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Effects of Ungulate Browsing on Aspen Regeneration in Northwestern Wyoming

Abstract

*Although clear-cutting has been demonstrated to be an effective means to regenerate aspen (*Populus tremuloides *Michx.), stand replacement may be retarded under conditions of intense browsing of regeneration, such as that experienced near elk (*Cervus elaphus*) feedgrounds in northwestern Wyoming. We studied the effects of ungulate browsing on regenerating aspen following clear-cutting on the National Elk Refuge. Nine deteriorating, aspen-dominated stands were clearcut in the spring of 1988, and regeneration characteristics were subsequently measured periodically through 1996. Big game exclosures were placed in three stands immediately following treatment. Post-treatment sucker densities were relatively low but theoretically sufficient for stand replacement. The percentage of "suckers" that obtained heights >2 m was significantly greater inside the exclosures after 9 years than outside the exclosures. Average heights of browsed and unbrowsed suckers were markedly taller within the exclosures. Our findings suggest that repeated annual browsing substantially increased sucker mortality, and limited the height achieved by aspen stems. Small-scale clear-cutting to regenerate aspen may not be effective in areas of winter ungulate densities similar to those adjacent to elk feedgrounds.*

Key words: aspen, *Populus tremuloides*, browsing, clear-cutting, exclosures, National Elk Refuge, regeneration

Introduction

Ecologists and resource managers have been concerned over the declining condition of aspen (*Populus tremuloides* Michx.) stands throughout northwestern Wyoming and elsewhere in the western United States, particularly on big game winter ranges. Although the relative importance of various factors involved is unclear, fire suppression, ungulate browsing, and natural succession all directly contribute to the lack of successful regeneration observed in western aspen (Krebill 1972, Schier 1975, Basile 1979, Gruell 1980, Kay 1985, Mueggler 1989, and Romme *et al.* 1995).

Aspen reproduces almost exclusively through vegetative propagation, and is therefore clonal in nature (Barnes 1966). Adventitious shoots (suckers) arise from shallow lateral roots that grow in a complex interconnecting network among the individual ramets comprising an aspen clone. Suckering is normally suppressed by a process called apical

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dominance, whereby auxin produced in the leaves and buds of mature aspen stems is transported to the roots and inhibits sucker growth (Farmer 1962, Schier et al. 1985). Death of overstory trees eliminates this regulatory control, thus permitting rapid sucker growth.

Management strategies, such as clear-cutting and prescribed burning, are effective because they mimic natural disturbances that kill the overstory trees and stimulate suckering (Schier *et al.* 1985). However, questions remain regarding sucker survival and growth following treatment under conditions of intense browsing pressure, particularly where ungulates are concentrated on winter ranges and near elk feedgrounds (Krebill 1972). In this paper we examine the influence of browsing on aspen regeneration and growth following clear-cutting under conditions of heavy ungulate use. Our objectives were to quantify regeneration after treatment and to determine whether subsequent browsing by ungulates would prevent new suckers from growing beyond the reach of browsers.

Study Area

Our study was conducted on the National Elk Refuge, located in Park County, northwestern Wyoming (43°30'N, 110°45'W). The refuge is located at the southern end of Jackson Hole, and is bordered to the east by the Gros Ventre Range and to the west by the Grand Teton National Park. The refuge encompasses over 10,000 ha with elevations ranging from 1900 to over 2200 m above sea level. Annual air temperature averages 3° C, and annual precipitation averages about 39 cm (Dept. of Commerce 1982). The refuge had 753 ha of aspen-dominated woodlands found in 143, mostly even-aged stands. Common understory associates included snowberry (*Symphoricarpos oreophilus*), serviceberry (*Amelanchier alnifolia*), willow (*Salix* spp.), *Calamagrostis rubescens*, *Poa* spp., *Lupinus argenteus*, *Helianthella uniflora*, *Epilobium augustifolium*, and *Geranium* spp.

