Interaction Among Cervids, Fungi, and Aspen in Northwest Wyoming

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Abstract—*Eighty-five 0.02-ha plots in the Gros Ventre River drainage of northwestern Wyoming with high elk usage had 39% fewer aspen stems in 1985 than in 1970. Sixty-five of these plots were remeasured in 1989 and 53 additional plots established in 1986 on the Hoback River drainage (lower winter elk usage) were remeasured in 1990. Overall mortality (average/year) of aspen stems >2.5 cm d.b.h. was 2.6% (1970–1985), 2.4% (1985–1989), and 2.3% (1989–1999) for the Gros Ventre plots, and 1.9% (1986–1990) for the Hoback plots. Larger stems (>15 cm) had lower mortality rates than smaller stems. Additional studies conducted near elk feedgrounds also showed that mortality caused by pathogenic fungi was correlated with the amount of prior cervid injury to stem boles. Aspen sprouts exposed to cervids rarely exceeded 1 m in height. These observations indicate that herbivory and disease may be reducing aspen distribution in these ecosystems.*

Introduction

The direct impact that elk browsing and barking have on aspen stands has been reviewed (DeByle 1985). Through the early sapling state, browsing reduces aspen growth, vigor, and numbers. Aspen (*Populus tremuloides*) is especially susceptible to gnawing or stripping of its bark by elk (*Cervus elaphus*) and moose (*Alces alces*) (Miquelle and Van Ballenberghe 1989). Deer (*Odocoileus* spp.) browsing prevented aspen regeneration in Utah (Mueggler and Bartos 1977) and Michigan (Westell 1954). A single, heavy late summer grazing by cattle (*Bos* spp.) after overstory removal practically eliminated aspen regeneration (Fitzgerald and Bailey 1984). Smith et al. (1972) reported that deer alone had little effect on the development of aspen reproduction, but when deer were present with cattle, aspen regeneration was virtually eliminated.

Severe browsing by elk in Michigan on aspen prevented the development of new stands following harvest (Spiegel et al. 1963), and in Montana 50% of the aspen sprouts were killed by elk during a single winter (Gaffrey 1941). Olmstead (1979) found that if more than 30% of the current year's production of twigs was eaten by elk, stand density decreased. He reported twig volume losses ranged from 43% to 79% on aspen stands in Rocky Mountain National Park. In the same area from 1968 to 1978, twig use averaged 69% and the number of mature stems declined in most aspen stands surveyed (Stevens 1980). During a five-year period in Yellowstone National Park, twig loss averaged 66%, and 76% of the stems under study died (Kittams 1959). Even much lower levels of defoliation may decrease plant fitness (Crawley 1985).

The nation's expanding elk, moose, and deer herds appear to be having a negative impact on aspen regeneration, especially in locations where the herds are protected from hunting (e.g., national parks). Most of the damage is restricted to winter ranges where elk are concentrated near feedgrounds. Aspen sprouts exposed to elk rarely exceeded 1 m in height on the Gros Ventre watershed in Wyoming (Krebill 1972; Hart 1986) or along Pacific Creek in

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Grand Teton National Park (Weinstein 1979). If unable to reproduce, these seral aspen stands deteriorate rapidly (Schier 1975) and may be replaced by communities with lower multiple-use values.

Relationships between cervids, aspen, and pathogenic fungi have been studied previously (Packard 1942; Graham et al. 1963; Hart 1986; Hart et al. 1986; Kittams 1959; Krebill 1972; Mielke 1943; Walters et al. 1982). The barking of aspen by elk or moose often has provided a point of entry for canker fungi that hasten the death of the stems. Sludge application to aspen stands in Michigan increased elk damage that altered growth form and created wounds, predisposing clones to pathogenic fungi (Hart et al. 1986). In areas of moderate to light herbivore pressure, the direct damage caused by the animals may not be severe enough to cause stand deterioration except for the secondary action of pathogens and insects. In some areas in Colorado where elk barking was light, no elk wounds became visibly infected with a pathogen (Walters et al. 1982). The reason for the disparity between the studies of Packard (1942), Krebill (1972) and Hart (1986), and those of Walters et al. (1982) is unknown.

