

## An Increase In Herbivory of Cottonwood in Yellowstone National Park

### Abstract

This study examined an effect of elk (*Cervus elaphus nelsoni*) on narrowleaf cottonwood (*Populus angustifolia*) in northern Yellowstone National Park, where stands consist of old trees and younger, densely-branched bushes. The elk herd increased from a census of 3,172 in 1968 to a census of 18,913 in 1988. The purposes of this study were to: 1) document the height-growth of cottonwood bushes, 2) determine if the height of browsing corresponded with snow depth, and 3) determine if there has been a recent increase in cottonwood herbivory. In 5 stands of different age (ranging ca. 9-45 y old), I measured the height of live previous-year-growth and the height of the oldest stems killed by browsing. The tallest previous-year-growth was 80 cm; all stems taller than 29 cm had been browsed. Stems were killed by browsing closer to the ground in younger stands (respectively, 87, 62, 28, 14, and 9 cm;  $P < 0.001$ ). There was no change in mid-winter snow depth during the period 1950-1994. The 2 stands established since 1977 had relatively small variances in the height at which stems were killed by browsing (21 and 15 cm<sup>2</sup>), a uniformity likely caused by intense herbivory since respective stand creation. The large variances in the height of browse-killed stems in older stands (745, 399, and 291 cm<sup>2</sup>) were likely caused by an initial period of light-to-moderate herbivory followed by an increase in herbivory that killed the stem tips at the heights existing at the time. The bush growth-form apparently results from an increase in herbivory that occurred between 1968 and 1977, a period in which the elk winter census increased from 3,172 to 8,981. The weight of evidence suggests that EuroAmerican influences have caused the northern elk herd to increase in number since the establishment of the park. If herbivory does not decrease, cottonwood may be eliminated from Yellowstone's northern range.

### Introduction

Over the past century, the elk (*Cervus elaphus*) population of northern Yellowstone National Park (YNP) has fluctuated in number. In response to studies that indicated range damage due to overgrazing (Wright and Thompson 1935), the herd was culled from 1935-1967 (Houston 1982). By 1968, the population declined to a low census of 3,172. Following the halt of the reduction program in 1968, the herd increased to a high census of 18,913 in 1988 (Coughenour and Singer 1996). The current condition of the northern range has become controversial (Chase 1987, Wagner et al. 1995).

There has been general agreement that some species of browse have declined since the establishment of YNP. Singer and Renkin (1995) reported a decline in big sagebrush (*Artemisia tridentata*) at lower elevations of the northern elk winter range. Kay and Chadde (1992) and Singer et al. (1994) reported the decline of willow (*Salix* spp). A decline of aspen (*Populus tremuloides*) was documented by Kay (1990, 1993) and Romme et al. (1995).

The effect of herbivory on other common browse plants such as birch (*Betula* spp.), alder

(*Alnus* spp.), and chokecherry (*Prunus virginiana*) has not been formally documented, however, the hedge-like appearance of young plants attests to significant herbivory. In areas where elk feed during the winter, lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*) that are about 10 - 15 years of age have the following growth form: stems ca. 1-1.5-m tall have live branches from 0 - ca. 0.4 m above ground level, the remainder of the stem being dead. Bite marks indicate that the upper stem was killed by browsing. The live foliage on the lower stem is apparently protected by snowcover. Older conifers are highlined, while younger plants are browsed to hedge-like bushes 20-40 cm tall.

There is disagreement on the cause of the declines. Proposed explanations can be placed into three general categories: 1) the declines are due to past fire suppression (Houston 1982, Despain et al. 1986), 2) the declines are due environmental change (Singer et al. 1994), and 3) the declines are due to EuroAmerican influences (Smith et al. 1915 unpub. rep., Graves and Nelson 1919, Cahalane 1941, Kay 1990). To be generally accepted, an explanation should account for the level of herbivory experienced by all browse species growing on the northern range.

