

# Historical Condition of Woody Vegetation on Yellowstone's Northern Range: A Critical Evaluation of the "Natural Regulation" Paradigm<sup>1</sup>

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**Abstract.** The Park Service's "natural regulation experiment" is predicated on the assumption that large numbers of elk (12,000 - 15,000) have wintered on Yellowstone's northern range for the last several thousand years. Agency biologists believe that the park's vegetation coevolved with these herbivores and reached equilibrium conditions, which they term "ecological carrying capacity." According to this model, elk influences on the vegetation are "natural" and represent the "pristine" condition of the park. If this paradigm is correct, early historic photographs of woody vegetation should show that aspen, willows, and conifers were as heavily browsed or highlined by ungulates in the early years of the park's existence as they are today, and aspen stem damage by elk was the norm then as it is now.

To evaluate these predictions and to test the "natural regulation" paradigm, we reviewed approximately 50,000 early images taken in the park. Photos of aspen stands on the park's northern range taken during the 1880s and 1890s do not show any evidence of elk-induced bark damage. Photos of aspen, willows, and conifers taken from 1872 to the 1890s do not show evidence of ungulate browsing or highlining. Some early photos do show occasional conifers that lacked their lower branches, but evidence indicates that this was caused by light groundfires burning or killing the lower branches and by human removal of branches. Previous authors apparently confused fire and human highlining with that caused by ungulates.

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Conifers and other woody vegetation in these 1870 - 1890 images were approximately 70-100 years old or older when they were photographed. Since they show no evidence of ungulate use, this suggests that few, if any, elk wintered in Yellowstone from the late 1700s through the 1870s. Thus, ungulate highlining of conifers and repeated browsing of other woody vegetation are not "natural" and represent a departure from conditions that existed before the establishment of Yellowstone National Park. These photographs do not support the Park Service's contention that Yellowstone was always a major elk wintering area and that the northern herd did not increase and alter the vegetation. Since these data do not support one of the key assumptions upon which "natural regulation" is based, that paradigm must be rejected.

## Introduction

The relationship between vegetation and ungulates in Yellowstone National Park has long been a subject of conflicting opinions and intense debate (Chase 1986; Despain et al. 1986; Houston 1982; Kay 1990). Before 1968, Park Service officials contended that an "unnaturally" large elk (*Cervus elaphus*) population, which had built up in Yellowstone during the late 1800s and early 1900s, had severely "damaged" the park's northern winter range, including aspen (*Populus tremuloides*) and willow (*Salix* spp.) communities (Tyers 1981). However, agency biologists now hypothesize that elk and other animals in Yellowstone are "naturally regulated," being resource (food) limited (Despain et al. 1986; Houston 1982), and that the condition of the ecosystem today is much as it was at park formation.

Under "natural regulation" (Kay 1990, 1-31) the following assumptions are made: First, predation is an assisting but nonessential adjunct to the regulation of ungulate populations. If wolves (*Canis lupus*) were reintroduced into the ecosystem, they would take only the ungulates slated to die from other causes, such as starvation, and hence predation would not lower ungulate numbers. Second, if ungulates and vegetation have coevolved for a long period of time and occupy an ecologically complete habitat, the ungulates cannot cause retrogressive plant succession or "range damage." The ungulates and vegetation will reach an equilibrium, called "ecological carrying capacity," in which continued grazing will not change plant species composition or the physical appearance of the plant communities. And finally, at equilibrium, competitive exclusion of sympatric herbivores caused by interspecific competition will not occur. In Yellowstone this means that competition by elk has not reduced the numbers of other ungulates or beaver (*Castor canadensis*) since park formation.

The Park Service's "natural regulation experiment" (cf. Despain et al. 1986) is predicated on the assumption that large numbers of elk (12,000 - 15,000) have wintered on Yellowstone's northern range for the last several thousand years. Park Service biologists now hypothesize that elk, vegetation, and other herbivores in Yellowstone have been in equilibrium for that period of time (Despain et al. 1986). The agency also holds that any changes in plant species composition since the park was established in 1872 have been primarily caused by suppression of lightning fires, normal plant succession, or climatic change, not by ungulate grazing. According to "natural regulation," elk influences on Yellowstone's vegetation are "natural" and represent the "pristine" condition of the park.

<sup>3</sup>Terms such as "overgrazing," "range damage," and "unnatural" elk populations are common in nearly all early government reports on the elk herds in the Greater Yellowstone ecosystem. Since these terms are value laden, they are used throughout this paper only in their historical context.