The primary responsibility of the refuge is to provide winter habitat and food for approximately 7500 Rocky Mountain elk (*Cervus elaphus canadensis*) annually. The number of elk supplementally fed on the refuge during 1988 - 1996 ranged from 7753 to 10004 elk (Smith and Anderson 1998). Another 150-300 elk wintered on the refuge but did not attend feedgrounds. Other browsers that wintered on the refuge included about 75 mule deer (*Odocoileus hemionus*), 20 moose (*Alces alces*), and 110-260 bison (*Bison bison*).

Methods

Nine aspen stands were selected for treatment from among 110 stands on the northern 6000 ha of the NER. Treated stands were 1.1-5.9 ha in size. Treated stands tended to be heavily browsed, lacked sufficient regeneration for stand replacement, and were experiencing significant mortality of overstory trees. Because the area of interest was under concentrated winter (15-20 moose and 150-300 elk), spring (7700-10,000 elk and 110-260 bison for 2-4 weeks), and summer (150-300 elk, 20-30 mule deer) ungulate use, treated stands were selected in clusters rather than in isolation to reduce the likelihood of ungulates congregating in any one stand (D. Bartos, N. DeByle, and W. Mueggler pers. comm.). Treated stands were located on generally north-facing slopes with similar soil types.

Each stand was clearcut during April-early May 1988. All aspen stems >5 cm dbh and all conifers, regardless of size, were cut. Afterward, rectangular (7x7 m) game exclosures were placed within three treated stands to measure the effects of ungulate browsing on aspen regeneration. Vegetation measurements were collected in each of the three stands with exclosures during late summer-early fall 1988 through 1996. Similar measurements were collected in the remaining stands during summer - early fall of 1988 and 1989, and every other year thereafter through 1995. A permanent transect was placed lengthwise through the middle of each stand. Five to 15 plots, depending on stand size, were permanently placed equidistantly along the length of transect. On each 1.6 m^2-plot, the number of aspen stems were counted and the level of browsing assessed. We measured the height of each stem and counted the number of years its terminal leader was browsed.

Data collected from each plot were pooled, and either a mean or proportion was estimated for each stand. We examined the effects of browsing by comparing vegetation measurements collected on plots within each exclosure to those outside the exclosure in a paired design. Statistical tests were conducted using SPSS 7.5 (SPSS Inc., Chicago, IL). Sucker density was tested for browsing effects, year effects, and treatment-year interaction using multivariate analysis of variance (MANOVA) with a repeated measures design (Norusis 1990). We tested for year effects on sucker density using MANOVA for data collected on plots outside of the exclosures from all nine stands. Year effects on browsing-related attributes and sucker height could only be examined descriptively because of missing data. Browsing-related effects were tested using a paired-samples t test, after calculating an average across years. Tests were considered significant at $P \leq 0.05$.

Results

Mean sucker densities within the exclosures ranged from over 60,000/ha in 1988 to a minimum of about 16,000/ ha in 1994 (n = 3). Sucker densities outside exclosures ranged from 17,200/ ha in 1990 to 12,133/ha in 1996 (Fig. 1).

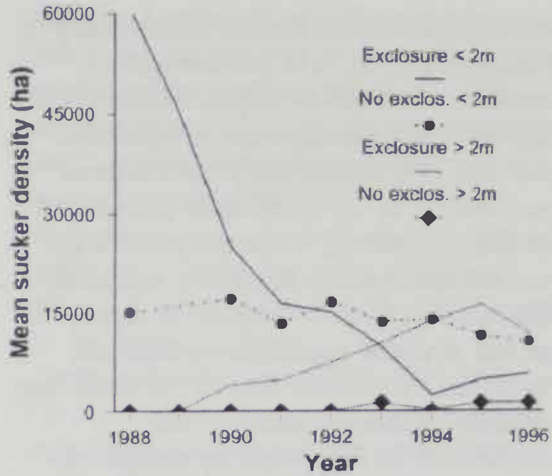

Figure 1. *Density of aspen suckers by treatment, 1988-1996.*

Sucker density was twice as great in the exclosures across all years, averaging over 28,000/ha (Table 1). We discerned no clear trends in average sucker density from all clearcut sites from 1989 to 1995, ignoring counts within the exclosures (F_{year} = 0.5, df = 4, 28, P = 0.719). Clearcut sites averaged 9136 suckers/ha, ranging from 7178 in 1989 to 10333/ha in 1991 (n = 9). With the exception of one treated stand, all stems recorded outside exclosures were <2 m tall over the course of the study.