The objective of this study was to conduct a long-term survey of aspen stands in northwest Wyoming to determine the relationships between aspen demographics and elk, moose, and disease.

Gros Ventre/Hoback Studies

Methods

In 1970 Krebill (1972) sampled one hundred 0.02 ha plots on the Gros Ventre River drainage (cervid injury common and severe) to determine the rate of overstory aspen mortality and its causes. Browsing and pests severely limited the replacement of dying trees. His data predicted a 44% reduction in aspen overstory by 1985.

To test Krebill's prediction, ninety-seven 0.02 ha circular plots were established on the Gros Ventre watershed in 1985. Using Krebill's original map, 85 of the plots were established in the same locale as his 1970 plots. Condition of aspen stems was recorded by diameter breast height (d.b.h.) in three size classes (2.5–15 cm, 15–30 cm, >30 cm). Occurrence of potentially lethal pathogens and insects and the amount of cervid injury to the bark 0.5–2.5 m above ground were recorded. The number of suckers, average height, and amount of browse on suckers were determined for each plot. Pathogens and insects were identified by field symptoms and signs.

In 1986, 55 similar plots were established in a drainage (Hoback River watershed) adjacent to the Gros Ventre in aspen stands with little or no cervid damage. In 1989, 65 plots were resurveyed and in 1999 32 plots on the Gros Ventre were resurveyed. Plots (53) on the Hoback drainage were resurveyed in

1990, thus the time between the initial and final samplings was the same (four years) for both areas.

Results

The 85 plots sampled in 1985 on the Gros Ventre drainage had 39% fewer stems >2.5 cm d.b.h. than in 1970, similar to the 44% decrease predicted by Krebill (1972). Mortality rates during 1985–1989 and during 1989–1999 based on the 32 plots sampled in 1999 were not significantly different ($p = 0.659$) (table 1). Smaller diameter trees died faster than larger diameter trees ($p = 0.001$) (table 1). Mortality was caused mainly by pathogenic fungi (primarily *Valsa sordida* [*Cytospora chrysosperma*], and *Encoelia pruinosa* [*Cenangium singulare*]) following prior cervid injury to stem boles.

Mortality during the 4-year period (1985–1989, Gros Ventre, or 1986–1999, Hoback) was significantly ($p = 0.0001$) greater for stems between 2.5 cm and 30 cm d.b.h. on the Gros Ventre watershed (high cervid numbers) compared to the Hoback watershed (low cervid numbers) (table 2). Most of the aspen in plots on the Gros Ventre drainage had more than 40% of the bark between 0.5 m and 2.5 m above groundline removed or damaged when the plots were sampled in 1985 (table 3). The aspen on only one of 55 plots on the Hoback drainage had damage above 40%. There was a significant difference ($p < 0.001$) in the amount of barking between locations. The number of dead aspen stems on the ground per plot correlated with the amount of prior cervid damage to the bark. Plots with stems having less than 40% of the bark damage averaged 4.5 dead stems per plot, while plots with stems with 40–70% and >70% damage averaged 15.1 and 17.7 dead stems per plot, respectively.

Number of suckers remained constant (table 4) as did their height ($p = 0.2064$) (table 5). On the Gros Ventre watershed, only 3–8% of the plots had suckers >1 m in height, while on the Hoback watershed over a third of the plots had suckers >1 m in height ($p < 0.0001$ for location) (table 5). Amount of browse on the current year's growth on suckers was lower ($p = 0.0331$) for plots sampled on the Hoback drainage compared to the Gros Ventre drainage (table 6). In 1999 the amount of browse was lower ($p = 0.0174$) in plots on the Gros Ventre

Table 1—Average annual mortality rates for aspen stems on the Gros Ventre drainage in northwestern Wyoming between 1985–1989 and 1989–1999. Number of live stems at the beginning of each interval is in parentheses.

