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Ungulate herbivory of willows on Yellowstone's northern winter range

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Abstract

Effects of unmanaged populations of large mammalian herbivores, especially elk *(Cervus elaphus)* on vegetation is a concern in Yellowstone National Park, since wolves *(Canis Lupus)* are extirpated, ungulate migrations are altered by human activities and the disruption of natural process is possible. Stands of low, hedged (height-suppressed) willows (*Salix* spp.) are observed throughout the greater Yellowstone National Park area where high densities of wintering elk or moose *(Alces alces)* exist. The height of 47% of the willow stands surveyed on Yellowstone's northern winter range has been suppressed. Mean leader use of willows of all heights was 22% in the winter of 1987-88, increased to 60% in winter 1988-89, following the drought and fires of 1988, then declined to 44% in 1989-90 and winter 1990-96. Height-suppressed willows (43 ± 2 cm, x̄ ± SE) were about one-half as tall as tall willows (83 ± 4 cm). Percent twig use of suppressed willows in summer (25%) and winter (59%) was significantly more than for intermediate or tall stands ($P<0.05$). Suppressed willows produced about one-fourth the aboveground annual biomass compared to taller willows; even after 27 or 31 years of protection, previously-suppressed willows produced only one-third the aboveground biomass of taller willows, suggesting suppressed willows grow on sites with lower growth potential. Growth conditions for willows on the northern winter range may have declined due to a warmer and drier climate this century, locally reduced water tables—because of the decline on beaver (*Castor canadenis*), or fire suppression may be responsible for the observed changes. Tall and intermediate-height willows contained higher concentrations of nitrogen and they exhibited more water stress than height-suppressed willows of the same species. More xeric growth conditions this century than last century, especially during the decades of the 1920's, 1930's, and 1980's, may explain the low growth rates and lower chemical defenses against ungulate herbivory for height-suppressed willows. We propose a more xeric climate and locally-reduced water tables likely contributed to the willow declines on the northern winter range, but that the proximate factor in the declines was herbivory by native ungulates.

Key Words: ungulate herbivory, browsing of willows, *Salix* ecology, willow water stress, and secondary compounds

Declines in willow (*Salix* spp.) abundance, distribution and stature on Yellowstone's northern range this century have been locally dramatic. Some willows were removed by park staff to facilitate hay culture during the early part of this century, but heavy browsing pressure, hedging, and declines were documented on many other stands (Houston 1982). Most of the declines in willows on the northern winter range apparently occurred during the 1920's through 1940's. Willow pollen in sediment samples decreased from 1900 to 1940 at 6 of 8 ponds (Engstrom et al. 1991), while willow cover declined from 1% to about 0.4% cover during the past century on the northern range based upon photographic comparisons (Houston 1982:129). Willows are a very minor component of this particular grazing ecosystem. Elk *(Cervus elaphus)* number 21 per km^2, but their diets are mostly grasses (75%) and <1% willows (Singer and Norland 1994). Moose *(Alces alces)* consume more willows, but their densities are very low (<0.1 per km^2). The willow declines may be due to: (1) possibly unnatural concentrations of wintering elk (Grimm 1939, Patten 1968, Lovaas 1970, Beetle 1974, Chadde and Kay 1991), (2) declines in beaver *(Castor canadensis)* numbers on the northern winter range during the 1920's and 1930's, (3) the colonization or reappearance and increase in moose numbers on the northern winter range during 1911-50 (Walcheck 1976, Chadde and Kay 1988), (4) plant stress as a result of the droughts of 1919-36 in the greater Yellowstone area, (5) reductions in wildfires due to modern fire suppression (Houston 1973, 1982), and (6) reduced concentrations of secondary defensive compounds for willows on dry or otherwise marginal growth sites.

Willows that invade fertile, recently disturbed sites typically grow beyond the height of browsing by large herbivores through rapid vertical growth rates and large belowground storage of nutrients and energy (Bryant et al. 1983). Willows of reduced canopy size and height, i.e., suppressed willows, are observed throughout the greater

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Yellowstone area including Yellowstone National Park (YNP) and the Jackson Hole areas where high densities of elk and moose spend the winter (Gruell 1980, Houston 1982, Chadde and Kay 1991). Photographs from the 1860 through 1890 period show no suppressed willows (Houston 1982, Chadde and Kay 1991) and park managers are concerned if the current reduced stature of willows is either a consequence of natural processes or the effects of European man on elk populations (National Park Service 1988).

Ungulate-vegetation dynamics on Yellowstone's northern winter range provides an opportunity to monitor the effects of natural regulation of ungulates by the National Park Service in a largely protected ecosystem. Yellowstone National Park managers embarked on a policy of natural regulation management of ungulates within the park's boundaries in 1968, following 35 years of intensive artificial reductions of elk and bison *(Bison bison)* populations (Cole 1971, Houston 1982). Natural regulation in Yellowstone is not a scientific experiment, in that no similar control situation [with wolves (*Canis Lupus*)] exist, and the extent of disruption of historic ungulate migrations by human activities outside of the park is unknown (Coughenour and Singer 1991). In spite of alterations in abundance, stature and form of limited types of woody browse (Salix spp., *Populus tremuloides* Michx., *P. trichocarpa* T.& G., P. *angustifolia* James) this century, Houston (1982) and Baur (1987) consider any plant changes following natural regulation to be within the bounds of expected changes. Grasses and forbs fluctuated more in response to climate changes than to ungulate densities (Houston 1982, Coughenour et al. 1994), while declines in woody riparian browse species this century were attributed to a lack of fires in an area that frequently burned, a drier and warmer climate, local reductions in water tables, and lower flooding frequency than during the 19th century (Houston 1982). Reductions in elk population to 20-30% of estimated ecological carrying capacity (ECC) in the 1960's (Houston 1982, Coughenour 1994) resulted in no significant difference in percent leader use of willows and only 11% increase in heights (Singer et al. 1994). Alternatively, Chase (!986) and Chadde and Kay (!988, 1991) concluded human activities, such as extirpation of wolves, alterations of elk migrations, increases in elk densities, and decline in beaver significantly altered ungulate-riparian vegetation relations this century on the northern winter range.