If this paradigm is correct, historical photographs of woody vegetation in the park should show that aspen, willows, and conifers were as heavily browsed or highlined by ungulates in the early years of the park's existence as they are today and that aspen stem damage by elk was the norm then as it is now. To evaluate these predictions and to test the "natural regulation" paradigm, we reviewed photographs taken in the park since 1870.

## Study Area

The work was conducted primarily on the winter range of Yellowstone's northern elk herd, though other parts of the park also were visited. Houston (1982) provides a description of the climate, physiography, and vegetation of Yellowstone's northern range.

## Methods

We searched archival photographic collections at Yellowstone National Park, the Montana Historical Society, the University of Montana, Montana State University, the Museum of the Rockies, the University of Wyoming, the Colorado Historical Society, the Library of Congress, the National Archives, and the U.S. Geological Survey's Denver Photographic Library for historical photos of the northern range. We reviewed approximately 50,000 images taken in the park and throughout the Yellowstone area. Only a small portion of these photographs were taken on the northern range and a still smaller number contained views of aspen, willows, or conifers of interest. From 1986 through 1989 we rephotographed the locations in the historical pictures to form sets of comparative photos, a process called repeat photography (Rogers, Maide, and Turner 1984). We evaluated the photosets under magnification to determine whether the plants pictured in the early photos showed evidence of ungulate browsing and then compared those data with our photos and notes on the condition of the vegetation in those same areas today. Houston (1976, 1982), Gruell (1980a,b), Cole (1983), and Despain et al. (1986) also used comparative photography to study vegetation changes on the northern winter range and other areas within the Greater Yellowstone ecosystem.

## Results and Discussion

### Conifers

One of the conspicuous characteristics of today's northern range, and indeed other parts of the park as well, is the browsing highline on conifers. Evident to the most casual traveler, the configuration is widely cut into all of the park's coniferous species (figure 1). Of the woody species in the park, conifers are among the least palatable to ungulates (Nelson and Leege 1982). If other foods are available, elk and other herbivores will take them in preference to conifers. When deep snows cover most vegetation and elk are facing starvation, however, they will turn to conifers in an attempt to satisfy their hunger. Thus, throughout most of western North America, ungulate highlining of conifers is usually viewed as a sign of overgrazing and range deterioration. According to Park Service biologist Houston (1982, 129). "High-lining of conifers (heavy browsing of lower branches) has [also] been interpreted as evidence of range deterioration" on Yellowstone's northern range.



Figure 1. Highlined conifers on Yellowstone's northern range. The lower branches on these Englemann spruce have been browsed off as high as the elk can reach. Of all the conifers in the park, Englemann spruce are the least palatable. For scale, the survey pole (lower left center) is 6 feet tall and is marked in one-foot segments. Photo by Charles E. Kay, August 15, 1986.

Park Service biologists who examined early photographs, however, observed what they interpreted to be ungulate-induced highlines on conifers. After reviewing 319 repeat photosets of the park and adjacent areas, 244 of which were taken on the seasonal ranges of the northern elk herd, Houston (1982, 129) concluded that "Early photos showed high-lined trees [conifers] on the northern range and adjacent areas." In his study of Yellowstone's Firehole elk herd, Park Service biologist Cole (1983) used "57 paired photographs taken at 58 and 104 year intervals" to evaluate vegetation changes. He also concluded that highlined conifers were common in early park photographs. Cole and Houston both implied that highlined conifers were natural and did not signify range overuse. The Park Service has taken these opinions as one line of evidence supporting its contention that elk have always been abundant in the park and that vegetative conditions today are similar to pre-Columbian conditions (cf. Despain et al. 1986).

We have carefully reviewed under magnification all photographs published by Houston (1976, 1982), Despain et al. (1986), and Gruell (1980a) as well as other archival photographs. In our judgment, there is no evidence that conifers or any other woody species had been highlined by ungulates in the earliest (1871 - 1890) photos. Instead, there is considerable evidence that few ungulates wintered in the area prior to park establishment. We base this conclusion on three grounds. First, even in those few photos in which Houston (1976, 1982) inferred ungulate highlining, we do not see convincing evidence. A few trees in those photographs apparently lack lower branches, yet other conifers in the same pictures have branches that extend down to the ground.