	2.5–15 cm d.b.h.	15–30 cm d.b.h.	>30 cm d.b.h.
	- - - - - - - - - - - - - - - *percent* - - - - - - - - - - - - - - - -		
1985–1989	4.2 (96)	2.0 (402)	0.1 (32)
1989–1999	4.6 (80)	1.8 (370)	1.9 (31)

Table 2—Average annual mortality rates during a 4-year period for aspen stems in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids.

	2.5–15 cm d.b.h.	15–30 cm d.b.h.	>30 cm d.b.h.
	- - - - - - - - - - - - - - - *percent* - - - - - - - - - - - - - - - -		
Gros Ventre[a]	5.0 (164)	2.0 (770)	0.4 (64)
Hoback[b]	2.7 (621)	1.1 (715)	1.3 (19)

[a]Number of live stems in 1985 is in parentheses.
[b]Number of live stems in 1986 is in parentheses.

Table 3—Amount of aspen bark that cervids have removed 0.5–2.5 m above groundline in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids.

% bark removed	Gros Ventre (1985) # of plots	Hoback (1986) # of plots
<10	0	31
10–40	9	23
40–70	53	1
>70	33	0

Table 4—Number of aspen suckers per 0.02 ha plot in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids. Number of 0.02-ha plots is in parentheses.

	1985/1986	1989/1990	1999
Gros Ventre	26 (97)	32 (65)	20 (31)
Hoback	18 (55)	20 (53)	

Table 5—Percent of 0.02 ha plots with aspen suckers >1 m in height in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids. Number of 0.02-ha plots is in parentheses.

	1970	1985/1986	1989/1990	1999
		- *percent* -		
Gros Ventre	3 (100)[a]	6 (85)	8 (65)	3 (31)
Hoback		33 (55)	40 (53)	

[a]1970 data from Krebill (1972).

Table 6—Percent of current year's growth of aspen suckers browsed by late August in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids. Number of 0.02-ha plots is in parentheses.

	1985/1986	1989/1990	1999
	- - - - - - - - - - - - - - *percent* - - - - - - - - - - - -		
Gros Ventre	72% (75)	66% (52)	30% (28)
Hoback	39% (36)	50% (36)	

than on the same plots in 1985 or 1989 (table 6). This reduction appears to be correlated with fewer cattle in 1999 compared to the 1980s.

Heart Six Studies

Methods—Study I

The winter of 1983–1984 was especially severe in western Wyoming, and elk were fed in 1984 near the Heart 6 Ranch, Moran, Wyoming, an area where elk had not previously wintered. Hence the aspen stems in this area were free of stem scars prior to the feeding program. The stems in the immediate area of feeding were severely damaged in early 1984, but nearby (300 m) clones were not attacked. No significant reinjury occurred during 1985, 1986, or 1987.

Although moose winter commonly in the willow flats below the feedground, they were not reported in the area where the elk were being fed.

Seven 0.02-ha plots were established in July 1985 in the injured (feedground) and in the nearby uninjured clones. The condition of stems 2.5 to 15 cm d.b.h. was recorded. The diameter, amount of injury, and presence of any pathogens were recorded for each stem >15 cm d.b.h. Stems were permanently marked and were examined again in July 1986 and August 1987, and their condition was recorded.

Results — Study I

From the data collected in 1985, it was estimated there were 428 stems 2.5–15 cm d.b.h. alive in the seven feedground plots in 1984 and 357 live stems in the seven control plots. In 1984, 82% (347/428) and 1.7% (6/357) of the stems received elk injury in the feedground and control plots, respectively. By 1985, 28% (97/347) of the injured stems had died in the feedground plots; the mortality dropped to 11% in 1986 and 1987. Mortality rates varied from 1.4% to 8.5% per year for the uninjured stems in the feedground area and from 5% to 14% per year in the control area. Cumulative mortality (1984 to 1987) was 43% for injured stems compared to 14% and 21% for uninjured stems in the feedground and control areas, respectively.