We examine 3 biological hypotheses:

1. Herbivory by large native ungulates is responsible for height suppression of willows on the northern winter range.
2. Drought-mediated water stress in willows results in reduced annual growth and contributes to height suppression of willows by large herbivores.
3. Drought or herbivore-mediated reductions in potential defensive metabolites or increases in primary nutrients in willows increase palatability of willows to ungulates and subsequent suppression of willows.

We examined these hypotheses by comparing willow stands that varied with respect to height, location, and by comparing willow stands protected within ungulate enclosures to adjacent browsed willows. We observed the short-term effects of drought on willow herbivory in 1988-90, following the most server summer drought of this century. Summer precipitation (June-August) in 1988 was only 36% of the 29-year average and June-August daytime temperatures were 3°C above average (Singer et al. 1989).

Study Areas

Our study was conducted primarily in a 148 km^2 area of Slough Creek, Soda Butte Creek, and Lamar River tributaries of the upper Yellowstone River on the upper elevations of the northern winter range as described in Houston (1982), and on 3 study plots at lower elevations (Mammoth, Blacktail, Junction Butte). Study sites were located both within Yellowstone National Park, and outside the park boundary on the Gallatin National Forest in upper Slough and Soda Butte Creeks. Elevations of sample sites ranged from 1,890 m to 2,448 m. Average annual precipitation ranged from 30 cm per year at the lowest site near Mammoth, Wyoming to 55 cm at intermediate elevations in the Lamar Valley, to approximately 100 cm at the highest study sites near Cooke City, Montana (Houston 1982). Snowfall typically accumulates to depths of 15-45 cm at the lower sites and 60-80 cm at the upper study sites. The climate is characterized by long, cold winters and short, cool summers.

The northern winter range is approximately 800 km^2 in size, of which approximately 41% is coniferous forest *(Pseudotsuga menziesii, Picea engelmanni, Abies lasiocarpa, Pinus contorta)* and about 55% is grassland or sagebrush/bunchgrass (mostly *Artemisia tridentata/Festuca idahoensis*). Only about 4% of the northern winter range is classified as riparian, and only about 0.4% of the northern winter range is dominated by willows (Houston 1982:87). Houston (1982) reported that most willow/sedge (*Carex* spp.) communities were dominated by Geyer willow (*Salix geyeriana* Anderss.), Bebb willow (S. bebbiana Sarg.), false mountain willow (*S. pseudomonticola* Bebb), Booth willow (*S. boothii* Bebb) and Wolf willow (*S. wolfii* Bebb), while a few willow stands on sand and gravel bars were dominated by linear-leaved willows (subfamily *S. exigua* Nutt., *S. farriae* Ball). Willow stands occur only on the most mesic sites, in swales, seeps, draws, and streamsides.

Four species of ungulates on the northern winter range were observed to browse willows, elk, moose, mule dear *(Odocoileus hemionus)* and bison, but of these, only elk in lower elevations, and moose in higher elevations of the northern winter range are important browsers. Elk densities on the northern winter range ranged from 21 elk per km^2 in 1987 to 18 elk per km^2 in 1990 (Singer et al. 1989, Mack and Singer 1994). Moose densities were about 9-15 moose per km^2 in early winter near the highest elevation willow stands (Mack and Singer 1991), but few moose wintered in the middle or lower portions of the winter range (<0.1 moose per km^2). Moose were the primary ungulate herbivore in the highest elevation willow stands in winter (2,100-2,250 m) and elk the primary ungulate herbivore in the lowest elevation stands (1,890-2,070 m), but both species potentially occurred at all elevations during winter. Beaver and hare (*Lepus* spp.) use of willows was insignificant at our study sites.

Methods

Landscape Level Measurements

We mapped willow stands in the northern winter range from the junction on the Lamar River and Slough Creek in the northeastern corner of the northern winter range and upstream to the head of Slough Creek and Soda Butte Creek. The mapping study area (148 km^2) totaled 19% of the entire northern winter range, and 23% of the northern winter range within Yellowstone National Park (YNP). We mapped all willow stands > 0.3 ha in size from 1:32,000 color aerial photographs and ground surveys in the study area. Areas of each willow stand were calculated from dot grids. Ungulate densities were obtained from fixed-wing aircraft surveys early each winter (Dec.-Jan.), 1985-90, in each of 66 count units on the northern winter range as described in Singer (1991). We additionally sampled 3 willow stands from lower elevation core elk winter range at Junction Butte, Blacktail Deer Creek, and Mammoth Hot Springs. Ungulate exclosures at these locations provided unbrowsed willow communities for sampling.