For example, in plate 72 of Houston (1976) and plate 38 of Houston (1982), he infers evidence of ungulate highlining in the c. 1885 Iddings photograph. Two trees in the upper right corner of the photo might support this inference, but the stronger contrary indication are the trees in the upper left corner with branches to the ground. Similarly, Houston (1976, plate 73) infers ungulate highlining in a c. 1871 Jackson photo. There, a single tree on the skyline in the upper center of the photo apparently lacks its lower branches, but the small trees on the skyline in the upper right all have a full complement of branches. We also do not see evidence of highlining in the c. 1885 Iddings photo in Houston's (1982) plate 1. On the contrary, there are numerous young trees with branches to the ground in the lower right corner and center right of the photo.

Our second line of evidence is the clear absence of highlining on photos we found in our search. Most significant are the conifers in William H. Jackson's c. 1872 photograph of Mammoth Hot Springs on Yellowstone's northern range, which show no evidence of ungulate browsing or highlining (figure 2a). The conifers in that picture are mostly limber pine (*Pinus flexilis*), juniper (*Juniperus scopulorum*), and a few Douglas-fir (*Pseudotsuga menziesii*). Limber pine is one of the most palatable conifers in the park, yet it shows no evidence of ungulate browsing in this photograph. The photo does not support Houston's (1976, 212) claim that conifers show "heavy ungulate utilization" in early (1870s) W.H. Jackson photos taken around Mammoth Hot Springs. Today those same trees have had all of their lower branches removed as high as the elk can reach (figure 2b). The conifers in Jackson's photo appear to be approximately 70 to 100 years old or older and show no evidence of ungulate use, which suggests that few if any elk wintered in that area as far back as 1800.

Regenerating conifers in Idding's c. 1890 photo of Rainy Lake (figure 3) and F. Jay Haynes' 1893 photo of Yancy's Hole (figure 10a) also show no evidence of ungulate browsing. Collectively, these photos, the early Mammoth Hot Springs images, and Houston's photos of unbrowsed conifers give no indication of the ubiquity of ungulate highlining that one sees on the northern range today.



Figure 2. Repeat photoset of conifers at Mammoth Hot Springs on Yellowstone's northern range. (a) Conifers in this William H. Jackson c. 1872 photograph show no evidence of ungulate browsing or highlining. The conifers between the camera and the hot springs are mostly limber pine and juniper. A few Douglas-fir in the left center background show evidence of fire-pruned lower branches. The hot springs apparently kept those fires from burning the conifers in the foreground. Dead trees around the hot springs were most likely killed by changing thermal water runoff patterns, as is often the case today. Regenerating conifers in left center background also do not show any evidence of ungulate highlining. W.H. Jackson photo No. 1,195 (F-28,835), Colorado Historical Society, Denver. (b) That same area in 1989. The conifers are now all highlined as high as the elk can reach. Charles E. Kay photo, No. 3,255-14, August 26, 1989.



Figure 3. Early photograph of Rainy Lake on Yellowstone's northern range southeast of Tower Junction. Based on the standing snags and height of the regenerating aspen in this c. 1890 photo, it appears that this site burned 10 to 15 years before the photo was taken. The aspen and regenerating conifers, mostly Douglas-fir, show no signs of highlining nor any evidence of ungulate browsing. The lower branches of older conifers have been killed by fire, as the highline height is variable, and the lower branches of some conifers have been removed higher than elk can browse. According to Houston (1976, p. 264), "A fire-scarred tree cut within 40 yards of the camera point showed fire dates of  $1876\pm$ ,  $1840\pm$ ,  $1810\pm$  and several earlier fires." Closeup from a photograph by J.P. Iddings, No. 148, U.S. Geological Survey, Denver.

The third basis for our conclusions is that other factors besides ungulate highlining may explain the absence of lower branches on conifers. These factors evidently account for most, if not all, of the infrequent cases of what appears to be highlining in the early photos. One factor is pruning by light groundfires that burn and kill lower branches. Fire pruning of the lower branches of conifers can be distinguished from ungulate highlining because fire-pruning height varies, producing an uneven highline instead of the near-constant height that results from ungulate browsing. Second, unless they are standing on packed snow, elk can typically browse to a height of only 3 m or less, while fires often kill conifer branches to a greater height.