After 1990, the density of aspen suckers >2 m tall was significantly greater inside exclosures than outside

Table 1. *Effects of year and protection of aspen from herbivory within exclosures on density (stems/ha) of aspen measured in 2 size classes on the National Elk Refuge, 1988-1996.*

	Mean Density (SE)		Test
Variable	Exclosure	No Exclosure	Result[2]
< 2 m tall	20,659 (3965)	13,074 (1824)	A
> 2 m tall[1]	9943 (1426)	590 (590)	B, C
Total	28,393 (4748)	13,533 (1771)	A

[1]estimated from 1990-1996

[2]A denotes a significant (P <0.05) treatment-year interaction

B denotes a significant treatment effect

C denotes a significant year effect

and the difference increased annually (Table 1, Fig. 1). The proportion of suckers >2 m tall averaged 51percent in the exclosures compared to 4 percent outside. We found the proportion of suckers >2 m tall continued to increase in the exclosures, while the proportion outside exclosures remained relatively stable (Fig. 2). The density of aspen <2 m tall was not significantly different between treatments due to the declining density of these suckers in the exclosures as they were recruited into the >2 m tall size class (Table 1, Fig. 3).

Both unbrowsed suckers and previously-browsed suckers were markedly taller within the exclosures than outside (Table 2). The average number of terminal leaders browsed was five times greater outside the exclosures, which showed an increasing trend over time (Fig. 3). No observable trends occurred within the exclosures for this variable. Thirteen percent of the suckers inspected within the exclosures showed evidence of browsing, as compared with 57 percent of suckers outside exclosures. The percentage of aspen suckers that were browsed was constant over time, in and out of the exclosures. Average height of suckers <2 m tall showed an increasing and asymptotic trend over time within exclosures. We observed no increase in average sucker height outside of the exclosures over time.

Discussion

Sucker densities outside the exclosures remained stable from 1988 to 1995, averaging 7000-10,000/ha nine years post-treatment. Since no pre-treatment data were collected, we have no basis for comparison to judge the effectiveness of clear-cutting in stimulating suckering on these sites.

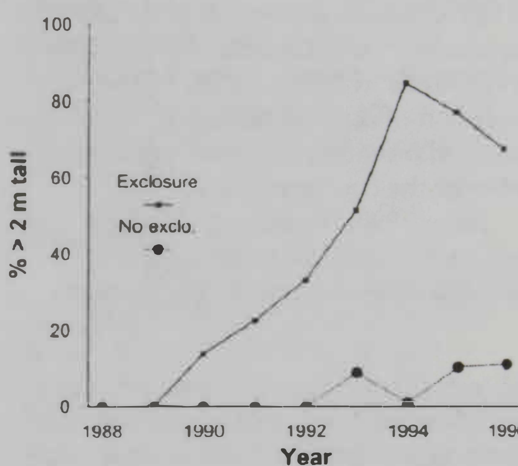

Figure 2. *Percent of aspen suckers > 2 m tall, 1988-1996.*

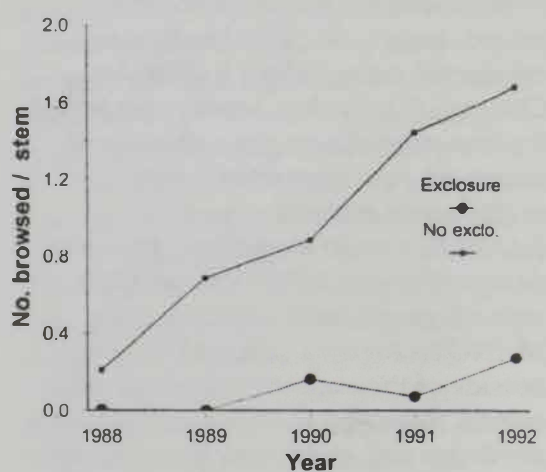

Figure 3. *Average number of terminal leaders browsed per aspen stem, 1988-1992.*