Willow Stand Measurements

Willow species abundance and production were measured in 15 randomly-located circle macroplots of 9.3 m^2 in size in each willow stand; only 5-10 macroplots could be placed in the smallest (<0.1 ha) willow stands. The height of the tallest live leader, widest shrub crown diameter, perpendicular shrub diameter, and the species of each aboveground willow clump were recorded. Percent dead portion of each willow clump was estimated. On every fourth individual shrub of each species, the number of rooted stems, number of shots per stem, length, height, and basal diameter of current annual growth (CAG), and diameter at the tip or browse point of 10 randomly selected shoots were recorded. Shoot measurements were gathered on the same stands on 1987, 1988, 1989, and 1990. Percent twig use of willows by ungulates was measured along 3-5 (depending on the size of the willow stand) permanently-marked 100 m transects located in a representative sample of willow stands. Along the transects, from 15 to 30 1-m^2 circular plots were randomly located and the center of the plot was inconspicuously tagged below the shrub crown. These marked shrubs were then relocated twice a year. Winter willow use was recorded prior to leaf bud break (May), and summer use was recorded prior to leaf-drop (August) 1987-90. The total number of shoots and the number browsed were recorded in each plot. Almost no willow growth occurred after the summer readings were taken in early August, therefore, nearly all summer leader use was assumed incorporated into the winter tallies of shoot use. The height and total diameter of the willow plant, length, basal diameter at browse point or tip, and the height from the ground to the apical bud or to the browse point were recorded on a sample of 50 browsed and unbrowsed shoots. Height classes were determined using summer height measurements at the end of each growing season (August) in 1986 to 1990. Heights of willow communities were divided into 3 categories based upon graphical analysis: (1) height-suppressed = nearly all plants were ≤80 cm, (2) intermediate = plants were 81-120 cm tall, and (3) tall willows = most plants were 121+ cm. Suppressed communities tended to be browsed at a uniform height, intermediate stands to a lesser extent, while tall stands were of diverse heights.

Bite size removed by ungulates was estimated from each browsed twig following the method of Pitt and Schwabb (1990). Bite size was calculated for winter and summer seasons from the formula:

$$BS = \frac{100\,(Dp-Dt)}{Db-Dt}$$

Where BS=bite size, Dp=twig diameter at the point of browsing, Db=basal diameter of browsed twig, and Dt=mean diameter of a representative sample of unbrowsed twig tips (Pitt and Schwab 1990). This equation differed from bite size determined by twig length differences by only 4-6% (Jensen and Urness 1981) and it accurately predicted bite size for 4 of 6 shrub species (Pitt and Schwab 1990).

Aboveground biomass estimates were calculated for each willow species in each willow stand according to methods used by MacCracken and Viereck (!990) following Telfer (1969) and Oldemeyer (1981). An average number of aboveground willow clumps per macroplot was calculated for each stand. The average number of twigs per shrub, average twig length, and average green diameter at base were calculated from the annual twig measurements on the 1-m^2 plots. Average twig weight was calculated from a linear regressions of dry weight (dependent variable) against twig length and basal green twig diameters at the base of the current annual growth (independent variables) (MacCracken and Viereck 1990). Log-log predictor regressions were calculated only for abundant species with adequate data (9 species in 1988, 5 species in 1989, and 5 species in 1990). Separate regressions were calculated for each willow species each year and each season (winter, summer) since the regressions varied between seasons and years. The r^2 values were high for each species (range r^2 = 0.78-0.97; r^2 = 0.87, SE = 0.13; n=19) and the plots of the residuals followed a normal distribution. The biomass of each willow species was estimated from the estimated twig weights x average number of twigs per plant x the number of shrubs per plot. Leaves were included in the summer twig weights; the presence of leaves accounted for the summer-winter differences in the regressions.

Plant Level Measurements

Forage quality was determined from shoots of height-suppressed, intermediate and tall willows for 3 species (Geyer, Wolf, and Booth willows) about 1 August of each year. At each study community, a minimum of 5 g of stem and leaf sample were taken from 5 randomly-selected shrubs. Twigs were gathered from the primary browse zone, 0.5-1.5 m. Samples were oven-dried for 48 hours at 50°C-60° C. Kjeldahl N (Assoc. Off. Anal. Chem. 1970) and in vitro digestibility (Tilley and Terry 1963), was analyzed at the Nutritional Analysis Lab, Colorado State University.

Moisture stress of willows was measured with a Scholander pressure bomb (PMS Instrument Co., Corvallis, Oregon) during the summer of 1989. Two readings were recorded from 10 plants of the 3 most common species per site. We sampled water stress of height-suppressed, intermediate, tall, protected (in ungulate exclosures for 27 or 31 years) and nearby unprotected height-suppressed willows at 3 exclosure sites. Water stress of willows was measured pre-dawn (0300-0600 hr) under conditions of minimum water stress and minimum transpiration for each plant to reduce variations due to fluctuations in day-time temperatures and cloud cover. The distal 12 cm of each willow shoot was cut, rushed to a Scholander pressure bomb, and the water potential was measured.

Twig collections for analysis of secondary metabolites paralleled the water stress sampling program; the same grazed and protected locations (height category x grazing) were sampled. Total tannins were analyzed by the butanol-HCl method. Approximately 300 mg of frozen tissue was ground under liquid nitrogen using a mortar and pestle, and then extracted in 70% acetone (3.5 ml x 3 times). Acetone was removed by passing nitrogen over the supernatant, reconstituted to 7 ml, and filtered (0.45 µm nylon filter). Buffered hemoglobin solution was used as the protein substrate. After the tannin containing willow extract was combined with the hemoglobin solution, unbound protein was read on a Coleman Spectrophotometer at 595 nm. The tannin content was expressed as mg/g dry weight.

Analysis for condensed tannins followed the methods of Porter et al. (1986) and Martin and Martin (1982) with all aspects optimized for each willow species analyzed. Twig and foliage tissue was freeze dried and foliage was separated from the twigs. In order to standardize the amount of twig and foliage tissue analyzed in each sample, 180 mg dry weight of twig tissue was combined with 120 mg dry weight of foliage tissue for each sample. This sample (300 mg) was added to 7ml H_2O and extracted by sonication for 5 min. An aliquot (0.2 ml) of extract was added to 4.8 ml methanol. One ml of the methanol/H_2O solution was placed in an 8 ml glass vial fitted with a teflon-lined screw cap. Six ml of 95/5 butanol/HCl solution and 0.2 ml of 2% (w/v) of ferric ammonium sulfate dodecahydrate in 2 M HCl was added to each sample. Hydrolysis was carried out in tightly-capped vials by thoroughly shaking and heating in an oven at 95° C for 40 min. Following cooling, the absorbance was determined at 520 nm which was the optimal wavelength for these species. Tannin concentration was calculated by comparing the resulting absorbances to a standard curve of tannin isolated from each willow species (0.02%, w/v in methanol) serially diluted across the concentration ranges known to occur for each species.

