Architecture of Cottonwood as an Index of Browsing History in Yellowstone

Richard B. Keigley

Abstract

*I determined the history of browsing by elk (*Cervus elaphus*) on narrowleaf cottonwood (*Populus angustifolia*) at a site in northern Yellowstone National Park (YNP). I aged cottonwoods in three stands by dendrochronology and classified them into four architectural categories that I postulated were produced by four browsing regimes: 1) uninterrupted-growth type (light-to-moderate browsing), 2) arrested-type (intense browsing), 3) retrogressed-type (a change from light-to-moderate browsing to intense browsing), and 4) released-type (a change from intense browsing to light-to-moderate browsing). Cottonwood trees established prior to 1947 were of uninterrupted-growth type architecture. Trees established between 1947 and 1968 were of uninterrupted- and released-type architectures. With the exception of individuals short enough to be protected from winter browsing by snowpack, all individuals established after 1968 were of arrested- and retrogressed-type architectures. Cottonwoods in the study area experienced the following browsing history: (1) light-to-moderate until 1951, (2) intense from 1952 to 1962, (3) light-to-moderate from 1963 to 1974, and (4) intense since 1975. Architecture-based methods can be used to determine the rank order sequence in which elk currently prefer different species of browse. Once determined, that rank order sequence can be used to test competing hypotheses about the declines in woody plants in YNP.*

Key words: architecture, browsing history, *Cervus elaphus*, elk, growth form, Yellowstone National Park

Introduction

The condition of elk (*Cervus elaphus*) winter range in northern YNP has been controversial for decades (Chase 1987, Despain *et al.* 1986, Kay 1990). Much of the controversy has focused on differing explanations for a decline in abundance of aspen (*Populus tremuloides*) and willow (*Salix* spp.).

Some believe that the northern range deteriorated because of overpopulation by elk (Wright and Thompson 1935, Leopold *et al.* 1963, Kay 1997). The northern elk herd increased in the late 1800s when elk were protected from hunting, predators were eliminated, and elk migration to ancestral winter range north of YNP was impeded (Pitcher 1905, Smith *et al.* 1915, Graves and Nelson 1919).

Houston (1982) and Despain *et al.* (1986) believe that the northern range has remained unchanged from the pristine condition that existed prior to the Park's establishment. Houston also contends that the northern elk herd fluctuates within natural limits of variation. Previous research attributes change in condition and abundance of vegetation to past fire suppression (Houston 1982, Despain *et al.* 1986) or climate change (Despain 1990, Singer *et al.* 1994).

Additionally, young cottonwood (*Populus* spp.), Engelmann spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga*

Richard B. Keigley, U.S. Geological Survey, Biological Resources Division, 632 Coulee Drive, Bozeman, MT 59718

menziesii), pine (*Pinus* spp.), juniper (*Juniperus scopulorum*), sagebrush (*Artemisia* spp.), greasewood (*Sarcobatus vermiculatus*), birch (*Betula occidentalis*), alder (*Alnus* spp.), and chokecherry (*Prunus virginiana*) are heavily browsed and dead plants are common (pers. obs.). The mortality of young plants suggests that these browse species are in decline. In national parks, ecologic changes caused by natural processes are to be preserved, while changes due to EuroAmerican influences may be mitigated (National Park Service 1988). An objective of my research was to develop an approach for evaluating two competing explanations: one which attributes the declines to EuroAmerican influences; the other attributes declines to natural processes.

Any evaluation of cause and effect must be based on how ungulate use of browse has historically varied in response to controlling factors. Some studies inferred levels of browse use that occurred at discrete points in time (Houston 1982, Kay 1990, Singer and Renkin 1995, Romme *et al.* 1996). For example, Houston (1982) and Kay (1990) interpreted browse use from historic photographs. Such interpretations are limited to the time and place documented by the photographs. I am aware of no study that describes a year-by-year history of browse use for any species. Here, I describe a year-by-year browse-use history of narrowleaf cottonwood (*Populus angustifolia*) that grow in one area on YNP's northern range. I also describe a method to test hypotheses about the causes of the decline in YNP's woody plants.