An excellent example is shown in figure 4, a photograph taken by J.P. Iddings on Yellowstone's northern range c. 1890. Iddings, who worked for the U.S. Geological Survey, apparently took this photograph to illustrate glacial erratic boulders, which are common in the lower Lamar Valley where this picture was taken. To the right of the boulder are one large and at least three smaller Douglas-fir trees. The lower branches on the large tree are all dead. If ungulates had highlined this tree, these branches would have been eaten or broken off. Instead, even the small, dead branch tips remain. Since this Douglas-fir grew by itself in the open, its lower branches did not self-prune as a result of lack of sunlight, as commonly occurs in dense forests. Based on the 20- to 25-year fire interval that Houston (1973, 1982) obtained for this area and the lack of sagebrush in this photo, we conclude that frequent light groundfires killed the lower branches on this large Douglas-fir.

The young Douglas-firs in figure 4 apparently grew after the last fire at the site and show no evidence of ungulate browsing or highlining. Today all the conifers on this site have been highlined by elk to a height of 3 m, including Englemann spruce (*Picea engelmannii*), which is the least palatable conifer (Bergerud and Manuel 1968; Miquelle and Van Ballenberghe 1989; Nelson and Leege 1982).

Other early photos also show fire pruning of the lower branches of conifers, including the conifers in the right center of figure 3 and in the upper center and upper left of figure 9. In both cases, the dead tree snags and clumps of young aspen shoots attest to the fire history of these sites. Fire-pruned conifers can also be seen in the upper right corner of figure 10a, again accompanied by dead snags.

A second explanation for the absence of lower coniferous branches is human pruning. Several historic photos, some as early as the 1880s, show conifers without their lower branches. Most of that highlining, however, was caused by human (European) use. Humans commonly removed lower branches for several purposes. During Yellowstone Park's early years, there were no designated camping areas and no regulations against cutting live trees (Haines 1977). Draft animals, primarily horses, were the main mode of transportation. Riders often removed a tree's lower branches so they could tie their animals directly to the main trunk, which was more secure than tying them to small branches.

Early park visitors also cut conifer branches to sleep on, since they did not carry the foam pads or air mattresses used by today's tourists. For example, William H. Jackson's early (1870s) photos of camp life in Yellowstone show pine boughs cut for bedding. Hamp (Brayer 1942, 284) refers to the "splendid bed of bows" he slept upon while camping in Yellowstone during the summer of 1872. Moreover, early tourists were no different from campers today, who remove lower branches from trees near their campsites to burn as fuel or for other camp activities.

In earlier times, people tended to camp near scenic attractions and hence tended to remove the lower branches from trees at those locations. Those same areas were also commonly photographed by early park visitors. Photography was much more difficult then than it is now, and people did not "waste" time and effort taking pictures that did not include major attractions, such as hot springs. The vast majority



Figure 4. Douglas-fir trees growing on the north side of a glacial erratic boulder in the lower Lamar Valley on Yellowstone's northern range c. 1890. Based on the 20-to 25-year fire interval determined by Houston (1973, 1982) for this area and the lack of sagebrush in this photo, the older Douglas-fir's lower branches were probably killed by low-intensity groundfires. The dead branches retain their fine tips, which would not be the case if elk had removed the foliage. Moreover, the branches have been killed to a height beyond the reach of elk or other ungulates. Three young Douglas-firs that have grown since the last fire at this site show no evidence of ungulate browsing or highlining. Photo by J.P. Iddings, No. 149, U.S. Geological Survey, Denver.

of the approximately 50,000 historic images we reviewed for this study were of major park features. Fewer than 1 percent contained vegetation subjects of interest, and most of those were taken for other purposes. For example, the only reason Haynes took photos in 1893 of aspen and willows on the northern range (figures 7 and 10a) was because his subjects happened to be standing in front of them.

William H. Jackson's c. 1883 photograph of Crested Hot Spring with Old Faithful erupting in the distance (figure 5) illustrates the effect of human highlining on conifers. The conifers in the right center and behind the cabin (left center) do not show evidence of highlining, but the conifers in front of the cabin, along the walkway, and in front of the tent camp on the bench above the Firehole River are all highlined. Apparently people removed the lower branches from these conifers to improve the view.

In total, we see no substantial evidence of ungulate-induced conifer highlining in photos depicting scenes in the first two decades of the park's existence. On the contrary, we see considerable evidence of its absence. The situation is clearly different today: the vast majority of conifers exposed to wintering ungulates on the northern range have had their lower branches removed by browsing animals (figure 1).