The purpose of this study was to examine the effect of herbivory on narrowleaf cottonwood (*Populus angustifolia*) in northern YNP. Narrowleaf cottonwood is a riparian tree that grows to 20 m tall (Harrington 1964). Establishment from seed is usually limited to the moist zone at the edge of streams, therefore, stands of different age often record a history of channel migration (Everitt 1968, McBride and Strahan 1984). Once established, recruitment from suckers is common (pers. obs.).

Herbivory can alter the form and size of woody plants. In some species, clipping initiates clusters of twigs at the ends of shoots (Cole 1958, Ferguson and Basile 1966, Riney 1982). Height growth may be inhibited (Gaffney 1941, Harlow and Downing 1968, Ross et al. 1970, Olmsted 1979). Intense herbivory may kill the top of a plant and cause young shoots to originate from the surviving lower stem (Garrison 1953, Patten 1968).

Snow depth influences the feeding behavior of elk (Nelson and Leege 1982, Skovlin 1982) and a change in snow depth could plausibly alter the height at which plants are browsed. An increase in herbivory could also affect the height at which stems were browsed. If, during a period of light herbivory, plants grow to heights that approximately correspond with age, an increase in herbivory could logically cause the stem tips of younger (shorter) plants to be browsed closer to the ground compared to the stem tips of older (taller) plants.

I observed that cottonwoods in northern YNP consisted of two age-related growth forms: old trees, and younger densely-branched bushes (Figure 1). One objective of this study was to document the height-growth of bushes. A second objective was to determine if the height of browsing corresponded with winter snow depth. A third objective was to determine if there had been an



Figure 1. A young cottonwood near Soda Butte Creek, Yellowstone National Park. Bite marks indicate that the bush-form habit was produced by herbivory. Virtually all young cottonwoods in the northern elk winter range are restricted to a bush-form growth habit.

increase in the herbivory of cottonwood since the end of the elk reduction program in 1968. Evidence consistent with an increase in herbivory would be: 1) if younger bushes were browsed closer to the ground compared to older bushes, and 2) if there was not a corresponding decline in snow depth.

## Methods

The study was conducted in northeast YNP on Soda Butte Creek 5.5 km upstream from its confluence with the Lamar River (elev. 2050 m). The average precipitation at Mammoth, WY is 412 mm. Substrates consisted of a poorly sorted alluvium with coarse clasts ranging from pebble-to-cobble in size.

Cottonwood bushes are presently uncommon in northern Yellowstone, so I designed a study to minimize coring and sectioning. The study was based on a comparison of stands of different age, thus reducing the need for the age determination of individual plants.

Five stands were assigned relative ages using aerial photographs. Stand 1 was visible on a 1954 photograph and was the oldest known stand of bushes in the area. Stand 2 was visible on a 1972 photograph, but not on the 1954 photograph. Stand 3 was first visible on a 1987 photograph. Stands 4 and 5 were not visible on the 1987 photograph.

I supplemented the relative ages indicated by photography with the dendrochronologic ages of plants presumed to be early colonizers of their respective stands. No plants in stand 1 were sectioned because all were dead and establishment date could not be fixed. Live, large plants were very rare in stand 2 and none were sampled. Relatively few large plants survived in stand 3 where 4 were sectioned. Twenty plants from each of stands 4 and 5 were sectioned. The bases of several plants from each stand were examined to determine if plants were established from seed or from root suckering.

Stand boundaries were defined so that plant height and density were approximately homogeneous within respective stands. Within each stand, 3 belt transects were placed at distance intervals along a baseline. Transects in stands 1 - 4 measured 2 x 25 m. Transects in stand 5 measured 1 x 10 m (plant density was about 5 times that of other stands).

Measurements were made in the summer of 1994. For each bush I recorded: 1) whether the bush was alive or dead, 2) the maximum height above ground level of live previous-year-growth, 3) whether or not that stem had been browsed, and 4) the height of the oldest browse-killed stem. Previous-year-growth was measured because it had experienced browsing during the winter of 1993-1994 while current-year-growth had not yet been browsed.

Browse-kill was defined to occur when at least 3 terminal twigs were dead, at least 1 of which was pruned by browsing. Within a bush, mortality may occur on a succession of shoots. The oldest such shoot was identified by: 1) a central position of the dead stem among a cluster of stems, and 2) condition of bark. A stem where bark was absent was interpreted to be older than a stem with frayed bark.