Statistical Analysis

Nutritional levels and plant moisture stress were compared among willow height categories and grazed and protected (exclosed) sites with ANOVA ($P<0.05$). Percent leader use, plant heights, and willow production were normally distributed and were analyzed with ANOVA and regression analysis. Differences in willow use between years, sites, and species, were compared with the non-parametric ranked Friedman 2-way analysis of variance because sample sizes on the permanently-marked utilization transects varied among years (some transects were lost and did not recover after the fires of 1988 or were inaccessible due to flooding some years), and their variances of means were not homogeneous. The Bonferroni approach (Neu et al. 1974, Miller 1981, Byers et al. 1984) was used to calculate experiment-wide confidence intervals on the proportional use of willows of each species by ungulates. Confidence intervals on percent leader use were compared to availability of willow species to evaluate disproportionate use. The terms use, avoided, and expected imply willow use greater than, less than, or equal to availability at the $P = 0.01$ level, respectively. Multiple regression analysis was used to compare percent leader use and annual biomass production with the variables of precipitation, a year effect, ungulate density in the same count unit containing each willow stand, and elevation.

Results

Landscape and Stand Level Observations

Willow herbivory was sampled in 42 browsed willow communities during 3 summers (1988, 1989, 1990) and 4 winters (1987-88, 1988-89, 1989-90, 1990-91). Ten browsed willow communities were classified as suppressed, 11 as intermediate and 21 browsed communities as tall. Suppressed and intermediate browsed stands were more prevalent at lower elevations and tall stands were more common at higher elevations (Fig. 1). Some tall stands, however, also occurred at lower elevations. Annual (summer plus winter) percent leader use varied significantly between years (Friedman test $P < 0.05$) and was highest during the severe winter of 1989 following the fires of 1988. Summer leader use did not vary between years ($P < 0.05$).

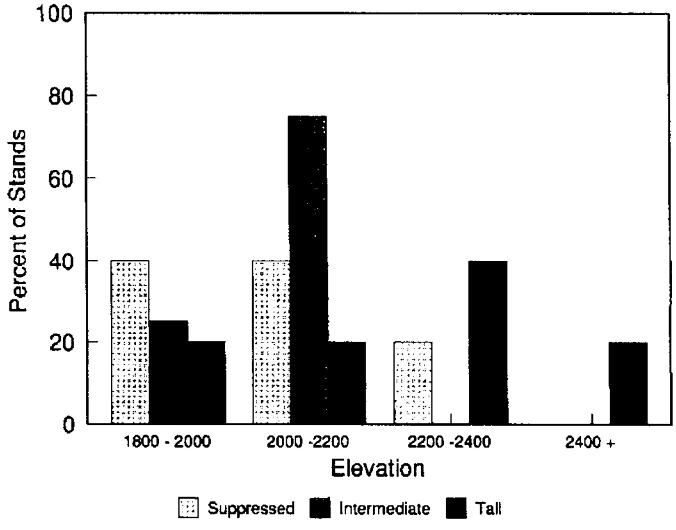

Fig. 1. The percentage of willow stands in each height class (suppressed, intermediate and tall) broken down by elevation. Missing bars indicate that there were no stands of that height class at that elevation.

Greater diversity of willow species was observed in taller willow stands (Table 1). An average of only 2.6 ± 0.3 species were found per macroplot in suppressed stands, 3.3 ± 0.3 species in intermediate, and 4.0 ± 0.5 species in tall stands (Mann Whitney U-tests, $P < 0.05$) Bebb and False Mountain willows were found only in low elevation, suppressed stands, while Drummond, Farr, and Barclay willows were found only in tall stands. Bebb willow reaches greater heights outside of study sites, where specimens 3-4 m in height were observed. False Mountain willow apparently competes poorly for shade in the absence of browsing; False Mountain is less abundant inside exclosures than in adjacent browsed stands (Chadde and Kay 1988, Singer et al. 1944).

Our hypothesis was that tall willows on the study area were better defended chemically, and therefore less preferred by herbivores than intermediate or suppressed willows. This hypothesis could only be examined in 3 willows that were found in all 3 height categories; comparatively taller growing Geyer and Booth willows, and the shorter, determinate growing Wolf willow. Browsing preferences varied amongst height categories for these 3 species. Geyer and Booth willows were used less than expected in tall willow stands, greater than expected in intermediate height stands, and greater than or at availability when occurring in height-suppressed stands (Table 1), a trend generally supporting our hypothesis. Wolf willow also was used proportionately less (0.088) in tall stands than in both intermediate and height-suppressed (0.233), but these patterns were not significant (Table 1).

Percent leader use during winter varied among willow species at only 19% of the 15 locations-winter (13 locations x 4 winters,

Table 1. Proportional availability and use of willow species within willow communities of 3 height categories by ungulates on Yellowstone's northern winter range during 4 winters, 1987-90.