Study Area and Methods

Narrowleaf cottonwood is a riparian tree that grows to 20 m tall (Harrington 1964). Trees established from seed along stream banks often form gallery forests where stands of different age provide a record of stream channel migration (Everitt 1968). Plants also may be established from root suckering. Outside YNP, narrowleaf cottonwood typically grows to a height of 1 m within 2-3 years of establishment (pers. obs.). On the northern range of YNP, narrowleaf cottonwood communities consist of older mature trees and younger plants so heavily browsed they have assumed a bush-like growth form (Keigley 1997b) (Fig. 1).

I conducted this study in 1992 near the confluence of Soda Butte Creek and the Lamar River in northern YNP (elev. 2010 m). This area was selected because of the diverse group of cottonwood age classes found there.

I examined three adjacent stands of cottonwoods growing in abandoned channels of the Lamar River. Stand 1 consisted of 14 very large trees up to 20 m tall and averaging about 1 m diameter at breast height (dbh). Stand 2 contained 45 trees up to 15 m tall and 30-50 cm dbh. Stand 3 consisted of 53 trees ranging up to 10 m tall, and many bush-form plants from 0.1-1.5 m in height.

Architectures

Ungulate browsing can permanently modify the architecture of woody plants (Cole 1958, Ferguson and Basile 1966, Riney 1982, Bergström and Danell 1987, Bilbrough and Richards 1993). Keigley (1997a) postulated that four general architecture types develop in response to four browsing regimes. A light-to-moderate browsing regime produces uninterrupted-growth type architecture of which a simple, non-forking trunk is characteristic. These are "typical" cottonwood trees.

Chronic intense browsing of a young plant produces arrested-type architecture (see Fig. 1). Browsing kills the tip of the terminal leader and promotes development of lateral branches from lower regions of the plant. Because browsing primarily occurs during winter, height of arrested-type plants is influenced by snowpack

Figure 1. *A bush-form (arrested-type) cottonwood about 50 cm tall growing adjacent to the Gardner River north of Mammoth Hot Springs, Yellowstone National Park. Ungulate bite-marks are visible on many branches. Above a height of about 20 cm, the primary stem branches profusely, indicating that stems were intensely browsed once they grew taller than the protection afforded by snowpack.*

Figure 2. *A retrogressed-type cottonwood about 75 cm tall growing adjacent to the plant in Fig. 1. In contrast to the flat-topped appearance of the plant in Fig. 1, this individual has three protruding stems. The ability of these stems to grow to 75 cm tall indicates that, early in its life, this plant experienced less intense browsing than the plant in Fig. 1. The upper portion of this retrogressed-type individual is dead. Leaves are borne on lateral branches that developed from the base of the plant.*

thickness. In a 17 year old stand of arrested-type cottonwoods located 5.5 km upstream from this study area (elev. 2050 m), average height was 18 cm; the tallest arrested-type individual was 42 cm (Keigley 1997b).

Retrogressed-type architecture is produced when browsing changes from a light-to-moderate level to an intense level. During the early period of light-to-moderate browsing, the plant may grow taller than the arrest zone (i.e., taller than 40-50 cm). When the browsing level changes to intense, the upper region of the plant's primary stem dies. A dense thatch of dead branches may form and protect new lateral branches that may develop from the lower region of the plant (Fig. 2). At the site previously described by Keigley (1997b), retrogressed-type cottonwoods grew as tall as 1.7 m before the upper stem was killed by browsing.

Released- type architecture is produced when the browsing regime changes from intense to light-to-moderate (Fig. 3). During the period of intense herbivory, an arrested- or retrogressed-type architecture develops. After the browsing level changes to a light-to-moderate level, a lateral branch assumes the role of a trunk. The individual is classified as "released" when the trunk grows taller than 2.5 m above ground level.

I assigned each individual cottonwood plant in my study to 1 of 3 categories: (1) uninterrupted-growth-type, (2) a combined arrested- and retrogressed-type, and (3) released-type. I assigned trees with trunks that did not fork within a zone between ground level

Figure 3. *A released-type cottonwood. In its youth, this tree resembled the cottonwood shown in Fig. 2. Evidence of retrogressed-type architecture is preserved in the dead stems at the right-hand side of the lower trunk. Above the point where retrogressed-type stems are attached to the trunk, trunk girth diminishes markedly. The large girth at point of attachment indicates that the dead stems were produced early in the tree's life. The near-vertical orientation of those stems indicates that they developed before elongation of what is now the trunk. A reduction in browsing intensity enabled a stem of the retrogressed-type plant to grow to ca. 4 m tall, producing the released-type architecture. Lateral branches within the browse zone have been intensely browsed, indicating that browsing level increased to intense after the trunk grew through the browse zone.*

and 1 m to the uninterrupted-growth-type category. The continuity of the primary stem was evidence of uninterrupted-growth when the terminal leader grew within that zone.