Transect data were pooled for statistical analysis. The variance of previous-year-growth height was homogeneous after natural log transformation and stands were compared by oneway ANOVA. Tukey's honest significant difference for unequal sample size, protected by a significant F-test, was used to test for differences between means. Variance of browse-killed stem height remained heterogeneous following natural log transformation (Hartley F-max = 2.9,  $P < 0.001$ ). Stands were compared by Kruskal-Wallis ANOVA using natural log transformed data. Tukey's honest significant difference for unequal sample size, protected by a significant H-test, was used to test for differences between means.

Snow depth at January 1, January 15, February 1, and February 15 was used to calculate a mid-winter average snow depth for years of record. Data from 1950-1994 were from the Tower Ranger Station located 23 km west at 1,910 m elevation. Trends in snow depth thickness were tested by regressing average mid-winter snow depth *on* year. On 8 March 1995 I took 10 snow depth readings at the study site to compare with the snow depth occurring at the Tower Ranger Station.

## Results

Based on the age of the oldest plants, stands 3, 4, and 5 were estimated to have been respectively created in 1968, 1977, and 1985. Using a combination of dendrochronology and photography,

stands 1–5 were inferred to be in sequence of decreasing age.

Stands 2 and 3 contained individuals that were established within a period ranging from respective stand creation to 1994. Recruitment in recent years was from root suckering. Stands 4 and 5 contained individuals established over the period from respective stand creation to 1991. Recruitment was from seed. The extent of root suckering in stand 1 could not be determined due to decay of the root system. The stems of many plants in all stands were decumbent.

Mean height of live previous-year-growth ranged from 12 to 33 cm tall (Table 1). The maximum height was 80 cm. All stems taller than 29 cm had been browsed. Mortality ranged from 100 % in stand 1 to 4 % in stands 4 and 5 (Table 1).

The mean height of the oldest browse-killed stems ranged from 9 to 87 cm tall (Table 1). Height was greater in older stands compared to younger stands (Kruskal-Wallis  $H = 358, P < 0.001$ ). The untransformed variance was greater in older stands compared to younger stands (stands 1 - 5 respectively: 745, 399, 291, 21, and 15 cm<sup>2</sup>).

Over the period 1950–1994, there was no long-term trend in the average mid-winter snow depth at the Tower Ranger Station ( $Y = 89.3 - 0.02 * X$ ; the standard error of the regression coefficient was  $\pm 0.16, P = 0.89, N = 45$ , Figure 2). On March 8, 1995 the snow depth at the Tower Ranger Station was 71 cm, 18 cm of which was new snow. On the same date, snow depth at the study site averaged  $71 \pm 0.7$  cm ( $\pm$  SE;  $n = 10$ ), 18 cm of

which was new snow, with no evidence of disturbance to the snow surface.

## Discussion

Narrowleaf cottonwood is capable of vigorous growth and in areas just outside of YNP, often attains more than 2-m height within a few years (pers. obs.). In contrast, the age of bushes in this study area represent a period of at least 45 years, yet the tallest live previous-year-growth was only 80 cm. The ubiquitous browsing of stems taller than 29 cm suggests that the bush growth-form has been maintained by intense herbivory. The survival of live stems to 80-cm-tall appears to result from the mechanical protection provided by thatches of browse-killed stems.

The average height of browse-killed stems measured in older stands was greater compared to the heights measured in younger stands. If a change in snow depth caused plants in younger stands to be browsed closer to the ground (compared to older stands), one would expect a corresponding decline in snow depth in recent time. There was no long-term decline in snow depth, indicating that this factor was not the cause of the change in the height at which plants were browsed.

Stands 4 and 5 appear to have experienced intense herbivory since establishment. The average height at which stems were killed by browsing was 14 and 9 cm respectively. Seventeen years after the creation of stand 4, the tallest live previous-year-growth was only 42 cm. The 17-year period

TABLE 1. Mortality, height of oldest browse-killed stems, and height of previous-year-growth.

