Effects of ungulate herbivory on aspen, cottonwood, and willow development under forest fuels treatment regimes

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1. Introduction

Ungulate herbivory is a chronic disturbance that can have dramatic effects on vegetation dynamics and other ecological processes in ecosystems throughout the world (Díaz et al., 2007). When ungulates suppress or eliminate preferred forage plants in favor of less preferred and less digestible plants, nutrient cycling and energy flow through an ecosystem can change substantially (Pastor et al., 1993; Pastor and Cohen, 1997; Schoenecker et al., 2004). A myriad of above- and below-ground processes can be affected (Wardle, 2002), including substantial changes in ecosystem productivity and the associated floral and faunal communities (Bormann and Gordon, 1989; Knops et al., 2000; Riggs et al., 2000; Schoenecker et al., 2004; Tiedemann and Berndt, 1972). Habitats and associated faunal communities can change entirely,
Herbivory-induced changes in deciduous plant communities also have serious implications for fire management. Reduction or elimination of deciduous shrub and tree recruitment in forest understories as a result of intensive ungulate herbivory, promotes in-growth of unpalatable conifers by reducing competitive interactions between conifer and deciduous tree seedlings. These conifers then serve as ladder fuels for stand-replacement fires (Hobbs, 1996; Vavra et al., 2007a,b). This condition is magnified by long-term fire suppression, which further accelerates in-growth of coniferous ladder fuels in forest understories, further increasing the frequency, intensity and extent of stand-replacement fires (Hann et al., 1997; Quigley and Arlberg, 1997; Vavra et al., 2007a,b).

The goal of our research was to document the effects of cattle, elk, and mule deer on the density and structural development of aspen, cottonwood, and willow species in western North American forests, and to evaluate the potential interactions of these herbivores with episodic disturbances of silviculture and fire. Our specific objectives were to (1) document differences in recruitment, density, height, canopy area, and canopy volume of aspen, cottonwood, and willow species under complete exclusion from ungulates versus extant herbivory by cattle, elk, and mule deer; and (2) to evaluate the potential differences caused by herbivory following intensive fuels treatment reductions, using mechanical removal and prescribed fire, versus no fuels treatment reductions. Our research took place in grand fir (Abies grandis) and Douglas-fir (Pseudotsuga menziesii) forests, which dominate much of interior western North America, and where little knowledge exists regarding ungulate herbivory-episodic disturbance interactions (Wisdom et al., 2006). While considerable research has focused on elk density, elk herbivory pressure, and predation of elk in relation to recruitment and survival of aspen and willow in western North America (Beschta and Ripple, 2010; Ripple and Beschta, 2003, 2007), this work has focused on riparian ecosystems rather than coniferous upland forests, which are the focus of our study.

2. Study area

Research was conducted at the Starkey Experimental Forest and Range (SEFR) in the Blue Mountains Ecological Province of northeast Oregon (Fig. 1), approximately 50 km southwest of La Grande, Oregon (45°12‘N, 118°3‘W). The 10,000-ha Experimental Forest and Range has been the site of long-term studies of cattle, mule deer, and elk during the past 50 years (Rowland et al., 1997; Skovlin, 1991), and is associated with one of the most extensive datasets on ungulate-environmental relations ever accumulated (Rowland et al., 1996; Wisdom, 2007). Conditions at the SEFR typify those of forest types occurring in interior western North America (Rowland et al., 1997; Wisdom, 2005). Elevations range from 1200 to 1500 m, and mean annual precipitation is approximately 400 mm, with most precipitation occurring as winter snow or spring rain, with a predictable drought during late summer-early fall (Rowland et al., 1997). Forests are composed of Douglas-fir, grand fir, and ponderosa pine (Pinus ponderosa) types (Franklin and Dymarski, 1973), intermixed with grasslands and meadows (Rowland et al., 1997; Wisdom, 2005).