I assigned plants to the arrested- and retrogressed-type category if a complete annual segment of the primary stem died due to browsing. Bite marks at the end of branches attest to ungulate herbivory as the principal determinant of growth form. Arrested- and retrogressed-type plants branch profusely as a result of pruning and appear bush-like. Both the arrested- and retrogressed-type architectures indicate intense current browsing.

I assigned plants to the released-type category in two steps. In the first step, I tentatively categorized them based on height growth that permitted the current primary stem to grow taller than the browse zone (ca 2.5 m), and on evidence of previous arrest or retrogression. Forking of a live stem from a dead, near-vertical stem was taken as potential evidence of arrest or retrogression. In the second step described below, I confirmed the assignment by determining whether or not forking was associated with release from a period of inhibited height growth.

Confirmation of Released-type Architecture

I determined ages of tree trunks at 0.3 and 1.0 m above ground level from increment cores. I used age at 0.3 m to estimate the year of tree establishment. If a tree had experienced intense browsing that limited its growth to less than 0.3 m for a period of years, a core taken from a height of 0.3 m would underestimate the age of the tree. Such browsing would cause development of multiple primary stems. Because trees at the site did not fork between ground level and 0.3 m, a core at 0.3 m provided a reliable estimate for establishment year of the initial primary stem. Growth to 1.0 m was selected as a benchmark height that corresponded with a browsing intensity that is markedly lower than the present level (Keigley 1997b).

I calculated the number of years required for growth from 0.3 to 1.0 m from the difference in annual-ring numbers between those heights. I termed this number of years the "elongation period," and considered it a measure of the rate of height growth. To identify periods of years with growth inhibition, I regressed elongation period for each plant on year of its establishment. If no inhibition occurred over a period of years, there would be a series of points with short elongation periods (1-3 years) on the ordinate spaced along a series of years on the abscissa. A value of 0 indicated that the stem grew through the 0.3 and 1.0 m levels the same year. If height growth was inhibited for a series of years and then released, the elongation period for each plant would increase by about 1 year for each year it was inhibited.

Consider a hypothetical case where plants were established each year over a period of 9 years and prevented from growing taller than 0.5 m during that period. At 9 years, there would be a group of 0.5-m-tall plants ranging in age from 0 to 9 years old. If in the tenth year all plants were allowed to grow taller than 1 m, the elongation period for plants established in the first year of treatment would be 10 years. Plants established in the second year of treatment would have an elongation period of 9 years, and plants established in the ninth year of treatment an elongation period of 1 year. If establishment years increase from left to right on the X-axis, the hypothetical series would be described with a regression slope of -1.0.

Height growth inhibition could be caused by unfavorable growing conditions (e.g., drought, insect herbivory). It also could be caused by a series of years during which the stems were browsed by ungulates, preventing the trees from growing to 1.0 m. If architectural evidence of ungulate browsing occurred, I assumed this to be the deterrent to plant growth. If there was no architectural evidence of ungulate browsing, I assumed that other factors principally inhibited the growth.

Development of a Browsing History

The architectures described above are produced during the period that the terminal leader grows within the browse zone. A history of browse use can be reconstructed by examining plants of different age (Keigley and Frisina 1998). Dendrochronology can be used to determine when browsing effects occurred.

If a period of intense herbivory followed a period of light-to-moderate browsing, I used the last year in which a tree grew to a height of 1.0 m tall to designate the final year of light-to-moderate herbivory. The presence of retrogressed-type plants established at about the same time offered evidence that browsing caused the latter period of growth inhibition.

Conversely, if a period of light-to-moderate browsing followed a period of intense browsing, the first year in which a tree grew to 1.0 m tall was used to designate the initial year of light-to-moderate herbivory. The presence of released-type individuals established prior to the transition year suggested that browsing influenced the early period of growth inhibition.