	Stands in sequence of older to younger				
	1	2	3	4	5
Mortality (%)	100	82	10	4	4
Live previous-years-growth					
N	0	6	143	199	180
Mean height (cm) $\pm$ SE	—	28 <sup>ab</sup> $\pm$ 1	33 <sup>a</sup> $\pm$ 1	18 <sup>b</sup> $\pm$ 1	12 <sup>c</sup> $\pm$ 1
Maximum height (cm)	—	47	80	42	33
Tallest unbrowsed height (cm)	—	0 <sup>2</sup>	29	24	22
Oldest browse-killed stem					
N	64	52	139	163	70
Mean height (cm) $\pm$ SE	87 <sup>a</sup> $\pm$ 1	62 <sup>b</sup> $\pm$ 1	28 <sup>c</sup> $\pm$ 1	14 <sup>d</sup> $\pm$ 1	9 <sup>e</sup> $\pm$ 1
Maximum height (cm)	173	101	85	30	22

<sup>1</sup> Similar superscript letters denote means which did not differ at  $P < 0.001$ .

<sup>2</sup> All stems were browsed.

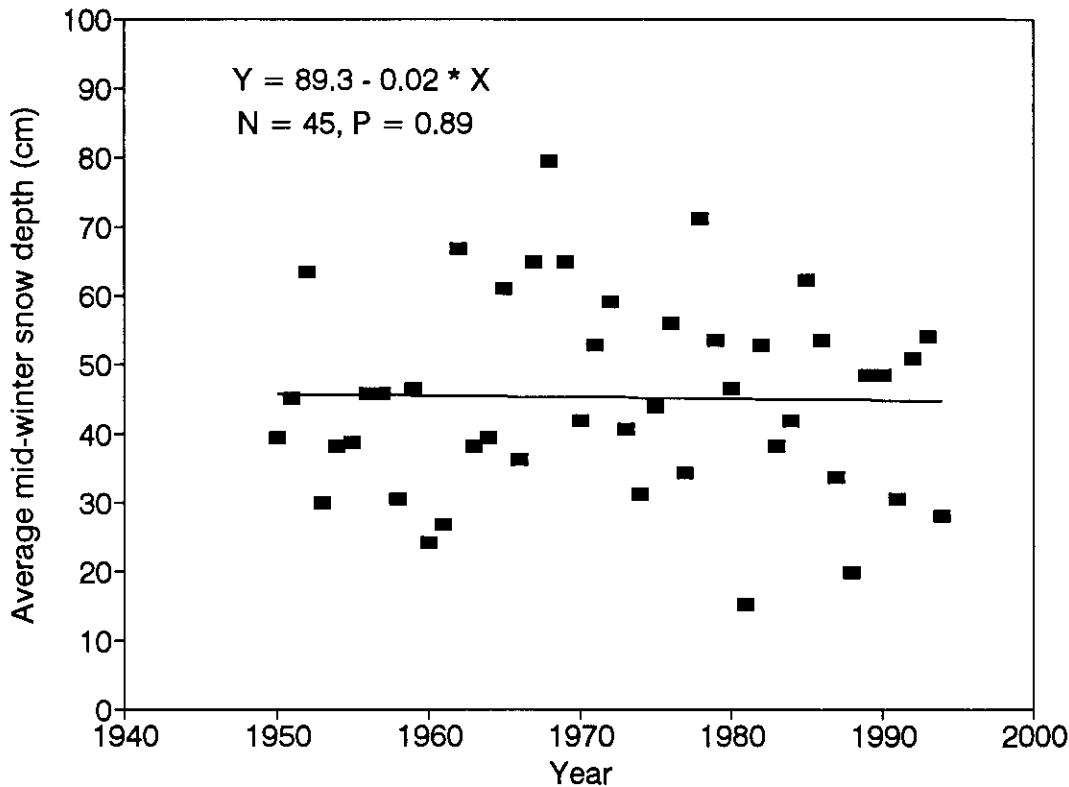


Figure 2. Snow depth can influence the height at which cottonwoods are browsed. Average mid-winter snow depth from 1950-1994 was examined to determine if a recent decrease in snow depth could have caused younger plants to be browsed more closely to the ground compared to older plants. Over that period there was no significant change in the average mid-winter snow depth.

of intense herbivory experienced by stand 4 provides an opportunity to explore the relationship between snow depth and season of browse use.

