INFLUENCE OF HERBIVORY ON REGROWTH OF RIPARIAN SHRUBS FOLLOWING A WILDLAND FIRE

Kathleen A. Dwire, Sandra E. Ryan, Laura J. Shirley, Danna Lytjen, Nick Otting, and Mark K. Dixon

ABSTRACT: Streamside vegetation frequently regenerates faster than upland vegetation following wildland fire and contributes to the recovery of riparian and stream ecosystems. Limited data are available, however, on the post-fire growth of riparian species and the influence of herbivory on regeneration. To determine post-fire regrowth of riparian vegetation, height, crown area, crown volume, and browse levels were measured for key riparian shrub species in streamside burned and unburned plots along second-order streams in western Wyoming. Shrubs in the burned plots were subject to high levels of browse – up to 84 percent of the leaders were browsed – by native ungulates in 2002, the second post-fire year (September 2001 to September 2002). In summer 2003, the burned watershed was also grazed by livestock, resulting in increased browse levels and decreased shrub heights for several species. In the third post-fire year, September 2002 to September 2003, four of the six most common species showed no increase in crown area or crown volume, indicating that the combination of native ungulate and cattle browsing suppressed their growth. Potential impacts of grazing on post-fire recovery of stream and riparian ecosystems are discussed. (KEY TERMS: wildfire; restoration; riparian ecology; post-fire regeneration; livestock; native ungulates.)

INTRODUCTION

Streamside vegetation influences critical functions of stream and riparian ecosystems, including cycling of nutrients and organic matter and regulation of sediment dynamics (Gregory et al., 1991). Riparian vegetation provides habitat and forage to a wide array of terrestrial and aquatic biota (Naiman et al., 1993; Kauffman et al., 2001), furnishes shade, large wood, and organic matter inputs to streams (Naiman and Decamps, 1997; Gregory et al., 2003), and increases hydraulic roughness and stability of stream banks and floodplains, thus dissipating hydraulic energy (Hupp and Osterkamp, 1996). Wildland fire is one of the primary natural disturbances influencing the heterogeneity, patchiness, and diversity of terrestrial and aquatic habitat (Resh et al., 1988; Foster et al., 1998). Although the impacts of wildland fire are research and management priorities, information on the effects of wildfire on stream and riparian ecosystems has only recently become available (Gresswell, 1999; Bisson et al., 2003).

Riparian species possess a range of ecological adaptations to disturbance that facilitates survival and regeneration following fire and can thus contribute to the rapid recovery of streamside habitats (McLean, 1969; Miller, 2000; Dwire and Kauffman, 2003). For example, many riparian shrubs and trees sprout from stumps, root crowns, lignotubers, and rhizomes (Stickney, 1986; Rood et al., 1994; Gom and Rood, 1999; Ellis, 2001). In some post-fire environments, streamside vegetation has been observed to regenerate faster than vegetation in surrounding uplands, and recovery rates of aquatic biota following fire appear to depend on the regenerative condition of riparian vegetation (Minshall et al., 1997). However, few studies have quantified the natural regrowth rates of common riparian species following wildfire or the impact of herbivory on post-fire recovery of riparian shrubs.


2Respectively, Research Riparian Ecologist, Research Hydrologist/Geomorphologist, and Biological Technician, USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect Road, Fort Collins, Colorado 80526-2098; Plant Ecologists, Duckfoot Survey Company, 2710 Emerald Street, Eugene, Oregon 97403; Hydrologist, USDA Forest Service, Rocky Mountain Research Station, Fraser Experimental Forest, Box 117, Fraser, Colorado 80442 (E-mail/Dwire: kadwire@fs.fed.us).
(Noste and Bushey, 1987; Busch, 1995). Limited data have restricted the ability to make recommendations for management of burned areas (Brown and Smith, 2000), particularly regarding the protection of stream and riparian ecosystems.