Results and Discussion

Chronologic Distribution of Architectures

All 14 trees in Stand 1 were of uninterrupted-growth-type architecture and of about the same height and dbh. All had heart rot and could not be aged fully. One individual contained 140-150 growth rings in the intact portion of the wood outside the rot. The establishment year for this tree must have preceded the 1840s-1850s. Heart rot in living trees and dead trees of similar stature indicated that trees in Stand 1 were reaching maximum longevity.

All 45 trees in Stand 2 were of uninterrupted-growth-type architecture and of about the same size and dbh. Heart rot also was common in these, and I could successfully age only 4 trees. Their years of establishment were 1877, 1892, 1893, and 1894. Given their similar size, all 45 trees were likely established within this approximate span of years.

All three architectural categories were represented in Stand 3. I successfully cored 51 trees at the 0.3 and 1.0 m heights. These trees were established between 1918-1968: 40 were classified as uninterrupted-growth-type and 11 tentatively as released type.

Approximately 3,000 individuals in Stand 3 ranged in height from ≤ 10 cm to 1.5-m tall. Most of these individuals were classified into the combined arrested- and retrogressed-type category. A few short individuals (≤ 20 cm) were classified into the uninterrupted-growth type category. Browsing by elk occurs primarily during the winter, so I attributed the uninterrupted-growth type architecture of smaller individuals to protection by snowpack. As described above, the youngest individual to grow to tree stature was established in 1968. Therefore, except for plants short enough to be protected by snowpack, all individuals established after 1972 exhibit arrested- or retrogressed-type architecture. One of the largest individuals in the combined arrested- and retrogressed-type category was 1.5 m tall and was determined to have been established in 1972.

Confirmation of Release

I plotted elongation period against establishment year for plants in Stand 3, which I could age at both 0.3 and 1.0 m (Fig. 4). A negative correlation between elongation period and establishment year occurred during two periods, 1924-1947 ($Y = 1278 - 0.66X$, $R^2 = 0.47$, $n = 33$) and 1947-1968 ($Y = 1965 - 0.74X$, $R^2 =$

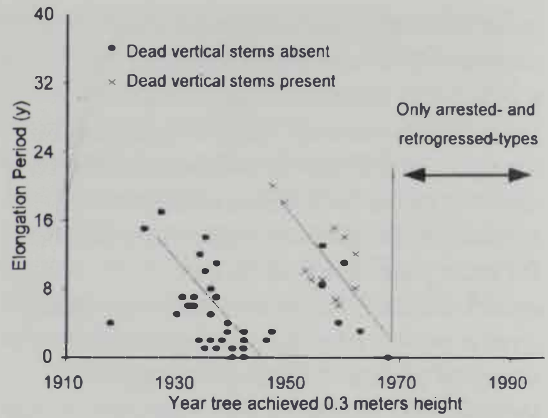

Figure 4. *Relationship between year of establishment and time required to grow from 0.3 m to 1.0 m. The negative slopes mark periods of inhibited growth.*

0.55, $n = 17$). A period of inhibited growth followed by release from that inhibition produced such a pattern.

The lower trunk of trees established from 1924-1947 did not fork, indicating that their terminal leaders were not intensely browsed when the plants were young and short. Other factors, such as drought (Houston 1982), must have played a role in growth inhibition. Although some browsing likely occurred, I attribute the height-growth inhibition that began in 1924 (Fig. 4) primarily to drought. Height growth resumed when the drought ended in the late 1930s (Fig. 4).

Eleven trees (the Xs in Fig. 4) established between 1947-1962 had live stems that forked from dead, near-vertical stems. Some of these dead stems were similar in appearance to heavily-browsed arrested- and retrogressed-type individuals nearby. For example, the dead stem at the base of the tree in Fig. 3 is similar in appearance to the retrogressed-type cottonwood shown in Fig. 2. These dead stems appeared to be the remains of terminal leaders that had been browsed when the plants were young.

The inhibition of growth during 1947-1962 was seemingly browsingrelated, which would confirm my tentative assignment of these individuals to the released-type category. Five of the remaining trees established during these years did not show clear evidence of intense browsing, but experienced some degree of inhibition.