The average mid-winter snow depth for the period since establishment of the stand (1977-1994) was 43 cm. If height of browsing is controlled by mid-winter snow depth, the variance of the height at which stems are killed by browsing should be similar to the variance in mid-winter snow depth. The variances of browse-killed stem height and average mid-winter snow depth were 21 and 199 cm<sup>2</sup>, respectively. A Hartley F-max ratio of 9.8 ( $P < 0.001$ ) indicates that the height of browsing is significantly more uniform than mid-winter snow depth.

Two lines of evidence suggest that herbivory occurs when snow is less deep than the mid-winter level. First, on average plants in stand 4 were browsed at 14 cm, ca. 30 cm below the mid-winter snow depth of 43 cm. Second, the height

of browsing does not reflect annual variation in snow depth, thus indicating that elk did not consistently remove 30 cm of snow to reach the buried plants. During autumn, snowcover becomes partially responsible for the increased use of browse relative to forbs and grass (Nelson and Legee 1982). The height at which stems were cropped in stand 4 (and stand 5) may record a snow depth at which browse becomes important in the elk diet.

Before browsing killed the tips of stems in stands 1, 2, and 3, those stems grew taller than the stems measured in stands 4 and 5. A stem in stand 1 grew to 1.7 m tall. Growth to this taller height suggests an early period of less intense herbivory compared to the present. A prior period of less intense herbivory would be consistent with the reduced elk population that was present during the late-1960's.

Herbivory would consistently inhibit the height growth of plants in a stand established after an

increase herbivory. In contrast, a stand established prior to an increase in herbivory would logically contain: 1) individuals established prior to the increase (the initial height growth of which would not have been limited by browsing), and 2) individuals established after the increase (the height growth of which would have been limited by browsing). Compared to the first stand described above, there would be greater variation in browse-killed stem-height in the second stand.

Pairwise comparisons of browse-killed stem-height variances suggest that herbivory increased between the creation of stand 3 in 1968 and stand 4 in 1977 (Figure 3). Chronic pruning since stand creation is inferred to have produced the relatively

low variances of stands 4 and 5 (21 and 15 cm<sup>2</sup>, respectively). The relatively large variance (i.e., compared to stands 4 and 5) of stand 3 (291 cm<sup>2</sup>) is inferred to have been produced when the growth of plants that had attained a variety of heights (approximately corresponding to each of their ages) was halted by an increase in herbivory. Plants in stand 3 that were established subsequent to the increase in herbivory would be cropped close to the ground.

Where recruitment is continuous, older stands contain a wider range of ages compared to younger stands. For this reason, significant differences in stem-height variance such as that found in the comparison of stands 1 and 2 are to be expected.