In this paper, results are presented from a study assessing the post-fire regrowth of riparian shrubs compared to unburned shrubs in the Little Granite Creek watershed in western Wyoming. Study objectives were to measure growth for common riparian shrub species in the first few years following fire and to assess the influence of herbivory by native ungulates and livestock on post-fire growth of riparian shrub species.

**METHODS**

**Study Area**

The study area is in the Little Granite Creek drainage (54.6 km²; latitude 43°17’N, longitude 110°31’W), a third-order stream and contributor to the Snake River system in the Gros Ventre mountain range in western Wyoming (Figure 1, Teton County). Nearly 75 percent of the drainage is in the Gros Ventre Wilderness Area, and is administered by the Bridger-Teton National Forest. The two main tributaries of Little Granite Creek are Boulder Creek (drainage area = 20.7 km²) and the upper basin of Little Granite Creek (referred to as Upper Little Granite Creek; drainage area = 19.7 km²) (Figure 1), both second-order streams. In August 2000, approximately 75 percent of the forested area in Boulder Creek and less than 5 percent of that in Upper Little Granite Creek burned with moderate to high severity in the Boulder Creek Fire (Figure 1). The two basins are similar in size, aspect, geology, and vegetation, so the burn pattern provided a unique opportunity for a paired watershed comparison of post-fire recovery processes (Ryan et al., 2003). Although the Boulder Creek Fire was suppressed along the eastern portion to protect in-holdings of private property, it was allowed to burn naturally in the Boulder Creek watershed.

Both of the study basins face south, range in elevation from 1,950 m to 3,200 m, and had similar prefire forest cover, composed of a mixture of conifers, primarily Engelmann spruce (Picea engelmannii), subalpine fir (Abies lasiocarpa), and lodgepole pine (Pinus contorta) (Steele et al., 1983). In confined and moderately constrained reaches, the floodplain is narrow and conifers dominate the overstory, with riparian shrubs occurring along the stream banks. In the broader valley bottoms, riparian vegetation is dominated by willow species (Salix spp.) (Youngblood et al., 1985). The underlying geology is composed primarily of deformed sedimentary rocks of marine origin. Mean annual temperature is 1.0°C; mean annual precipitation is 52 cm (Western Regional Climate Center, 2004a; National Climate Data Center, 2004), and most precipitation falls as snow from November through March. Average annual snowfall between 1948 and 1999 was 340 ± 125 cm (mean ± 1 standard deviation; measured at Bondurant, Wyoming) (Western Regional Climate Center, 2004b). For the growing season (May 1 to September 30), average annual rainfall between 1988 and 2003 was 20.16 ± 6.83 cm (mean ± 1 standard deviation; measured at Bondurant, Wyoming; National Climate Data Center, 2004). The growing season rainfall was below average for the two years of the study and similar between years (2002 = 14.99 cm; 2003 = 13.72 cm; measured at Bondurant, Wyoming; National Climate Data Center, 2004).

Prior to the Boulder Creek Fire, the Little Granite Creek drainage had been grazed season long on a pasture rotation system. During the second post-fire year, 2002, the unburned Upper Little Granite Creek watershed was grazed by cattle (about 250 cow/calf pairs) from late June to late September. Although no grazing was scheduled in the Boulder Creek watershed during the first two post-fire years, 2001 and 2002, cattle occasionally moved into burned portions of Boulder Creek from Upper Little Granite Creek in summer 2002. In 2003, cattle (about 250 cow/calf pairs) grazed the Boulder Creek basin from late June to mid-September. A range rider was employed to periodically move the cattle and ensure sufficient distribution and proper range use. Despite efforts to keep livestock in upland portions of the basin, cattle were frequently observed in the valley bottom along Boulder Creek throughout the summer. For riparian sites, maximum forage (shrubs and herbaceous) utilization levels were set at 65 percent of a year’s growth; this target applied to grazing by livestock, wildlife, and recreational stock. Native ungulate herbivores are moose (Alces alces), elk (Cervus elaphus), mule deer (Odocoileus hemionus) and white-tailed deer (Odocoileus virginianus).