Our study focused on Douglas-fir and grand fir forest stands in the SEFR. In addition to grand fir and Douglas-fir, other canopy tree species present in these stands include western larch (Larix occidentalis), ponderosa pine, lodge pole pine (Pinus contorta), and Engelmann spruce (Picea engelmannii). Common understory grass and grass-like species include Idaho fescue (Festuca idahoensis), elk
Fig. 1. Starkey Experimental Forest and Range, ungulate herbivory sites, and conceptual layout of the ungulate herbivory experiment. Three sites were fuels treated and burned, and a 1-ha ungulate exclosure constructed at each site, with a paired 1-ha plot established on the same site, but open to extant herbivory by free-ranging cattle, elk, and mule deer. Three other sites of the same vegetation type as treated sites were established as control sites, where no active silviculture had occurred for >40 years. Eighteen additional stands were fuels treated but not excluded from ungulate herbivory, and sampled using the same methods used at the experimental fuels treated and control sites.

Sedge (Carex geyeri), pinegrass (Calamagrostis rubescens), western fescue (Festuca occidentalis), Kentucky bluegrass (Poa pratensis), and annual bromes (Bromus spp.). Common shrub species include bearberry (Arctostaphylos uva-ursi), big huckleberry (Vaccinium membranaceum), grouse huckleberry (Vaccinium scoparium), rose (Rosa spp.), snowberry (Symphoricarpos albus), shinyleaf spiraea (Spiraea betulifolia lucida), and twinflower (Limneum borealis). Common forbs include lupine (Lupinus spp.), strawberry (Fragaria spp.), tall annual willowherb (Epilobium paniculatum), and western yarrow (Achillea millefolium).

SEFR has a long history of grazing by domestic and wild ungulates on the area's shared summer range (Skovlin, 1991). During the past 25 years, approximately 500 cow–calf pairs of cattle have grazed SEFR from mid-June through mid-October of each year under a deferred rotation grazing system (Rowland et al., 1997; Wisdom, 2005). During this same period, approximately 200 mule deer and 350 elk (spring population estimates) have grazed the SEFR during spring, summer, and fall (April through November) of each year (Rowland et al., 1997; Wisdom, 2005). Population densities of cattle (7.15/km²), elk (4.55/km²) and mule deer (1.95/km²) at SEFR are typical of densities on shared summer ranges in western North America (Wisdom and Thomas, 1996).

3. Materials and methods

3.1. Silvicultural treatments and exclosure establishment

During 1999 and 2000, we identified 80 grand fir and Douglas-fir stands (between 10 and 50 ha in size) in SEFR for potential application of silvicultural treatments to reduce extremely high fuel loads (Vavra et al., 2004b). The high fuel loads had developed during the late 1980s through the 1990s as a result of an extended outbreak of western spruce budworm (Choristoneura occidentalis), an insect that intensively defoliated and killed nearly all overstory grand fir and Douglas-fir in these stands (Vavra et al., 2004b; Wisdom, 2005). Of the 80 available stands, 46 were randomly selected to apply fuels reduction treatments, with the remaining 34 stands identified as control sites where no silvicultural treatments would be applied.

Silvicultural treatments were applied to the 46 stands between 2000 and 2003 (Bull et al., 2005; Vavra et al., 2004b). Treatments included mechanical thinning of overstory trees and removal of fine conifer fuels in the understory. Before treatment, fuel loads often exceeded 150 tons/ha (Bull et al., 2005). The main treatment objective was to reduce fuel loadings to <35 tons/ha, compatible with fuel loads considered unlikely to carry stand-replacement fires (Vavra et al., 2004b, 2007a). All stands were mechanically thinned with a feller-buncher to achieve the objective for overstory removal. Mechanical thinning occurred between May and October of each year. Thirty-eight of the 46 stands were then broadcast burned following mechanical thinning and removal of fuels (Bull et al., 2005). Controlled burns were implemented during the fall of the same year, or on occasion, the following year due to time and logistical constraints. See Bull et al. (2005) for additional details regarding treatment objectives and applications.