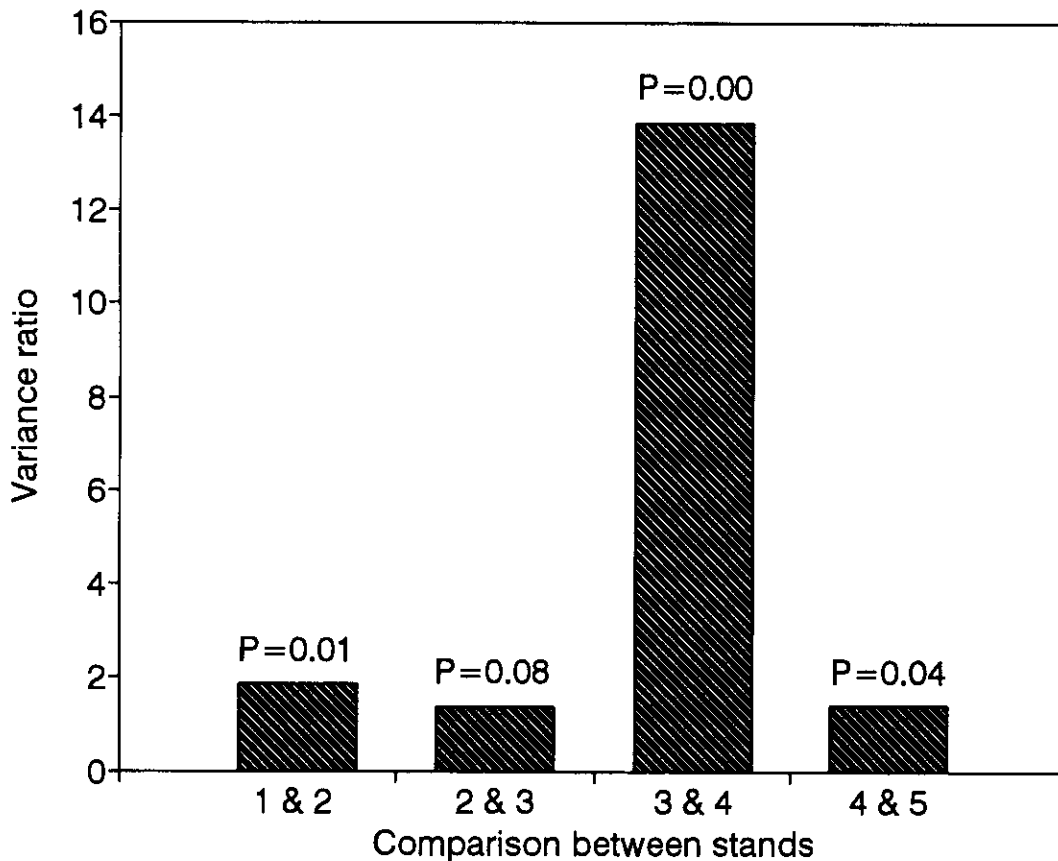


Figure 3. The cottonwood stands were mixed-aged due to continued recruitment after stand creation. Stands established prior to an increase in herbivory would contain cottonwoods whose height growth was not limited by herbivory, and cottonwoods whose height growth was limited by herbivory. Herbivory would kill stem tips at diverse heights above ground level. Plants in stands established after an increase in herbivory would be browsed at a more-uniform height. In sequence of decreasing stand age, pairs of variances of browse-killed stem height were compared by ratio test. The seven-fold difference between the variance ratio of stands 3 and 4 and the ratio of other variance pairs is distinct in magnitude. The ages of those stands mark a period within which browsing intensity increased.

It is the magnitude of difference that suggests that the comparison of stem-height variances of stands 3 and 4 is distinct from the other paired comparisons.

The increase in browsing intensity appears to have occurred some time between the creation of stands 3 and 4 (1968–1977). Over this period, the number of elk counted during the winter census increased from 3,172 to 8,981 (Houston 1982; Figure 4). I hypothesize that the increase in cottonwood herbivory was caused by an increase in the northern elk herd.

The pre-1968 period of less-intense herbivory may have been brief. Plants in stand 1 have decumbent stems that are similar in form to the stems found on young cottonwoods that are currently intensely browsed. In autumn 1961, the northern elk herd was estimated to number 10,000 (Howe, unpublished YNP report). During the

1961–1962 elk reduction, 5,135 animals were culled from the herd. It is plausible that a herd reduction of this magnitude could have a significant effect on herbivory. I hypothesize that plants in stand 1 experienced: 1) intense herbivory from ca. 1950 (i.e., since establishment) to 1961, 2) a reduction in herbivory beginning in 1962, and 3) an increase in herbivory sometime between 1968–1977. The decumbent stems observed in stand 1 could have been produced during that initial period of intense herbivory.