Table 2. *Browsing effects on regenerating aspen (<2 m tall) on the National Elk Refuge averaged from 1988 to 1996. Measurements obtained inside and outside exclosures were compared with paired Student's* t *tests.*

	Mean (n = 9 years)			
Variable	Exclosure	No exclosure	Differ. (SE_d)	P
Browsed sucker height (cm)	133	79	+54 (17)	0.086
Unbrowsed sucker height (cm)	120	42	+78 (9)	0.014
No. of terminal leaders browsed	0.3	1.5	-1.2 (0.2)	0.034

Crouch (1983) reported sucker densities approaching 76,000/ha one year following clear-cutting, as compared with 2500 on uncut control stands in southwest Colorado. Schier and Smith (1979) reported first year sucker densities averaging about 129,000/ha, in comparison with 8500/ha on the controls on a clearcut in Utah. In the same study, twelfth-year densities averaged over 14,000/ha, and were 4000/ha more than that recorded in our ninth year. Bartos and Mueggler (1982) reported sucker densities exceeding 45,000/ha two years post-clear-cutting in northern Utah, while uncut control sites averaged < 5000/ha.

Based on the results of these studies, we conclude that sucker generation substantially increased on our clearcut sites. The relatively low production of suckers may be related to the declining condition of the stands prior to treatment, or to site characteristics (Schier 1975). Regardless, initial sucker densities post-treatment should have been sufficient for stand replacement (Bartos et al. 1991). In contrast, sucker densities estimated in our exclosures followed trends typically observed in western aspen, i.e., a first year irruption, followed by a sharp decline in abundance in subsequent years (Bartos *et al.* 1991). We are uncertain if the difference in first year sucker densities between treatments was related solely to browsing-related effects.

The beneficial effects of clear-cutting in regenerating aspen stands are best demonstrated by the number of suckers that grow beyond 2 m tall. We considered 2 m the effective height beyond which young aspen stems will likely escape further browsing of terminal buds (Kay 1985). We found that sucker densities > 2 m tall were significantly greater in the exclosures across all 9 years, and more importantly, that the proportion of suckers recorded in this size class also was far greater inside exclosures than outside. During the ninth year post-treatment, <5 percent of the suckers outside of the exclosures were > 2 m tall, and these stems were restricted to a single stand. In contrast 68 percent of the suckers recorded in the three exclosures were >2 m tall during the ninth year. Browsing apparently inhibited aspen growth and recruitment on these sites. This conclusion is corroborated by our observation that the proportion of suckers browsed was four times greater outside exclosures than inside (also indicating that our exclosures, as physical barriers to ungulates, were less than completely effective).

As expected, we observed an increasing trend in the frequency of terminal leader browsing over time outside of the exclosures, and average sucker heights were considerably taller in the exclosures than outside. We also observed that suckers, which had never been browsed, were considerably shorter outside of exclosures than inside. This suggested that repeated annual browsing substantially increased mortality, stimulated further suckering, and in effect, created younger sucker age classes. This also would explain the lack of declining trend in sucker densities outside of the exclosures. If true, continued browsing may expedite the decline of these treated stands as food reserves in the clonal root systems are exhausted (Schier *et al.* 1985). In fact, clear-cutting may have actually hastened the demise of these stands.

It is clear from our data that browsing-related effects prevented young suckers from growing beyond the reach of further browsing and reduced the rate of recruitment for overstory replacement. Increasing the size of clearcuts may help mitigate this problem in areas of high ungulate use. Mueggler and Bartos (1977) concluded that, "Without control of ungulate use, clear-cutting or burning less than about

5 hectares of mature aspen might be futile." Our results support their conclusions. Persistent ungulate browsing on the refuge may necessitate treating much larger areas of mature aspen in the future, or reducing elk numbers to facilitate maintenance of multi-aged aspen stands on the landscape.

Acknowledgements

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