Following fuels reduction, six enclosures ranging in size from five to seven hectares were constructed on six different units to exclude all ungulates (Vavra et al., 2004b). Three of the six enclosures were constructed on fuels reduction units subjected to mechanical thinning and broadcast burning (fuels treated sites, Fig. 1). The other three enclosures were constructed on units where no fuels reduction treatments or any other silvicultural treatments had been implemented in >40 years (control sites, Fig. 1). The control sites were similar in forest structure and composition to pre-treatment conditions of the fuels treated sites. Information on each enclosure, associated management history, and assigned fuels treatment levels, are summarized in Table 1.

The six enclosures were established by constructing an 8-foot high fence that excluded all ungulates (cattle, elk, and mule deer), but allowed for other wildlife to pass under, over, or through. The enclosures were constructed in the year following fuels treatment on each site (Table 1). The size and shape of each enclosure varied with site conditions, including topography, slope, forest structure, and the shape of the forest patch, to minimize site variation within and among enclosures.

We also established a 1-ha paired plot near each enclosure that was subjected to extant herbivory by free-ranging cattle, elk, and mule deer (Fig. 1). These paired extant herbivory areas were located in the same forest types as the associated enclosures, and were subjected to the same background silvicultural treatment (fuels treated or control) as implemented for the associated enclosures (Fig. 1).

3.2. Data collection

We sampled the six enclosures during the third growing season after fence construction (Table 1) to identify, count, and measure recruitment of black cottonwood, quaking aspen and willow species. Data collection occurred from 2005 to 2007, depending on the date of enclosure construction. Surveys to locate aspen, cottonwood, and willow species were done with a field crew of 4–6 persons, who systematically searched the enclosures and paired extant herbivory areas on three separate occasions during the first growing season after enclosure construction. When encountered, all individual aspen, cottonwood, and willow were identified,
measured, given a unique ID number and tag, and geo-referenced with a global positioning system (GPS) unit (Trimble Pathfinder ProXRS, Trimble Inc., Austin, TX).

Measurements of each individual plant included height (cm), dbh (when applicable for cottonwood and aspen), canopy surface area (cm²), and canopy volume (cm³). Canopy surface area was estimated by measuring the longest perpendicular length and width measurements along the canopy plane of each plant. Canopy volume was estimated with methods described by Thorne et al. (2002), as derived from the basic ellipsoid volume formula of \( \frac{2}{3} \pi H \sqrt{A_1 A_2} \) where \( H \) = plant height, and \( A_1 \) and \( A_2 \) are perpendicular diameter measurements taken at 50% of the plant height across the plane of photosynthetically-active material. This approach overcomes concerns associated with other formulas to estimate canopy volume because it is elastic and accurately accommodates a wide range of plant shapes and sizes (Thorne et al., 2002). This method specifically accommodates a variety of plant shapes that are non-concentric about the horizontal axis and are either compressed or elongated along the vertical access, which are common characteristics of plants in the field, especially browsed plants (Thorne et al., 2002).

We used these same methods to identify, count, and measure recruitment of aspen, cottonwood, and willow present in the plot area as defined by the fuels treatment exclusion zone, and are either compressed or elongated along the vertical access, which are common characteristics of plants in the field, especially browsed plants (Thorne et al., 2002).

To further expand the inference space of our study, we complemented this dataset by using these same sampling methods to identify and estimate the density and structural development of aspen, cottonwood, and willow in 408 additional plots located within 18 of the 46 units that were fuels treated but not selected from the exclosures, allowing us to examine the individual and joint effects of ungulate herbivory with episodic disturbances (fuels treatment or control sites) on recruitment, density, and structure of aspen, cottonwood, and willow.