History of Browsing at the Site

Stands 1 and 2 (the oldest stands) contained all uninterrupted-growth-type individuals. Stand 3 contained (1) older uninterrupted-growth-types, (2) middle-aged, uninterrupted-growth- and released-type individuals, and (3) younger-aged uninterrupted-growth and arrested- and retrogressed-type individuals. These architectures indicated a four-phased browsing history (Fig. 5).

In phase 1, the older uninterrupted growth individuals in Stands 1, 2, and 3 grew to tree stature during a period of light-to-moderate browsing. However, there are substantial gaps in the phase 1 record from the 1800s to 1924 and the browsing levels that existed during these gaps was not determined from the architectural evidence present at this site. From 1924 to the end of phase 1, the record is nearly continuous and the validity of the reconstructed history is more certain.

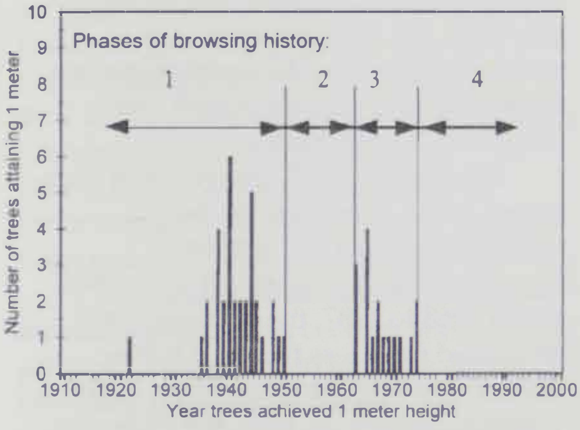

Figure 5. *Frequency diagram describing the number of trees attaining 1.0 m in a given year. Over the past century, cottonwood at the study site experienced a four-phase browsing history, the transition years of which were based on whether or not browsing permitted tree-growth to 1.0 m tall.*

The released-type trees established between 1947 and 1962 are evidence of a period of intense browsing followed by a period of light-to-moderate browsing. The period of intense browsing, phase 2, followed the early period of light-to-moderate browsing, phase 1, identified above. Growth of the released-type plants to tree stature suggests a subsequent period of light-to-moderate browsing (phase 3). The arrest and retrogression of individuals established since 1968 suggests intense browsing at the present time (phase 4).

No cottonwoods attained a height of 1 m during the period 1952 to 1962 (Fig. 5) even though individuals were established during this period (see distribution along the X-axis, Fig. 4). I attributed inhibition of height growth during this period to browsing. The transition between phase 1 (light-to-moderate browsing) and phase 2 (intense browsing) is marked by the final year (1951) that a tree grew to a height of 1 m. Phase 2 occurred between 1952 and 1962, when no trees grew to 1 m tall.In 1963, three individuals grew to a height of 1.0 m (Fig. 5), which marked the beginning of a period of light-to-moderate browsing: phase 3. The arrested- and retrogressed-type plants of stand 3 suggest that current browsing is intense: phase 4. The year of transition between phase 3 and phase 4 is marked by the final year (1974) that a tree grew to a height of 1 m (Fig. 5). Retrogressed-type individuals in stand 3 experienced an early period of light-to-moderate browsing, phase 3, followed by intense browsing: phase 4. The largest, possibly oldest, retrogressed-type individual in stand 3 was established in 1972. The retrogression of this individual a few years after its establishment conforms closely with the 1974 date for transition to intense herbivory as determined by final tree growth to 1.0 m.

I do not imply that browsing levels of cottonwood changed abruptly in the exact years described above. The methods I used provide a consistent way to identify and describe transitions in browsing intensity.

History of Elk

The size of the northern elk herd prior to the establishment of YNP is unknown and the accuracy of early numbers reported after that are subject to question. After a period of market hunting during 1871-1877, Norris (1877) described YNP's northern elk herd as "decimated." After the grey wolf (*Canis lupus*) was reduced and elk were protected from hunting inside the park, the northern herd increased (Norris 1879). By 1886, it was reported that there was more game in the park "than was ever known before" (Wear 1886). In 1915, Smith *et al.* (1915) reported the northern herd to number 27,800 elk. The number of elk wintering in the park was believed to have increased because settlement and hunting along the park's borders blocked the elk's access to an ancestral winter range that extended north of the park (Pitcher 1905, Smith *et al.* 1915, Graves and Nelson 1919).