Height category: willow species	No. shoots sampled	Proportionate availability	Proportionate use	Use compared to availability
Suppressed (High Elevation):				
Wolf	25,481	1.000[1]	.230	[2]
Suppressed (Low Elevation):				
Bebb	2,578	.345	.297	-
False Mountain	2,245	.301	.318	0
Geyer	1,554	.208	.244	+
Booth	1,090	.146	.141	0
TOTAL	7,467			
Intermediate:				
Wolf	8,805	.445	.235	-
Geyer	1,808	.091	.169	+
Booth	9.160	.463	.596	+
TOTAL	19,773			
Tall:				
Wolf	8,820	.095	.088	0
Geyer	12,979	.140	.123	-
Booth	20,399	.220	.175	-
Drummond	40,549	.438	.523	+
Farr	7,796	.084	.059	-
Barclay	2,039	0.22	0.32	+
TOTAL	92,582			

[1] Only Wolf present, no preference analysis conducted.
[2] Bonferroni ∞ = 0.10 experiment-wide confidence intervals.
+denotes use greater than, 0 use at, and - use less than availability, according to the Neu et al. (1974) test. The test was conducted on each height category separately.

Table 2. Ungulate abundance, estimated bite sizes and percent of CAG length removed on browsed shoots in suppressed, intermediate and tall willow stands on Yellowstone's Northern Winter Range 1987 to 1991.

	Suppressed		Intermediate		Tall	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Unbrowsed shoot length, (cm)	11.8	1.5a	25.2	2.8b	17.9	1.9b
Summer:						
Ungulate species browsing	E,M,D,		M,ED		M	
Percent leader use	25	3a	14	3b	14	2b
Estimated bite size (cm removed)	8.9	1.2a	4.6	0.7b	8.4	1.9a
Approximate % length of shoot removed (unbrowsed length minus cm removed)	75%		18%		47%	
Winter:						
Ungulate species browsing	E,M		E,M,B		M	
Elk and moose density[1]	49	4a	52	3a	8	1b
Percent leader use	59	5a	43	8c	32	3c
Estimated bite size (cm removed)	5.7	0.9a	9.6	1.4b	10.4	1.6b
Average % length of each shoot removed (unbrowsed length minus cm removed)	48%		38%		47%	

[1] Elk and moose density were the combined average of actual counts of the species from fixed-wing aircraft in count units surrounding the sample stands, winters 1987-91. Percent leader use and bite size are described in the "Methods" section.

n = no. of 1 m^2 utilization plats read each season. Ungulate species: E-elk, M-moose, D-deer, B-bison. different letters indicate a significant difference between height categories (ANOVA, $P<0.05$).

Friedman tests, $P < 0.05$), and all species at a site were therefore pooled for subsequent analysis. Percent leader use varies among the 3 height classes of willows during winter and was greatest for suppressed willows (ANOVA, F = 17.3, $P < 0.0001$. Table 2). Length of twig removed (cm), or bite size, was least for suppressed willows (ANOVA, F = 10.06, $P < 0.0001$, Table 2).

Ungulate winter densities were higher in the valley bottoms near willow stands ($\bar{x} = 36$ elk/km^2) than for the northern winter range as a whole ($\bar{x} = 21$ elk/km^2). Ungulate winter densities were less near tall willow stands ($P < 0.05$, Table 2) compared to the other height categories, but there was no difference between suppressed and intermediate stands ($P > 0.05$).

Suppressed willow twigs were also browsed more in summer ($\bar{x}$ = 25% leader use) than were intermediate or tall willows ($\bar{x}$ = 14%). Bite sizes were largest during summer on suppressed willows, and least on intermediate willows (ANOVA, F = 74, $P < 0.001$, Table 2). Unbrowsed shoots of suppressed willows were 21% shorter than shoots from intermediate and tall willows (Table 2, $P < 0.05$). Willow bite size relative to current annual growth (CAG) was equivalent in winter among the height classes of willows. Relative bite size during summer was largest (75% of shoot length) for suppressed willows.

Aboveground willow production varied between years (Friedman test, $P < 0.05$, Fig. 3). Production increased markedly in 1989 following the wettest winter of the decade, but production was least in 1990 following 2 winters of heavy browsing pressure. Suppressed willows produced only 28% as much biomass as did tall willows, and intermediate willows produced 73% as much biomass as did tall wil-

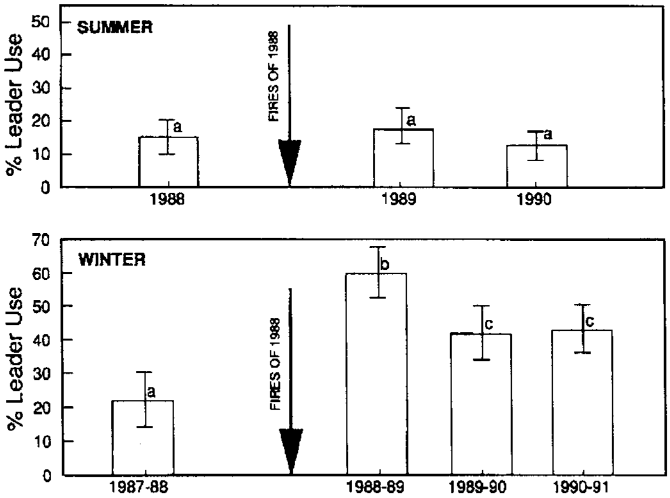

Fig. 2. Percent leader use on all willows summers and winters 1987-88 through 1990-91 on Yellowstone's northern winter range ($\bar{x}$ ± SE). Different letters denote significant differences in use levels between years according to Friedman test ($P<0.05$).