The reduction in herbivory hypothesized to have begun in 1962 only permitted growth to 1.7 m tall. If the period of less-intense herbivory spanned on the order of 10 years, this height is short compared to the potential 10-year-growth of young cottonwood. Height growth during that period may have been limited by stress due to herbivory prior to 1962, moderate herbivory from

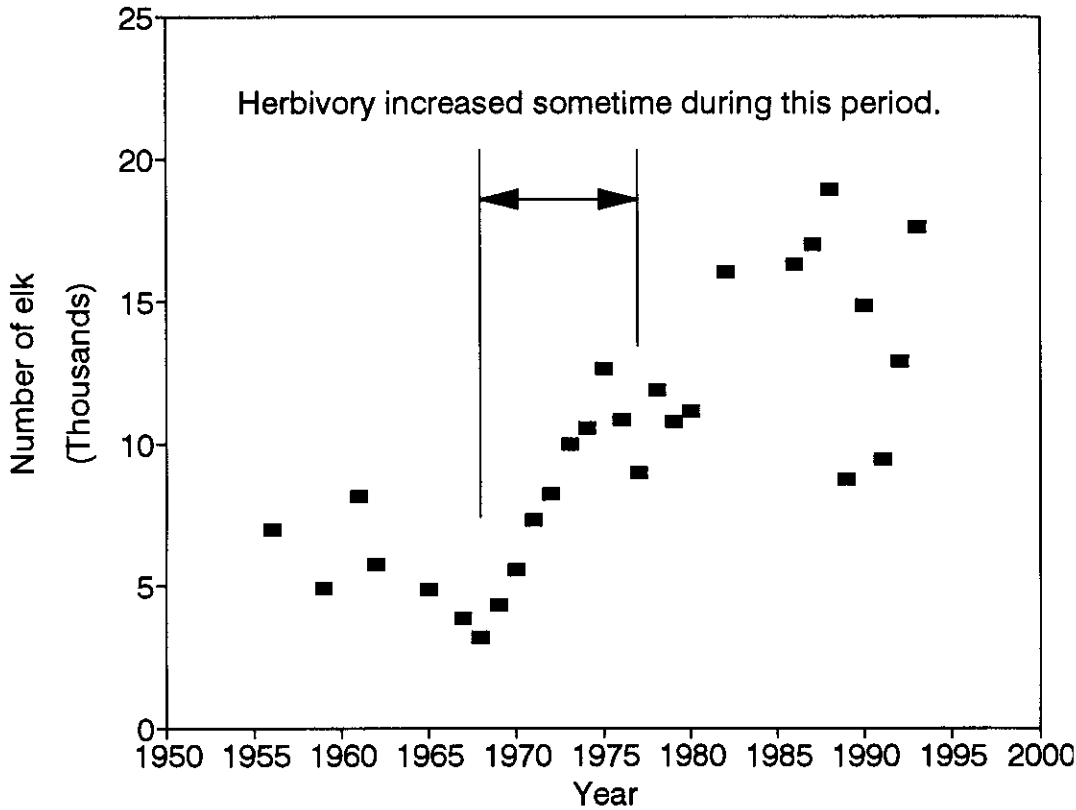


Figure 4. Browsing was inferred to have become intense some time within the period 1968–1977. During this period the elk population increased from a winter census of 3,172 to 8,981. Data are from Houston (1982) and Coughenour and Singer (1996).

1962 until the increase in 1968–1977, or unfavorable site conditions.

Mortality in stands 1 and 2 (respectively, 100 and 82%) was greater than the 4% measured in stands 4 and 5. The difference in mortality may reflect the number of young, latent buds protected by snowcover. The chronic cropping of young plants may increase the number of buds that are produced close to the ground. As the tips of stems are browsed, replacement branches can develop from the activation of latent buds. Plants in stands 4 and 5 may owe their high rate of survival to chronic intense herbivory that has occurred since establishment.

Compared to stands 4 and 5, plants in stands 1 and 2 may have experienced a period of rapid elongation, thus producing fewer buds close to the ground. If the plants were topkilled by an increase in herbivory, there may have been few young, latent buds protected by snowcover from which to replace the browse-killed stems. Plants that rapidly attain 1-to-2-m height may be especially vulnerable to a subsequent increase in herbivory.