Wright and Thompson (1935) reported the northern range in "deplorable" condition in 1929 due to overgrazing. From 1935 to 1968, the northern herd was culled to prevent further range deterioration (Houston 1982). By 1968 the northern herd had been reduced to less than 4,000 elk (Coughenour and Singer 1996). But the killing of elk in a national park was controversial (U.S. Senate 1967), and the culling program was halted in 1968. The northern elk herd then increased to more than 23,000 by 1987 (Coughenour and Singer 1996).

Hypotheses Testing

There are two general schools of thought regarding the decline of YNP's woody plants. According to one school, the declines were caused by increased browsing pressure from increased numbers of elk that winter on the northern range (Wright and Thompson 1935, Leopold *et al.* 1963, Kay 1990). According to the other school, the number of elk wintering on the northern range has fluctuated within the natural limits of variability, and decline in woody plants has been influenced by a complex interaction between climate change, fire, mammalian predators, and beaver abundance (Singer and Cates 1995). To date, neither of these hypotheses has been tested, nor have methods of supporting or refuting them been developed.

Here I offer a method to test the hypothesis that the decline in woody plants is primarily due to increased browsing pressure by an increasing elk population. This method is based on the premise that elk prefer some browse species over others.

For example, at a site where aspen is intensely browsed, Douglas fir may be moderately browsed, and spruce may not be browsed at all (pers. obs.). When highly preferred browse species are depleted, elk then consume less preferred species. The onset of intense browsing may occur in a rank order sequence of preference.

In northern YNP, the nature of such a rank order sequence can be determined from the history of browsing that has occurred since 1968. From 1968 to 1987, the northern herd increased from less from 4,000 (the census was 3,172) to more than 23,000 (census, 18,193). In 1974, the browsing intensity of cottonwood at the study site changed from light-to-moderate to intense. The northern herd was censused at 12,607 in that year (Coughenour and Singer 1996). Cottonwood browsing intensity since 1968 has consisted of two phases, an early phase of light-to-moderate browsing, and a later phase of intense browsing. There was no comparable two-phase change in climate. The post-1968 increase in browsing intensity best corresponds to a four-fold increase in elk number.

Architecture-based methods can determine the post-1968 browsing history of aspen, lodgepole pine, Douglas fir, and spruce. Over much of the northern range, these species appear to exhibit a pattern similar to that of cottonwood: older individuals exhibit uninterrupted-growth type architecture, while younger individuals exhibit retrogressed- and arrested-type architectures. Based on the post-1968 browsing histories, the species can be ordered in the sequence in which intense use began. Because elk use varies across the northern range, the actual transition years may vary. However, because the sequence is an expression of current browse preference by elk, the sequence should be identical throughout the northern range.

The cause of the post-1968 increase in browsing intensity is understandable given the six-fold increase in elk number. It is the cause of the pre-1968 increase in browse use that has been controversial. For example, was the increase in cottonwood browsing in 1952 at the study site caused by climate change? By use of the methods I describe, we can determine the rank order sequence in which browse species were intensely used prior to 1968.

I hypothesize that the increase in browse use early this century was primarily caused by an increase in browsing pressure by the elk population. That hypothesis will not be supported if the following are not upheld: 1) the rank order sequence of change in browse use earlier this century will be the same as the rank order sequence of browse use that occurred after 1968, and 2) all sites on the northern range will exhibit a similar pre-1968 rank order sequence.

It seems unlikely that the influences, such as climate-change, fire, and beaver abundance, described by Singer *et al.* (1994) would produce, earlier this century, the same rank order sequence of browse use that occurred after 1968 in response to a six-fold increase in elk number. The influence of such factors should vary with topography and location. I would expect different rank order sequences to occur in different parts of the northern range. The methods and test that I propose provide a way to address a controversial issue on northern YNP elk winter range.

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Literature Cited

Bergström, R. and K. Danell. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. J. Ecol. 75:533-544.

Bilbrough, C.J. and J.H. Richards. 1993. Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms of tolerance. Ecol. 74:481-492.

Chase, A. 1987. Playing God in Yellowstone. Harcourt Brace Jovanovich, Publishers. New York, NY.