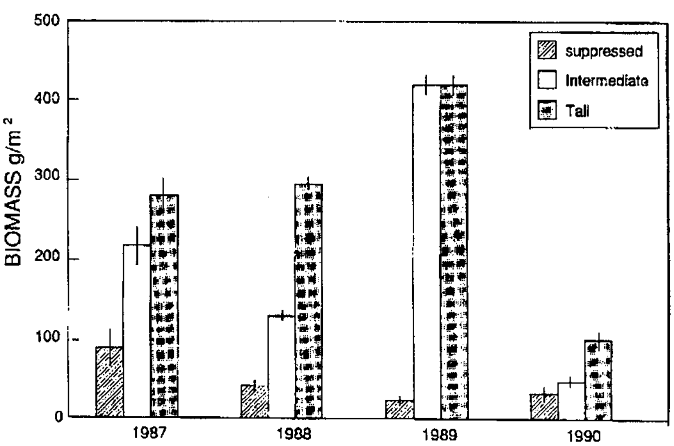

Fig. 3. Annual aboveground production of current annual growth ($\bar{x}$ ± SE, g/m^2) in suppressed, intermediate and tall willow communities, 1988-90, on Yellowstone's northern winter range.

lows (Friedman test, $P < 0.05$, Fig. 3). Formerly suppressed willows, after protection for 31 years inside exclosures, still produced only 35% as much biomass as did tall willows (94 g/m^2 for protected formerly-suppressed willows, n = 60 plots located inside of four exclosures, versus 272 g/m^2 for tall willows).

Aboveground willow production increased with increasing elevation and increasing precipitation during the previous year and decreasing ungulate density the previous winter (multiple regression, $r^2 = 0.44$, F = 5.2, $P < 0.008$). The relation was significant in 1988 ($r^2 = 0.67$, F = 9.3, $P < 0.001$) and in 1989 ($r^2 = 0.94$, F = 36.9, $P < 0.001$), but not in 1990 ($r^2 = 0.12$, F = 0.52, $P = 0.68$). Elevation and precipitation are positively correlated on the northern winter range (Houston 1982), and aboveground biomass was best explained when both elevation and precipitation were used together ($r^2 = 0.67$, $P < 0.001$). The relationship between biomass and ungulate density during the previous winter approached statistical significance (F = 2.75, $P = 0.11$), but there was no association between willow biomass and ungulate density 2 winters prior ($r^2 = .02$, F = 0.49, $P = 0.49$). Willow biomass was negatively associated with percent leader use 2 winters before ($r^2 = 0.53$, F = 23.3, $P < 0.001$).

Percent leader use was associated with aboveground willow biomass produced the previous summer, by ungulate density and by year (F = 14.2, $P < 0.0001$). However, only 24% of the variation in leader use was explained by these 3 variables. Percent leader use in the current year was not associated with either bite size ($r^2 = 0.02$, F = 0.56, $P = 0.46$), or by percent leader use the previous year ($r^2 = 0.04$, F = 1.19, $P = 0.18$).

Tall willows had higher nitrogen (N) concentration than suppressed willows in 1988 and 1989, and higher in vitro digestibility than suppressed willows in 1990 ($P<0.05$, Table 3). Intermediate willows had higher N concentration in 1990, but lower N concentration in 1988 ($P<0.05$) compared to suppressed willows. There was tendency for higher N concentration in the shoots of tall and intermediate willows in comparison to suppressed willows, except for 1988, (a severe drought) when drought-stressed intermediate willow plants had low N values. Low water potentials of -5 to -9 bars were associated with the low N concentrations in drought stressed and dying willows.

Plant Level Measurements

Booth and Wolf willows from tall communities contained higher N concentrations than height-suppressed individuals of the same species (Mann-Whitney U tests, U = 21 and 30, respectively, $P<0.001$), but no relationship was observed between height class and nitrogen concentration for Geyer willow (U = 78 $P = 0.64$). Nitrogen concentrations in intermediate height Booth and Wolf willows were also less than for individuals from tall communities (U = 13, 3, $P<0.52$). Percent digestibility was higher in tall than suppressed Booth, Wolf and Geyer willow (U = 37, 56, 14, $P<0.01$), and digestibility was higher in tall than in intermediate Wolf willow (U= 3, $P<0.05$).

Significant differences in water potentials were found between browse-suppressed and adjacent protected willows (F = 30.33, $P<0.0001$), and between locations (F = 7.6 $P<0.0008$), but interactions were significant (F = 6.94, $P=0.001$). Unbrowsed Bebb and False Mountain willows showed a greater water stress (xylem pressure potential range =-2.4 ± 0.85 bars) compared to browsed plants (-1.17 ± 0.68 bars), ($P<0.01$, 2-way ANOVA, Table 4.

Lower water potential were observed for intermediate height willows ($\bar{x}$ = 2.86 ± 1.35 negative bars) than for suppressed willows $\bar{x}$ 1.71 ± 0.68 negative bars, $P=0.01$, 1- way ANOVA). Tall and intermediate willows have a larger canopy and leaf surface area and, therefore, a larger demand for water than do suppressed willows. The effects of location (F = 25.74, $P<0.0001$) and interactions (F = 14.38, $P<0.0002$) were also significant. Lower water potential readings suggest Wolf and Bebb willows were more vulnerable to drought stress in 1988, which was consistent with observed deaths of these 2 species in 1988 and 1989. No individuals of the other willows species died in 1988 or 1989. Nine percent of the Wolf willow individuals at the Lost Creek site died in 1989, and by 1990, 30% were dead (n=96). All 8 marked Bebb willows on a transect in the Lamar Valley died in 1989, the year after the severe drought.

For all willow species combined, height-suppressed willows produced significantly less condensed tannin ($\bar{x}$=39.9 ± 20 mg/g dw) compared to intermediate willows (ANOVA, $P<0.05$, n=64 tissue samples, 48.2 ± 17 mg/g dw). Since Wolf willow never grows beyond the reach of ungulates, and is chemically better protected (as is the determinant, and slow growing willow *S. lapponum* from Europe, Tahvanainen et al. 1985, an ecological equivalent of Wolf willow), we excluded Wolf willow from the remaining analyses. When all species were combined except for Wolf willow height-suppressed willows had lower tannin concentrations (42.7 ± 22 mg/g dw) compared to intermediate and tall willows (50.5 ± 16, 50.5 ± 23, respectively). Intermediate and tall willows were not significantly

Table 3. Nitrogen concentration and percent dry matter digestibility (IVDOM) of willow shoots from suppressed, intermediate and tall willow stands on Yellowstone's Northern Winter Range, 1988-90. All species values were pooled at a site.