The bulk (72%) of the first-year mortality of injured stems 2.5–15 cm d.b.h. was the result of elk completely girdling the stem; the remaining mortality in 1985 and nearly all of the mortality in 1986 and 1987 was the result of elk wounds being colonized by canker fungi. *Valsa sordida* (*Cytospora chrysosperma*) was the pathogen present except for one case in 1986 when *Encoelia pruinosa* (*Cenangium singulare*) was identified. In addition, 61 of the 198 wounded stems still alive in 1987 in the feedground plots had active *Cytospora* cankers in 1987.

There were 141 and 136 live stems >15 cm d.b.h. on the feedground and control plots, respectively. Ten injured stems over 15 cm d.b.h. died between 1985 and 1986, but only one death resulted from colonization of an elk wound by a pathogenic fungus (*Cenangium*). Five more stems died in 1987, but none died from cankers associated with elk damage. Cumulative mortalities (1985–1987) of elk-damaged and healthy stems were 2.7% and 1.5%, respectively.

Methods — Study II

During 1988, elk and moose were again fed near the Heart Six Ranch, Moran, Wyoming, in areas free of stem scars prior to the feeding program. During August 1989, 14 plots of 0.02 ha were established in areas where some barking had occurred; seven of these plots were the "control" plots for Study I. The condition of 529 stems 2.5 to 10 cm d.b.h. was recorded; 54% of the stems had damage caused by elk or moose. The diameter, the number of cervid wounds, the percent of the circumference girdled, the presence of canker fungi, and the presence of the heartrot fungus *Phellinus tremulae* were recorded for each stem >10 cm d.b.h. There were 163 stems that received some damage and 99 undamaged stems. Plots were sampled annually in late summer from 1989 to 1995, with the year of death recorded for each stem that died. There was little new damage after 1988, but a few stems had to be eliminated because of üubsequent damage.

Results — Study II

From 1989 to 1995, 55% of the damaged and 46% of the undamaged stems 2.5–10 cm d.b.h. died. Seventy-two percent of the mortality of the damaged

Table 7—Annual mortality rate of aspen stems in northwestern Wyoming with and without *Phellinus tremulae* and with or without cervid damage to the bark, 1988–1995. Number of stems is in parentheses.

	percent
Healthy	2.4 (76)
Cervid wounds only	2.9 (129)
P. tremulae, no wounds	1.9 (23)
P. tremulae, cervid wounds	5.9 (34)

stems occurred by 1991. As in Study I, most of the mortality was from mechanical injury followed by infection of wounds by *V. sordida*.

The annual mortality of stems >10 cm d.b.h. was 3.5% for damaged stems and 2.3% for stems not injured by cervids. Stems that had fruiting bodies of *P. tremulae* and cervid damage were three times more likely to die than unwounded stems with *P. tremulae* fruiting bodies and twice as likely to die as wounded stems without *P. tremulae* or healthy stems (table 7). Wounded stems that died by 1995 had an average of 69% of the circumference of the trunk girdled in 1988 compared to 37% girdled for wounded stems that did not die by 1995 ($p = 0.0001$). Wounded stems that became infected with canker-causing fungi had an average of 53% of the circumference girdled in 1988 compared to 40% girdled for wounded stems that did not become infected by 1995. Reduction in the percent of the trunk girdled between 1988 and 1995 was 41% and 23% for stems that did not and stems that did become infected with canker fungi, respectively. The 56 stems that died between 1988–1995 had an average d.b.h. of 17.3 cm, while the average d.b.h. of the 206 stems that did not die was 18.7 cm ($p = 0.849$).

Goosewing Exclosure

Methods

Near the Goosewing ranger station (Gros Ventre watershed) there was an exclosure that contained a considerable number of aspen. During 1985 and 1986, moose broke a hole in the fence and scarred a number of stems, most injury apparently being the result of a single feeding episode.