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Table 1

<table>
<thead>
<tr>
<th>Exclosure</th>
<th>Size (ha)</th>
<th>Fuels treatment date</th>
<th>Exclosure construction date</th>
<th>Sampling date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bally Camp</td>
<td>6.75</td>
<td>2001</td>
<td>2002</td>
<td>2005</td>
</tr>
<tr>
<td>Louis Spring</td>
<td>7.34</td>
<td>2001</td>
<td>2002</td>
<td>2005</td>
</tr>
<tr>
<td>Bee Dee</td>
<td>5.68</td>
<td>Not treated</td>
<td>2003</td>
<td>2006</td>
</tr>
<tr>
<td>Dong Prairie</td>
<td>7.26</td>
<td>Not treated</td>
<td>2003</td>
<td>2006</td>
</tr>
<tr>
<td>Kaenta Spring</td>
<td>7.30</td>
<td>Not treated</td>
<td>2004</td>
<td>2007</td>
</tr>
</tbody>
</table>

a Included partial overstory thinning, removal of fuels on forest floor followed by broadcast burn.

A similar approach was needed to examine differences in abundances between extant and ungulate excluded treatments within the fuels reduction sites. Again, few individuals of most species were found in the extant herbivory treatments, and thus we again pooled species and conducted a chi-square test to evaluate differences in the observed versus expected pooled plant abundances between the extant and ungulate excluded treatments. In addition, we calculated and graphed the densities of aspen, cottonwood, and willow species. The willow species were divided into two categories, one containing a single species, Scouler’s willow and the other group containing all of the other Salix spp. encountered, including S. boothii, S. bebbiana, S. exigua, S. lasiolepis, S. lucida, and S. monochroma. This was done because all Salix spp. except S. scouleriana were not abundant enough on their own for summary. We calculated and graphed these densities for each ungulate exclosure and paired extant herbivory area at each fuels treated and control site. In addition, we calculated and graphed densities for these species across the 18 fuels reduction treatments that had been selected for additional sampling and analysis. These summaries and graphs provided important descriptive insights of the overall patterns of density of the deciduous plant species in response to individual and joint effects of fuels treatment and ungulate herbivory.

We used permutation tests to evaluate differences in the median values of height, canopy surface area, and canopy volume of deciduous species between areas of ungulate exclusion versus areas of extant herbivory in the three fuels treated sites (Bally Camp, Louis Spring, Half Moon). One of the three fuels treated sites (Half Moon) had considerably larger plants than the other two fuels treated sites. Consequently, instead of pooling data from the three sites for analysis, we conducted two sets of permutation tests; one was conducted for Half Moon and the other with data from Louis Spring and Bally Camp combined. We conducted permutation tests for the two most abundant species, Scouler’s willow and cottonwood.

Permutation tests were conducted in JMP 9.0 with 2000 resamples (SAS Institute Inc., 2010). For each response variable (height, canopy surface area, volume), individuals were randomly assigned to one of the two treatment groups (areas of ungulate exclusion versus extant herbivory on fuel treated sites) and the medians calculated for each group. This resampling process was done 2000 times, and differences in medians between the two groups were then calculated for each of the 2000 resamples. The permutation distribution and \( P \)-values were then determined by dividing the number of instances that the permutation median differences from resampling were greater than the observed median difference between the two categories, divided by the total number of resamples.
4. Results

4.1. Abundance and density in fuels reduction and control treatments

Large differences in abundance were found between the fuels treated and control sites (Fig. 2), with a significantly greater proportion of aspen, cottonwood, and willow species found in fuels treated sites ($X^2 = 119.168$, $DF = 2$, $P < 0.0001$). These significant differences were reflected in large differences in density of each species or species group between the fuels treated sites and the control sites where no silvicultural treatments were applied (Fig. 2). In all, a total of 2143 individuals were recorded, of which 82% were found at the fuels treated sites. This resulted in an overall density of deciduous species that was >4 times greater in response to fuels reduction (844 individuals/ha) compared to control sites (19.7 individuals/ha). Cottonwood was the most abundant species at the fuels treated sites ($N = 824$), and densities ranged from 21.0 to 59.9 plants/ha (median = 41.6 plants/ha). By contrast, we found only two cottonwoods at the three control sites (range 0–2; median density = 0 plants/ha).