Although plants in stands 4 and 5 appear to tolerate chronic intense herbivory, it is uncertain whether the cottonwood population can be maintained. Recruitment in stands 4 and 5 was from seed. Because the bushes do not produce seed (pers. obs.), continued recruitment depends on the survival of older seed-producing trees. As the surrounding trees die, the local cottonwood population may significantly decline. Elsewhere on the northern range I have not observed cottonwood bushes to grow as vigorously as they do in the vicinity of Soda Butte Creek. The cottonwood stands in the Soda Butte Creek area likely represent a best-case scenario with respect to cottonwood regeneration on the northern range.

Throughout much of this century, intense herbivory in YNP has been attributed to an overpopulation of elk caused by EuroAmerican influences (Graves and Nelson 1919, Wright and Thompson 1935, Kay 1990). Keigley and Wagner (ms in review) estimate the pre-YNP northern elk herd numbered ca. 5,000–6,000 and that the herd was more migratory compared to the present. In the winter elk migrate from high elevations in YNP to lower, less-snowcovered elevations. Prior to the establishment of YNP, elk were reported to use an ancestral winter range north of YNP

(Graves and Nelson 1919). Elk use of that range was inhibited when it was settled in the late 1800s. After the establishment of YNP, hunters concentrated just outside the park border. Hunting at the YNP border has been found to cause an artificial concentration of elk in the park through conditioned avoidance behavior (Houston 1979). Predation was essentially eliminated by the extirpation of the wolf (*Canis lupus*) and protection from human hunters. In combination, these factors would cause an increase in the number of elk using the present winter range.

In the past 25 years, two additional explanations have been proposed. Houston (1982, p. 136) and Despain et al. (1986, p. 104) attributed the declines of aspen to be primarily because of past fire suppression by the NPS. Houston was of the opinion that, "The effects of fire suppression may be largely reversible as fires are again permitted to burn." In 1988 YNP experienced widespread fire. Romme et al. (1995) found that elk continued to prohibit the growth of aspen to tree stature in burned areas.

Singer et al. (1994) speculated that "...a more xeric climate, lowered water tables, and/or changes in hydrological patterns contributed to the willow declines and changes in chemistry production on the northern winter range." Their principal evidence was the observation that heavily-browsed willows contained lower levels of chemical defense compounds compared to less-heavily-browsed plants. By this scenario, the environmental factors listed above caused a reduction in chemical defenses that then attracted increased elk use.

In a response to Singer et al. (1994), Wagner et al. (1995) pointed out that reduced levels of chemical defenses can be a *result*—as well as a *cause*—of intense herbivory. The data presented by Singer et al. support this interpretation. In their study, Singer et al. found that heavily browsed willows outside of an exclosure produced significantly less condensed tannin than did protected willows inside the exclosure. Because the environment inside and outside the exclosure is similar except for herbivory, this relationship suggests that the reduced chemical defenses are a *result* of herbivory. In response to Wagner et al. (1995), Singer and Cates (1995) presented the case that a "complex, multi-causal situation, where interactions between elk abundance, climate change, fire,

mammalian predators, and beaver abundance, might all influence the status and recruitment of willows." No specific model was described.

The fire suppression and environmental change theories (i.e., Houston 1982, Singer et al. 1994) were based primarily on the physiology and ecology of aspen and willow, respectively. A more realistic assessment of probable cause should begin with a complete description of the browse species that are in decline as a result of elk use. In my opinion, that list would include most of the woody plants on the northern range. If a broad spectrum of species is confirmed to be intensely browsed, it may become difficult to support the theories above. For example, it is questionable whether the degree of environmental change observed in YNP would reduce the vigor or production of chemical defenses of all members of such a physiologically-diverse group of plants.

The episodic nature of disturbance may make it impossible to define the natural vegetation or the natural disturbance regime in many areas

(Sprugel 1991). Could the intense herbivory in YNP be part of a natural—but infrequent—cycle? If the present intense herbivory is to be generally accepted as a natural circumstance, it will be necessary to identify the natural processes responsible. To date, this has not been accomplished. On the other hand, the potential effect of predator elimination is well understood: prey populations may increase. And as a matter of practice, game management agencies take into account the possibility that elk migratory behavior can be altered by a variety of human influences. At the present time, the weight of evidence appears to favor the explanation that EuroAmerican influences are responsible for the decline of cottonwood and other browse species in northern YNP.

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