## Aspen

Aspen are more palatable to ungulates than conifers and are readily eaten by elk during winter as well as during other times of the year (Nelson and Legee 1982). The animals affect aspen stands in four ways. First, they eat the soft bark, digging their lower front teeth into the bark and then moving their heads upwards, applying pressure to the tree. This enables the animals to gnaw or strip off large pieces of bark, often down to the sapwood (DeByle 1985, 118-119; Krebill 1972). In response to this injury, the trees develop black scar tissue. When the bark damage is extensive, as is characteristic in Yellowstone, the lower 3 m or so of aspen trunks are black instead of the normal white (figure 6).

Second, in areas of heavy elk use, the animals perennially browse off any young shoots that grow from the clone's root mass. Thus, any trees tend to be uniformly older ones that somehow escaped browsing. There are no young regenerating sprouts greater than 2 m tall. These characteristics can be seen in figure 6.

Third, those aspen stems that have managed to escape elk browsing and grow into trees characteristically have no lower branches, i.e., they are highlined. Branches within the animals' reach are browsed off (figure 6).

And finally, in areas of heavy elk use, the understories of aspen stands have a parklike appearance, the vegetation made up largely of grasses (often exotic) and low forbs (Kay 1990; figure 6). Stands not subjected to heavy use, like those outside Yellowstone Park and in enclosures on the park's northern range, have a diverse understory of shrubs and tall forbs (Kay 1990).

Park biologists agree on the above characteristics of contemporary aspen stands on the northern range. But according to the "natural regulation" hypothesis, they contend that aspen in Yellowstone have always exhibited these characteristics (Despain 1991, 94-101; Despain et al. 1986). If this is true, ungulate use should be apparent in early photos of aspen stands on the northern range.

Figures 7 and 8 are 1893 and 1899 photos of aspen on the park's northern range. They show white, unscarred trunks down to ground level; branches or branch scars on their lower 2 m; multisized (aged) stems; and understories that appear to be dominated by tall forbs and shrubs, not grasses. By 1910, however, photos show that elk had started to highline aspen and inflict bark damage.



Figure 5. Conifers in William H. Jackson's c. 1883 photograph of Crested Hot Spring with Old Faithful erupting in the distance show evidence of human highlining. (a) Trees in the right center and behind the cabin (left center) do not show any evidence of highlining, whereas conifers in front of the cabin, along the walkway, and in front of the tent camp above the Firehole River have all been highlined. People apparently removed the lower branches from these conifers to improve the view or to facilitate camp activities. (b) Closeup of the area around the cabin. W.H. Jackson photo, No. 235 (F-33,110), Colorado Historical Society, Denver.



Figure 6. A typical aspen stand on Yellowstone's northern range today, showing extensive black scar tissue induced by elk bark wounding on the lower 3 m of trunks. Almost all aspen on the northern range have been similarly affected and identical bark coloration patterns are clearly visible in any photograph. Compare this with figures 7 and 8. Charles E. Kay photo, No. 3,272-24, August 28, 1989.

Early photos of other aspen stands on Yellowstone's northern range, such as those depicted in figures 3 and 9, show dense, relatively short-statured aspen that apparently regenerated after fire. None of these trees show any sign of ungulate browsing. Kay (1990) evaluated more than 460 recently burned aspen stands in the Greater Yellowstone ecosystem. In photographs of those stands several years after they were burned, the only ones that had the same physical appearance as stands on the northern range, c. 1870 to 1890, were those that experienced little or no ungulate use. Aspen stands on the northern range that were burned by the 1988 wildfires have not been able to grow new stems greater than 2 m tall because of repeated elk browsing (Kay, unpublished data).

In sum, none of the aspen in early photos show any signs of ungulate browsing or highlining. Instead, stands photographed on Yellowstone's northern range during the late 1800s resemble contemporary stands found within ungulate-proof enclosures and outside the boundaries of the park (Kay 1990).



Figure 7. Company D, Minnesota National Guard camp at Little Blacktail on Yellowstone's northern range in 1893. (a) Aspen stands in background show no elk-induced bark injury; multisized (aged) aspen; tall-forb-dominated understory; and little or no use by elk or other ungulates. Stumps in stand indicate some aspen have been cut, probably related to camp activities. In all likelihood, those woodcutting activities injured surrounding aspen and produced the few black scars evident in this photo, as any bark injury will produce black scar tissue. Other black marks are branch scars that aspen normally produce when lower branches die as the trees grow. (b) Closeup of aspen. These aspen clearly do not look like today's heavily scarred trees; compare this photo with figure 6. Photo by F. Jay Haynes, H-3070, courtesy Haynes Foundation Collection, Montana Historical Society, Helena.