Salix spp. and quaking aspen followed a similar pattern and were nearly absent at the control sites, with only two Salix spp. and no aspen encountered. Densities of Scouler’s willow also were higher at the fuels reduction sites (median = 32.4 plants/ha; range = 32.4–36.6 plants/ha) than at control sites (median = 17.7 plants/ha; range = 7.7–32.4 plants/ha).

4.2. Ungulate herbivory and fuels reduction interactions

Within the fuels reduction sites, a significantly higher abundance of aspen, cottonwood, and willow were found when ungulates were excluded ($X^2 = 142.875$, $DF = 2$, $P < 0.0001$; Fig. 3). These significant differences were reflected in large differences in the density of each species or species group between fuels treated sites excluded from ungulate herbivory versus fuels treated sites subjected to extant herbivory (Fig. 3). Densities of cottonwood were >5 times higher in exclosures on fuels treated sites (122.5 stems/ha) versus the paired areas of extant herbivory (24.3 stems/ha). Density patterns for the other species followed a similar trend. Populus spp. and Salix spp. had a combined density of 211.6 stems/ha within the exclosures compared with a density of 66.1 stems/ha in areas of extant herbivory.

Results from the additional 18 fuels reduction forest stands further supported the findings from our controlled experiment that Populus spp. and Salix spp. densities are disproportionately higher following fuels reduction when ungulates are excluded. Of the 6.8 ha sampled across the 18 stands, only 85 individuals were encountered, nearly all of which were Scouler’s willow ($N = 76$). Seventeen cottonwoods and one Salix spp. were also encountered, while no aspen were found. Plant densities in these stands were also much lower than in the exclosures: density of Scouler’s willow ranged from 0 to 25 (median = 7.6/ha), followed by cottonwood (median = 0/ha; range: 0–17.1) and Salix spp. (median = 0; range: 0–1.3). Evidence of past herbivory was prevalent and 89% of plants encountered showed evidence of past ungulate browsing.

Results from our permutation tests also revealed that deciduous species subjected to extant ungulate herbivory were significantly smaller in height, canopy surface area, and canopy volume than the same species inside the ungulate exclosures (Figs. 4 and 5). Height, canopy surface area, and plant volume were significantly different for cottonwood. Cottonwood showed the greatest differences in height, while Scouler’s willow showed greatest differences in canopy surface area and volume.

5. Discussion and management implications

Our results demonstrated the benefits of episodic ground disturbances in facilitating recruitment of deciduous plant species that are highly palatable to ungulates in forests of interior western North America (Irwin and Peek, 1983). In our study, fuels reduction and burning were key episodic disturbances that facilitated recruitment of aspen, cottonwood and willow. By contrast, areas of ungulate exclusion at control sites, in the absence of episodic disturbances, resulted in little recruitment of aspen, cottonwood, or any species of willow except Scouler’s willow.

Effects of ungulate herbivory on density and structural development of aspen, cottonwood, and willow also were dependent on the prior benefits of fuels reduction and burning that facilitated recruitment and growth of these deciduous plant species, particularly in the absence of ungulate herbivory. These results support hypotheses and associated models that have described the potential synergy...
of ungulate herbivory with episodic disturbances in changing the composition and structure of aspen, cottonwood, and willow in forests of interior western North America (Vavra et al., 2007a,b; Wisdom et al., 2006). These hypotheses and associated models suggest that episodic disturbances initially favor recruitment of deciduous plants that are highly palatable to ungulates. In turn, areas of episodic disturbance become focal points for ungulate herbivory. The resulting high level of chronic ungulate herbivory then
reduces or eliminates the palatable deciduous plant species in such areas, and in the process, favors in-growth of unpalatable coniferous. In-growth of unpalatable conifers results in a substantial increase in volume of understory ladder fuels, in turn increasing the probability, intensity, and extent of stand-replacement wildfires (Vavra et al., 2007a,b). Long-term studies, spanning multiple decades of forest development, are needed to evaluate these relationships empirically (Wisdom et al., 2006).

