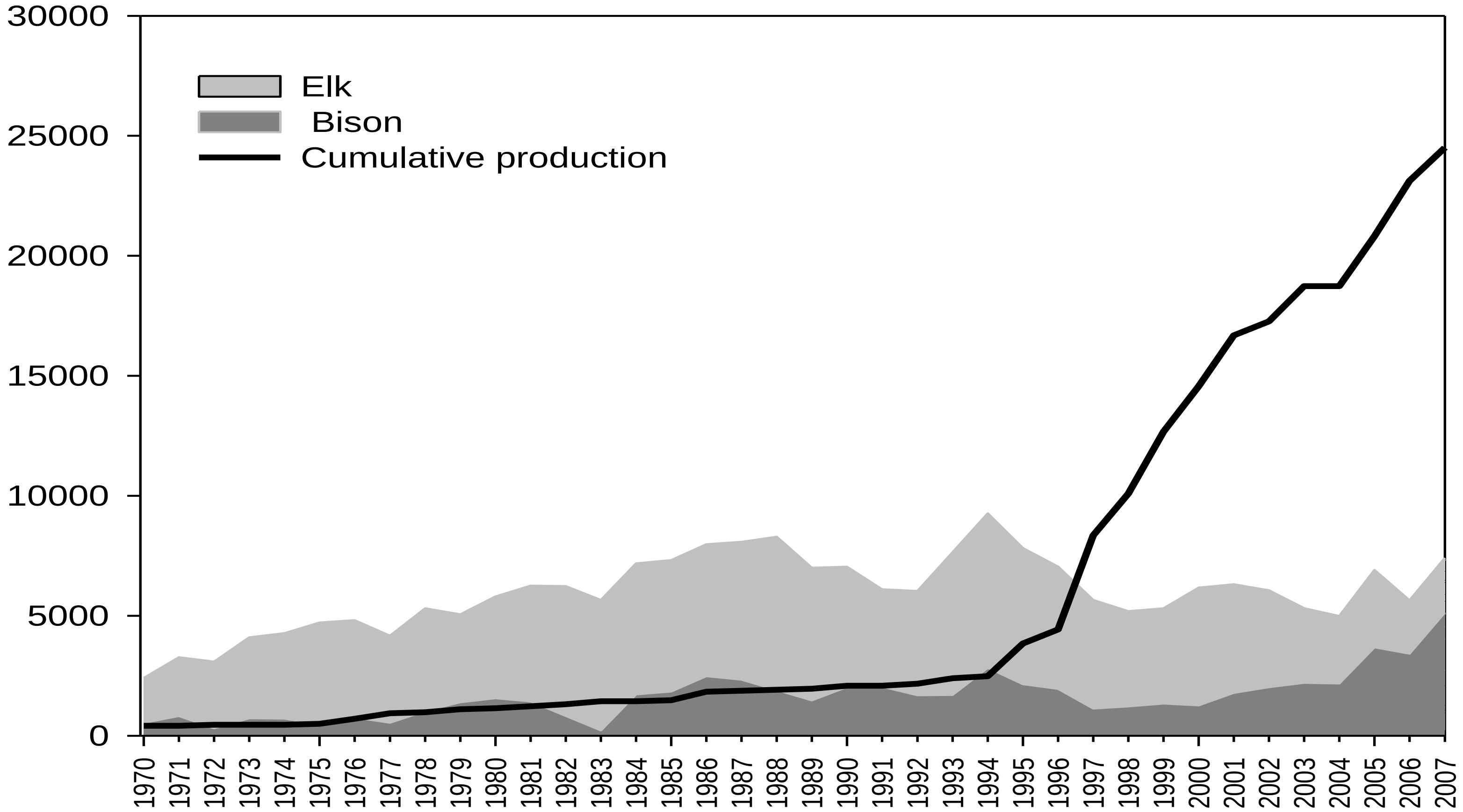

Figure 13: Hypothetical model using the 1% consumption rate at a 3 months duration for bison and 2 months for elk plotted against cumulative total production for the Lamar River and Soda Butte Creek. Consumption values for bison and elk are stacked. The horizontal axis is the number of animals and the vertical axis is the total consumption and cumulative production in kilograms.

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