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EFFECTS OF ELK BROWSING ON ASPEN STAND CHARACTERISTICS, RAMPART RANGE, COLORADO

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Quaking aspen (*Populus tremuloides*) forests provide important wildlife habitat and forage throughout the American West (Reynolds 1969, Patton and Jones 1977, DeByle 1985, Romme et al. 1995). They also are important at landscape scales by providing "firebreaks" within otherwise combustible forests (Brown and Simmerman 1986). North American elk (*Cervus elaphus*) browse on bark of mature aspen and consume young shoots (e.g., Reynolds 1969, Hobbs et al. 1981, Kay 1997, White et al. 1998, Suzuki et al. 1999, Kay and Bartos 2000). Several years of bark browsing by elk can completely arrest flow of sap and kill aspen stems (Packard 1942) or leave open scars causing the stems to be more susceptible to insects and disease (Loope 1971, DeByle 1985).

Elk populations have increased markedly in North America from the 1800s to the present (Kay 1997). Estimates compiled by Bunnell (1997) from elk managers show an increase from 100,000 elk in North America in 1907 to 967,000 in 1995. The present North American elk population may be higher than at any time in the last 10,000 years (Kay 1997). Estimates compiled from elk managers in Colorado show that the population roughly doubled in the 20 years from 1975 (105,000) to 1995 (203,000) (Bunnell 1997).

In some areas, perhaps especially on winter ranges (Suzuki et al. 1999), high elk populations are preventing significant regeneration of aspen stands through very heavy browsing of young shoots (DeByle 1985, Romme et al. 1995, Baker et al. 1997, Kay 1997, White et al. 1998, Ripple and Larsen 2000). This is a recent phenomenon and, based on historical photos, did not occur prior to about 1900–1920 (Baker et al. 1997, Kay 1997, White et al. 1998, Ripple and Larsen 2000).

In this study in the Rampart Range of Colorado, we compare effects of elk herbivory on aspen between heavily browsed and minimally browsed stands within 5 km of each other. We include comparisons of growth rates of mature aspen stems, a growth response not previously reported in the literature to our knowledge.

We gathered data in the Rampart Range east of Woodland Park, Colorado. A mosaic of grassy meadows and forests covers the rolling landscape. On forested south-facing slopes, areas dominated by quaking aspen occur along with stands of ponderosa pine (*Pinus ponderosa*). Forests on north-facing slopes are a mixture of Engelmann spruce (*Picea engelmannii*), Colorado blue spruce (*Picea pungens*), and Douglas-fir (*Pseudotsuga menziesii*). The entire area has forbs, grasses, and shrubs typical of high montane plant communities and receives an average of 45 cm of precipitation per year (J. McDermott, U.S. Air Force Academy, personal communication). Bedrock for all stands is Pikes Peak Granite.

The heavily browsed aspen stands are located on the United States Air Force Academy Farish Memorial Recreational Area (38°59′N, 105°00′W). Because hunting is not permitted, this 242-ha property is used year-round by a large elk population (100 to 200 animals), which has grown slowly through time (B. Davies, Colorado Division of Wildlife, personal communication). This property is surrounded by Pike National Forest where hunting is allowed. In the minimally browsed stands (39°00′N, 104°58′W) in the national forest, terrain, elevation, vegetation, soils, and size of mature

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aspen stems are very similar to the Air Force property. Elevations of heavily browsed stands range from 2800 m to 2815 m and for minimally browsed stands 2795 m to 2830 m. Slope inclinations are gentle, which makes aspect relatively unimportant. Aspects are mixed within each browsing intensity and range from northeast to southeast for heavily browsed stands and northeast to southwest for minimally browsed stands.

Although several species of wild and domestic ungulates can affect aspen regeneration (Kay and Bartos 2000), elk are the only species significant in this area. Estimates of mule deer (*Odocoileus hemionus*) densities are very low due to the poor habitat, an estimated 0.4 to 0.8 animals · km^{-2} (B. Davies, Colorado Division of Wildlife, personal communication). Livestock grazing is not permitted in the Farish Area, and there is not a grazing allotment in the national forest study area. In addition, no evidence was seen of livestock grazing in either area.

We determined degree of browsing pressure by proportion of bark scarred by elk stripping bark. The 2 study areas showed a remarkable divergence in this character. On the unhunted Farish Recreation Area, elk browsing is extremely heavy, with all mature aspen stems virtually completely covered to about 2.25 m aboveground with the rough black bark created by bark stripping. On the nearby U.S. Forest Service land, aspen bark shows nearly zero evidence of bark stripping.