In 1985, the d.b.h. (average 9.1 cm, 4.3–26.1 cm) and percent of circumference girdled were recorded for 80 recently scarred stems. The d.b.h. (average 8.8 cm, 3.4–22.9 cm) was also determined for 75 uninjured stems, and all 155 stems were permanently numbered. Similar data were recorded for 25 stems injured in 1986. All stems were observed annually until 1995 except for 1988.

Results

Annual mortality of stems was 3.5% and 1.3% for stems injured by moose and uninjured stems, respectively, results very similar to those obtained from the Heart Six, study II. Annual mortality for the 25 stems injured in 1986 was 1.8%. Wounded stems that died by 1995 and wounded stems that remained alive had nearly identical amounts of girdling in 1985: 37.3% and 36.0% ($p = 0.633$), respectively, which differs from the data collected from the Heart Six, study II. As reported in the previous studies, smaller d.b.h. stems were more likely ($p = 0.0648$) to die than stems with a larger d.b.h. Average d.b.h. of uninjured stems

that died was 7.7 cm versus 9.0 cm for stems remaining alive. For injured stems, those that died had an average d.b.h. of 7.8 cm versus 9.7 cm for stems that lived.

Discussion

These results support previous research which has demonstrated that aspen has a difficult time maintaining itself when subjected to intense herbivory from cervids (Kay 1997; Romme et al. 1995; Bartos and Mueggler 1981; Krebill 1972). Mortality increased as the amount of bark injured increased (Miquelle and Van Ballenberghe 1989). Death of overstory stems coupled with heavy browsing of suckers, especially when fire was excluded from the environment, resulted in the reduction of the aspen type over time.

Increased grazing pressure resulted in increased pathological stress. Injured stems usually succumbed to invasions by pathogenic fungi rather than from mechanical injury alone. These fungi are secondary in time (not in importance) because changes in host condition are required for their successful attack. The canker fungi are part of the natural biota that occur on the trees. Aspen are highly resistant to these secondary pathogens until wounds enable them to succeed. Yet most injured trees were not attacked by canker fungi or were able to recover over time. The combination of *P. tremulae*, ungulate barking, and canker fungi was a deadly combination for most stems.

The effect of herbivory or disease on a clonal plant may differ significantly from the effect on a non-clonal plant, especially in evolutionary terms. Predation or disease on a clonal plant may have no influence on fitness if the predator removes only what would have died later from density-dependent processes. The birth and death rate for stems may represent a population behavior distinct from but interacting with the birth and death rates of clones. Perhaps by reducing the amount of energy-requiring stem tissue, dieback of part of the clone (usually the smaller diameter stems) adjusts the clone's energy balance to its environment without significantly reducing clonal fitness.

The major role of most mammalian herbivores is related to their indirect effects rather than those related directly to energy consumption. These herbivores, while minor participants in ecosystem energy flow, can have important effects out of proportion to the quantity of energy consumed. Damage by animals to the cambium of trees or to the apical meristem may have effects far greater than the fraction of the plant body eaten, particularly when the effect is to change the morphology of the plant. Thus by altering growth form or by creating wounds for pathogens, herbivores may cause significant successional consequences.

Kay (1997) has reviewed the literature which strongly suggests that cervid populations in much of the West are higher now than in the past. Feedgrounds (three of which are on the Gros Ventre watershed) further concentrate these animals during the winter. To persist, aspen must not only be resistant to disease and competition by conifers, but also be inaccessible to cervids or be resistant to herbivory. Historically, periodic winter die-offs reduced cervid populations (at least before winter feeding) and allowed aspen to grow above browse levels before cervid populations recovered. Under current conditions (reduced fire frequency; high, constant cervid populations), the future of aspen in this area is limited by the intensity of herbivory in the winter and competition with conifers. Hence, more fires and/or fewer cervids would favor the growth of aspen.

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