Figure 8. Closeup of aspen felled by beaver on Yellowstone's northern range in 1899. Aspen show no elk-induced bark injury, branch scars or branches on lower 2 m of trees, multisized (aged) aspen, shrub-tall-forb-dominated understory, and little or no use by elk or other ungulates. Compare this photo with figure 6. Photo by Aven Nelson, N213p-y-nc, courtesy American Heritage Center, University of Wyoming, Laramie.



Figure 9. Early photo of aspen on Yellowstone's northern range. The dense aspen regeneration in this c. 1890 photo taken northeast of Tower Junction is not highlined and does not show any evidence of ungulate browsing. Based on the height of the aspen and lack of sagebrush, it appears this site burned 10 to 15 years before the photo was taken. The lower branches of older conifers, mainly Douglas-fir, have been removed or killed by fire. According to Houston (1976, p. 252), "Fire scarred trees cut in this area suggest a historic fire frequency of one fire every 20 - 25 years for the past 300 - 400 years." Closeup from a photograph by J.P. Iddings, No. 152, U.S. Geological Survey, Denver.

## **Willows**

Willows, like aspen, are highly palatable to elk. Willows today seldom exist as tall shrubs in the riparian zones of the park's northern range. Instead, most willows are hedged snags 1 m or less in height that seldom exceed the depth of the previous winter's snow. If the premises of the "natural regulation" paradigm are valid, willow vegetation along streams should have exhibited these characteristics in pre-Columbian times and in the late 1800s, at and following park formation (Despain et al. 1986; Dodd 1991).

Early photos of tall willow communities on the park's northern range, such as those in figure 10, however, show no evidence of ungulate browsing or highlining. Willows photographed on Yellowstone's northern range during the late 1800s resemble those found today within ungulate-proof enclosures and in riparian zones outside the park (Chadde and Kay 1991; Kay 1990). Thus, conditions inside the enclosures more closely approximate the level of ungulate use that existed when Yellowstone Park was established than do current park conditions. This evidence also implies that, historically, few elk or other ungulates wintered in what is now Yellowstone National Park.

## **Conclusions**

Photos of conifers, aspen, and willows on Yellowstone's northern winter range show little or no impact of elk browsing when the park was established in 1872. From 1900 to 1920, those same woody species showed increasing evidence of heavy elk use — conifer highlining, aspen bark stripping and highlining, and hedging of willows — became common. Thus, we conclude that the northern range vegetation is not "natural" — if that term is defined as the condition that prevailed at European contact — and represents a departure from the conditions that existed before the creation of Yellowstone Park.

The condition of the woody vegetation in early photographs and in repeat photosets supports the view that Yellowstone was not historical winter range and that the northern herd increased to unprecedented numbers and profoundly altered the park's vegetation. These photographs do not support Houston's (1982) conclusion that Yellowstone was always a major elk wintering area and that the northern herd did not increase or alter the system. Instead, the evidence points to a significant increase in elk that altered the northern range ecosystem. Since these data also disprove one of the key assumptions upon which "natural regulation" is based — i.e., that thousands of elk always wintered in the park — that paradigm must be rejected as well.



Figure 10. Early photographs of tall willows on Yellowstone's northern range. (a) None of the tall willows in this 1893 photo of Yancy's Hole near Tower Junction shows any evidence of ungulate browsing or highlining. Today, no tall willows exist at this site because of repeated elk browsing (Chadde and Kay 1991, p. 237). Conifers in right center-top show the results of frequent low-intensity groundfires. The lower branches of older trees have been fire pruned, as the highline height is variable, and the lower branches of some conifers have been removed higher than elk can browse. Young conifers show no evidence of ungulate browsing or highlining. Photo by F. Jay Haynes, H-3080. Courtesy Haynes Foundation Collection, Montana Historical Society, Helena. (b) Willows in this c. 1896 photo of the lower Soda Butte Valley show no evidence of ungulate browsing or highlining. Today, no tall willows exist at this site because of repeated elk browsing (Chadde and Kay 1991, p. 240). Photo by A.E. Bradley, courtesy A.E. Bradley Collection (72-158), Mansfield Library, University of Montana, Missoula.

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