In September 1999 we chose 5 stands of similar structure and mature stem size in both the heavily browsed and minimally browsed areas. These were essentially pure aspen stands; only occasional, small conifers were present. Within each stand we randomly chose one 10 × 10-m plot. In each plot we counted live and dead suckers (stems <2.5 m tall) and live and dead mature stems. From living stems 13 to 14 cm dbh, average size of the mature stems in the stands, we selected and cored 10 stems in each plot at breast height on the south side of the stem. If we were unable to find 10 stems that met our criteria in the plot, we used stems in the same stand as close as possible to the plot. Growth rates were determined by gluing cores to a board, removing the top portion with a razor blade, and measuring radial increment of the last 10 years to the nearest 0.5 mm under a dissecting microscope.

Densities and percentages of suckers and mature stems were tested for differences between the 2 treatments with 1-way ANOVA or with the Kruskal-Wallis test when parametric assumptions were not met. Nested ANOVA was used to compare growth rates.

Heavily browsed stands had about 60% fewer live mature trees (P = 0.00) and over a 3-fold higher percentage of dead mature stems (P = 0.02, Table 1). Total stem density (live plus dead) was one-third lower in heavily browsed stands (P = 0.02), and dead stem density showed a trend toward being higher (P = 0.09).

Suckers in heavily browsed stands had a lower live stem density (P = 0.00) and a higher percentage of dead suckers (P = 0.00), since we found no live suckers in any heavily browsed plot. Total (live plus dead) sucker densities showed a trend toward being lower in heavily browsed stands (P = 0.08), and dead sucker densities were not different between the 2 browsing intensities (P = 0.39).

Mature stems in heavily browsed stands had radial increments about 1.7 times those in minimally browsed stands (P = 0.00).

Comparing minimally and heavily browsed aspen stands that are close to each other and in ecologically similar situations provides additional strong evidence that elk browsing of suckers can drastically reduce or even eliminate vegetative reproduction of aspen. This has been shown by studies in other locations in western North America (DeByle 1985, Romme et al. 1995, Baker et al. 1997, White et al. 1998, Suzuki et al. 1999, Kay and Bartos 2000, Ripple and Larsen 2000). It also appears that densities of larger stems may be decreased by heavy elk browsing through increased mortality of mature stems. The lack of significant differences in dead sucker densities (Table 1) may well be caused by some suckers in heavily browsed stands being completely consumed or falling after dying.

The previously undocumented increase in radial growth increment of mature stems in heavily browsed stands has 2 possible causes: decreased competition and fewer resources allocated to suckers. Several studies have shown that increased competition for water, light, and nutrients among aspen stems is negatively correlated with diameter growth rates (Graham et

TABLE 1. Characteristics of aspen stands heavily and minimally browsed by elk, Rampart Range, Colorado. Suckers are stems <2.5 m tall. *P*-values are from ANOVAs as described in the text unless otherwise indicated. Sample size is 5 within each treatment except for radial increment, where it is 50.

Stem type	Heavily browsed		Minimally browsed		
Characteristic	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	*P*
Mature stems					
Radial increment, last 10 years (mm)	10.53	0.51	6.26	0.30	0.00
Live stem density (per 100 m^2)	12.4	2.96	33.0	2.77	0.00
Dead stem density (per 100 m^2)	13.6	3.17	6.0	2.39	0.09
Total stem density (per 100 m^2)	26.0	3.22	39.0	3.11	0.02
Dead stems (%)	51.1	11.16	14.7	5.17	0.02
Suckers					
Live stem density (per 100 m^2)	0	0	27.2	9.18	0.00[a]
Dead stem density (per 100 m^2)	18.6	5.30	13.2	2.63	0.39
Total stem density (per 100 m^2)	18.6	5.30	40.4	9.49	0.08
Dead (%)	100	0	37.7	8.68	0.00[a]

[a]Kruskal-Wallis test

al. 1963, Jones and Trujillo 1975 as cited in Jones and Schier 1985). In addition, thinning stands can drastically increase growth rates of stems (Jones and Shepperd 1985). In heavily browsed stands of this study there would likely be less intraclonal competition both in the present, due to the lower density of live mature stems (Table 1), and in the recent past as indicated by the lower density of live and standing dead stems combined. In addition, when suckers are produced in aspen stands, carbohydrate reserves in the root system supply energy necessary for bud development and shoot outgrowth (Scheir et. al. 1985). Because all suckers were apparently killed in heavily browsed stands, clones presumably allocate more resources to growth of mature stems.

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