	Suppressed		Intermediate		Tall	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1988:						
%N	1.3	0.06 (46)^a	1.1	0.05 (32)$^{b1/}$	1.5	0.08 (41)^b
%DMD	50.2	1.3	52.9	0.4	52.4	0.9
1989:						
%N	1.4	0.05 (53)^a	1.5	1.0 (85)^a	1.5	0.06 (19)^b
%DMD	48.8	1.5	45.2	2.1	48.9	1.1
1990:						
%N	1.4	0.03 (75)^a	1.7	0.08 (53)^b	1.6	1.0 (21)^a
%DMD	49.3	1.1	48.6	1.3	53.8	0.9*

Different letters indicate a difference between intermediate or tall willows compared to suppressed willows within a year according to Mann-Whitney U tests ($P<0.05$).

[1] Includes low protein values from willow individuals that were drought stressed at the Lost Creek site and which later died. 1988 was the most severe summer drought since 1934 in Yellowstone National Park.

( ) = no. of samples.

Table 4. Species differences in negative water potentials (negative bars) between browsing suppressed and nearby protected willow plants (1-way ANOVA).

	Willow Species	
Exclosure Location	Bebb	False Mountain
Junction Butte:		
Suppressed-browsed	1.79±0.4	1.04±0.14***
Unbrowsed	3.38±0.91	2.04±0.45***
Mammoth:		
Suppressed- browsed	2.59±0.38	1.73±0.48***
Unbrowsed	2.5±0.5	2.38±0.53
Lamar:		
Suppressed-browsed	2.27±0.47	0.96±0.14***
Unbrowsed	2.08±0.38	1.3±0.45***

*$p<0.05$, **$p<0.01$, ***$p<0.001$

different from one another at ≤0.10).

Willow species inside (unbrowsed) the grazing exclosured were compared to willows outside (suppressed-browsed) the exclosures. Browse-suppressed willows produced significantly less condensed tannin (30.3 ± 13 mg/g dw, n=78) than did protected willows inside the exclosure (38.1 ± 13, ANOVA, $P<0.05$, n=23 tissue samples).

Discussion

Levels of large mammalian herbivory on Yellowstone's willows was moderate although ungulate herbivory clearly was the proximate factor in height suppression of willows. All plants (100%) were browsed each winter and about 37% of the current aboveground biomass of willows was removed from suppressed willows. By comparison, moose on Isle Royale browse less individual deciduous shrubs (36-76%) and remove only 3% of the current biomass (McInnes et al. 1992). Higher biomass removals similar to those we observed are sustained by willows and birches elsewhere (Danell et al. 1985, Fox and Bryant 1984).

As predicted by our second hypothesis, many browse-suppressed willows apparently grew on sites with lower growth potential than did tall or intermediate height willows, and thus were more vulnerable to the effects of large herbivore browsing. Suppressed willows produced only about 28% the aboveground biomass of tall and 38% the biomass of intermediate height willows. Even after protection from ungulated for 31 years, formerly height-suppressed willows still produced only about 35% the aboveground biomass that tall willows did. We conclude that less than optimum growth conditions and lower biomass production coupled with less defense chemistry compounds were the ultimate factors contributing to height suppression of willows. Willows are capable of rapid height growth, and vigorous willows can escape ungulate browsing in as little as 2-5 years following disturbances such as fire (Wolff 1978, MacCracken and Viereck 1990). Patten (1968) reached a similar conclusion for willows in the Gallatin drainage, Montana. Willows located further from a stream experienced greater mortality from elk browsing, while willows growing in the stream channel survived the same browse pressure (Patten 1968). In the absence of fires and beaver activity for nearly 70 years, competition from sedges and grasses likely has increased to the detriment of willow production.

Three possible explanations exist for the reduced productivity of some willow communities on Yellowstone's northern range. First, Yellowstone's northern winter range very is slightly warmer (0.5-1.0°C warmer) and drier (1-2 mm less rainfall annually) this century than during the last century (Houston 1982). A 15-year drought period 1919-1934, coincided with most of the reported willow declines (Jonas 1955, Houston 1982, Engstrom et al 1991). Secondly, declines in beaver undoubtedly contributed to localized declines in water tables (Jonas 1955). Thirdly, increased competition from grasses and sedges growing in the abandoned beaver ponds also likely reduces the potential for seedling establishment of willows.

As we predicted, height suppressed willows possessed reduced concentrations of tannins, they were more highly preferred by ungulates, and off-take levels were higher than for taller willows. Browsing mammalian herbivores select forages primarily on the basis of lower concentrations of defense compounds (Bryant and Kuropat 1980, Bryant 1981, Picman et al. 1982, Cooper et al. 1985, Basey et al. 1988), as our data also indicated. Bryant et al. (1983) concluded that defense compounds influenced food selection by vertebrate herbivores more so than did plant nutrients or digestible energy concentrations. A number of studies suggest plant stress lowers defense chemistry and increases palatability of browse. Ruffed grouse (*Bonasa umbellus*), and Capercaille preferentially fed upon water- or injury-stress woody browse (Guillion 1970, Pullianien 1970). Similar responses are observed with intense clipping or herbivory. Lower resins and lowered tannins were observed in intensely clipped or browsed birch and willow (Reichardt et al. 1984, Chapin et al. 1985, Suter 1991). A substantially larger proportion of height-suppressed compared to tall willows leaves are unshaded and exposed to strong sunlight. Sun leaves, those leaves exposed to strong sunlight, senesce more quickly, export N more quickly, and are preferred by herbivores more than are shade leaves (White 1984).