Cole, G.F. 1958. Range Survey Guide. State of Montana Department of Fish and Game. Helena, MT.

Coughenour, M.B. and F.J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecol. App. 6:573-593.

Despain, D.G. 1990. Yellowstone Vegetation. Roberts Rinehart Publishers. Boulder, Colorado.

Despain, D.G., D. Houston, M. Meagher, and P. Schullery. 1986. Wildlife in Transition. Roberts Rinehart, Inc. Publishers. Boulder, CO.

Everitt, B.L. 1968. Use of the cottonwood in an investigation of the recent history of a flood plain. Am. J. Sci. 266:417-439.

Ferguson, R.B. and J.V. Basile. 1966. Topping stimulates bitterbrush twig growth. J. Wild. Manage. 30:839-841.

Graves, H.S. and E.W. Nelson. 1919. Our national elk herds: A program for conserving the elk on national forests about the Yellowstone National Park. USDA Circular 51. US Government Printing Office. Washington, D.C. 34 pp.

Harrington, H.D. 1964. Manual of the Plants of Colorado. Swallow Press Inc. Chicago, IL.

Houston, D.B. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publishing Company, Inc., New York, New York. 474 pp.

Kay, C.E. 1990. Yellowstone's northern elk herd: A critical evaluation of the "natural regulation" paradigm. Dissertation, Utah State University, Logan, Utah. 490 pp.

Kay, C.E. 1997. Viewpoint: Ungulate herbivory, willows, and political ecology in Yellowstone. J. Range Manage. 50:139-145.

Keigley, R.B. 1997a. A growth form method for describing browse condition. Rangelands 19:26-29.

Keigley, R.B. 1997b. An increase in herbivory of cottonwood in Yellowstone National Park. Northwest Sci. 71:127-136.

Keigley, R.B. and M.R. Frisina. 1998. Browse evaluation by analysis of growth form. Montana Fish, Wildlife, and Parks. Helena, MT. 149 pp.

Leopold, A.S., S.A. Cain, C.M. Cottam, I.N. Gabrielson, and T.L. Kimball. 1963. Wildlife management in the national parks. Trans. NA Wild. Conf. 24:28-45.

National Park Service. 1988. Management Policies. U.S. Government Printing Office, Washington, D.C.

Norris, P.W. 1877. Annual report of the superintendent, Yellowstone National Park. U.S. Government Printing Office, Washington, D.C.

Norris, P.W. 1879. Annual report of the superintendent, Yellowstone National Park. U.S. Government Printing Office, Washington, D.C.

Pitcher, J. 1905. Annual report of the superintendent, Yellowstone National Park. US Government Printing Office, Washington, D.C.

Riney, T. 1982. Study and management of large mammals. John Wiley and Sons. New York, New York.

Romme, W.H., M.G. Turner, L.L. Wallace, and J.S. Walker. 1996. Aspen, elk, and fire in northern Yellowstone National Park. Ecol. 76:2097-2106.

Singer, F.J. and R.G. Cates. 1995. Response to comment: Ungulate herbivory on willows on Yellowstone's northern winter range. J. Range Manage. 48:563-565.

Singer, F.J., L.C. Mark (sic), and R.C. (sic) Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. J. Range Manage. 47:435-443.

Singer, F.J. and R.A. Renkin. 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. Great Basin Nat. 55:201-212.

Smith, C.L., A.A. Simpson, and V. Bailey. 1915. Report on investigations of the elk herds in the Yellowstone region of

Wyoming, Montana, and Idaho. United States Bureau of Biological Survey and United States Department of Agriculture Forest Service. Unpublished report in Yellowstone National Park Archives, Yellowstone National Park, Wyoming. 56 pp.

U.S. Senate. 1967. Hearings before a Subcommittee of the Committee on Appropriations of the United States Senate on Control of Elk Population, Yellowstone National Park. U.S. Government Printing Office, Washington, D.C. 142 pp.

Wear, D.W. 1886. Annual report of the superintendent, Yellowstone National Park. U.S. Government Printing Office, Washington, D.C. 3 pp.

Wright, G.M. and B.H. Thompson. 1935. Wildlife management in the national parks. Fauna of the National Parks No. 2. US Government Printing Office. Washington, D.C. 142 pp.