Ungulate herbivory can dramatically affect the density and structure of aspen, cottonwood, and willow in areas of high recruitment of these species after episodic disturbance. Our results further demonstrate that reductions in density and structure of these highly nutritious plant species can occur over very short time periods, immediately following ground disturbances that facilitate recruitment of these deciduous species. It is likely that in many coniferous forests of western North America, that the absence of aspen, cottonwood, and willow species as understory species may reflect the very short time periods over which these plant species can be substantially reduced or eliminated in response to high ungulate herbivory that typically follows episodic ground disturbances.

Our results further suggest that aspen, cottonwood, and willow species are potentially common components of upland forests of grand fir and Douglas-fir communities of interior western North America. This pattern is new and surprising, given that these deciduous species are common on wetter sites, especially riparian areas, but not considered common in upland coniferous forests (Franklin and D’Antonio, 1993; Johnson and Simon, 1997). For example, other than Scouler’s willow, none of our other study species (cottonwood, aspen, other willow species) are even mentioned as components of Douglas-fir and grand fir forest in the region (Johnson and Simon, 1997). Yet cottonwoods were the most of the abundant species measured in fuels treated areas when ungulates were excluded. Additional research is needed to determine if seedlings of cottonwood, willow, and aspen continue to persist as succession continues following episodic disturbances.

Aspen, cottonwood, and willow species can exist as shrubs or trees, and our results indicate that these species have the potential to be dominant or co-dominant members of upland forest sites previously considered as strictly coniferous forest types. Recruitment and long-term survival of aspen, cottonwood, and willow species in these upland forests are likely to require a combination of episodic disturbance such as silviculture and fire to facilitate plant recruitment, followed by reductions in grazing pressure by domestic and wild ungulates between periods of episodic disturbance to facilitate long-term plant growth and survival (Romme et al., 1995; Vavra et al., 2007a). The recruitment and establishment of deciduous species of high nutritional value to ungulates is greatly influenced not only by the distribution and abundance of ungulates, but also by the size, shape, and distribution of episodic disturbances and subsequent forage areas across the landscape (Wisdom and Thomas, 1996). For example, small, isolated disturbances (e.g., small scale fuels reduction treatments) may concentrate ungulate herbivory in small areas thereby suppressing or eliminating these species from the landscape, while larger and more frequent disturbances (e.g., wildfire) may spread ungulate herbivory across the landscape, thereby increasing the likelihood that species can escape herbivory and successfully establish. Alternatively, small, fragmented patches created by smaller disturbances may create a landscape where some patches are undetected by ungulates, resulting in greater dominance of the deciduous trees species in certain areas. Thus, the management implications are potentially profound.

Further evaluation of our findings will require manipulative, controlled experiments that vary the density levels of each ungulate in relation to episodic disturbances to identify potential threshold densities of ungulates, above which the establishment and growth of aspen, cottonwood, and willow species are substantially affected, and below which the growth and survival of these deciduous species is likely (Wisdom et al., 2006). Our experiment did not evaluate the effects of different density levels of ungulates beyond complete exclusion versus extant herbivory, and thus our work could not be used to identify potential threshold densities of ungulates. Deciduous plant responses to multi-density manipulation of ungulates remains a strong and unmet need. Moreover, it remains unclear if cottonwood, aspen, and willow establishment and survival will continue as forest succession progresses, or if other environmental or biotic factors reduce survival. Such long-term experiments are needed to gain quantitative knowledge about the specific combinations of episodic ground disturbances and levels of ungulate herbivory needed to meet vegetation management goals in upland forests of interior western North America.

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References