Lower secondary compound concentrations were apparently of overriding importance in the higher preference for suppressed willows than were nutrients or digestibility. We observed reduced N concentration and lower digestibility height-suppressed willows on Yellowstone's northern range than for intermediate or tall willows. Ungulates clearly did not select willows based on forage quality. Either or both drought stress or intense browsing may explain the decreased nutritive values in willows. Drought stress reduces the N content of grasses and woody browse (Tevini et al. 1983, Hayes 1985). Shoots from severely clipped birches had less N, Ca, Na, and more fiber than unclipped controls; N levels were reduced to only one-third to one-half the level of unclipped birches (Danell and Bergstrom 1987). Intense herbivory or clipping reduced aboveground production, heights, root biomass, dry matter digestibility and N concentrations in shoots of willows and birches (Åhlen 1975, Oldemeyer 1981, Wolfe et al. 1983, Neuvonen and Haukiohja 1984, Danell and Huss-Danell 1985, Danell and Bergstrom 1987).

Water stress per se is not currently a major factor in the height-suppression of willow communities on the northern winter range, and we can not infer that willow declines in the previous century were due to water stress alone. We observed only moderately low stomatal pressure (5 to 9 negative bars) in a number of intermediate-height willow individuals, some of which died following the drought of 1988. The death of many willows this century (Houston 1982, Chadde and Kay 1991), however, suggests that willows on most marginal sites on the northern winter range were likely eliminated well before our study. Additionally, height suppression of willows may later root:shoot ratios to a more desirable relationship on marginal sites. Welker and Menke (1990) reported a similar situation when severely defoliated oak seedlings demonstrated higher water conductance and a longer growing season due to the removal of transpiring tissues and reduced shoot:root ratios. Georgiadis et al. (1989) also reported improved water status of grazed African grasses. Low biomass production in protected willows provides strong circumstantial evidence that some environmental factor (water stress, competition from sedges and grasses, etc.) has contributed to the height-suppression of willows.

Intermediate-height willows were apparently more vulnerable to water stress than suppressed willows. Significant willow mortality occurred at 2 intermediate stands following the drought of 1988, while no death was observed in height-suppressed willows that year. Intermediate willows are taller, and have more transpiring leaf tissue than suppressed willows, they likely have lower root:shoot ratios and, consequently, they may be more vulnerable during drought than shorter willows with higher root:shoot ratios. Height suppression may permit willows to cope with intense herbivory. Gradual height reduction, readjustments to more favorable root:shoot ration, survival on wet subirrigated sites (most willows that died, 1920-1940, were probably on the driest sites), and the ability to root sprout might preadapt height-suppressed willows on the northern winter range to survival during drought.

Fire suppression this century on Yellowstone's northern range might have contributed to the willow declines. There is considerable evidence that the northern winter range and adjacent areas was subjected to high fire frequencies (as high as every 25 years), prior to extensive fire suppression about 1900 (Houston 1973, Barrett 1993). Fire stimulates willow production, vigor, and recruitment (Wolff 1978, Gruell 1980, MacCracken and Viereck 1990). More than a century of fire suppression on the northern range increased the distribution and density of conifers and big sagebrush adjacent to willow stands. These invading species might have increased transpiration rates, reduced local water tables and runoff patterns, and reduced soil moisture available to willows. Fire suppression, acting synergistically with fewer beaver ponds, increased competition from encroaching trees and shrubs, and locally reduces water tables, might explain the willow declines.

Height-suppression may permit willows to survive adverse environmental and herbivore influences in the short term (several decades), but severe reduction in heights results in the entire plants within the reach of browsing ungulates, and intense herbivory reduces seed production. Willow catkins are produced only on shoots that were unbrowsed the previous year; most willow seed from northern range willows is produced on unbrowsed crowns that grow above the reach of elk and moose. Reduced seed production, reduced recruitment, and little or no expansion of willow communities has been observed on Yellowstone's northern range over the past several decades (Chadde and Kay 1991). Willows of suppressed height are remarkably persistent and almost no deaths have been observed for the past 3 decades on a series of transects (Singer et al. 1994), but in the absence of recruitment, these stands will eventually disappear. Limited recruitment of willows does occur, even under existing conditions. Willows establish on new sites disturbed by floods (Houston 1982), tall willows that grow beyond the reach of ungulates, or shoots protected in the center of clumps (refugia) still produce seed, while root suckering due to ungulate browsing results in a larger number of smaller willows than in protected stands (Singer et al. 1994). However, willow declines of the magnitude observed this century on the northern range are suggested several times in the pollen record over the past 1,000 years (Engstrom et al. 1991). Extirpation of willows seems unlikely; sufficient willows will likely survive into the next wet and cold period to sustain yet another period of willow abundance.

Conclusions

We conclude that ungulate herbivory alone does not explain the declines and height reductions of willows on the northern winter range. Height suppression of willows was not correlated to wintering ungulate density, at least during our admittedly brief study period (5 years), while formerly height-suppressed willows produced far less aboveground growth and showed no community expansion even when protected from ungulates for 3 decades. Suppressed willows produced less defense compounds, resulting in a higher preference by ungulates and greater relative rates of offtake. Suppressed willows are so highly palatable that large elk reductions to 20-30% of ECC in the 1960's did not reduce percent leader use of suppressed willows (Singer et al. 1994).Willow deaths observed following the drought of 1988 were not correlated to intensity of ungulate browsing. One stand subjected to drought-related mortality was intensely browsed, but the other was not. Both stands were located on dry, marginal sites on higher stream terraces left behind by meandering stream. We speculate 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, but that the proximate factor in the declines has been intense herbivory by native ungulates. Well designed manipulative experiments should test the relative influences of herbivory, water stress, and burning.

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