**Vegetation Sampling**

Streamside vegetation plots were permanently established in the Boulder Creek drainage in September 2002 and in the Upper Little Granite Creek drainage in July 2003 (Figure 1). Within the moderately to severely burned portion of the Boulder Creek...
watershed, five streamside plot locations were selected at approximately 350 m intervals along the stream riparian corridor. Due to the burn pattern of the Boulder Creek Fire, the plots were located along moderately constrained reaches where the conifer overstory had burned completely and the riparian area was fairly narrow, dominated by shrubs with a forb graminoid understory. Similarly, in the Upper Little Granite Creek drainage, three streamside plot locations were selected. Three plot locations, rather than five, were established in the unburned drainage because a limited portion of the stream riparian corridor was analogous to the sampled reaches in the Boulder Creek drainage with respect to preburn riparian vegetation and geomorphology.

At each plot location, multiple belt transects 5 m wide and perpendicular to the stream channel were permanently delineated and monumented. The transects were arranged adjacent to each other, and each transect extended from the stream edge through the riparian area. The extent of the riparian area was determined based on vegetation, fluvial surfaces and geomorphological characteristics (Youngblood et al., 1985; Crowe and Clausnitzer, 1997). The goal was to sample a minimum area of 350 m$^2$ at each plot location, so transect lengths (5 m to 25 m) and number of transects per plot (five to eight) varied, depending on the dimensions of the valley bottom (range 50 m to 100 m wide) and the extent of the riparian area. The target minimum area (350 m$^2$) was selected to assure that a representative area was sampled and to
allow comparisons with other studies conducted in forested riparian zones (Crowe and Clausnitzer, 1997).

Data were collected on all shrubs occurring within a 2 m wide strip on the upstream side of each transect center line. In the plots at Upper Little Granite Creek, the total area sampled for shrubs was approximately 700 m², and in Boulder Creek plots, a total of 900 m² was sampled. For nonclonal species (Table 1), the following data were collected for each shrub: species, location on transect (distance from stream, distance from transect center line), height, two widths (\(w_1 = \text{maximum crown diameter, and } w_2 = \text{perpendicular diameter at the shrub midpoint}\)), and an estimate of percentage of browsed stems. The distance measurements allowed relocation of individual shrubs during subsequent sampling periods. Percentage of browsed stems was determined for each plant by estimating the number of browsed leaders or stems and dividing by the total number of stems. The number of observers was limited to reduce the variability in observer measurement of browse (Hall and Max, 1999). Crown area was calculated by multiplying the two crown widths. Crown volume was calculated by multiplying the crown area by height for each shrub. For clonal species (Table 1), the area of the 2 m wide portion of the belt transect occupied by the species was recorded, in addition to five to ten randomly located height measurements. Percentage of browsed stems for clonal species was also determined by estimating the number of browsed stems and dividing by the total number of stems. To estimate shrub mortality, the location of burned shrub stumps that had not resprouted was recorded during each sampling period. In the burned plots, vegetation sampling was conducted September 17-24, 2002 (second post-fire year) and June 5-27, 2003, and September 17-24, 2003 (third post-fire year). In the unburned plots, vegetation was sampled July 15-31, 2003. For purposes of this study, a sprout was defined as any shoot arising from either the base of a shrub (Sutton and Titus, 1983) or a rhizome, a creeping, underground stem (Miller, 2000). Clonal species were those that appeared to be sprouting primarily from rhizomes and were assumed to have been derived from single individuals (Sutton and Titus, 1983) (Table 1).

**Data Analysis**

Mean percentage of browsed stems was calculated by species for the burned and unburned basins for each sampling period. Summary statistics for height, crown area, and crown volume were calculated for the six most abundant species. For data collected in the burned plots, differences among the three sampling periods were evaluated using repeated measures analysis of variance. A “plot effect” variable was designated as the subject in the analysis model to account for potential correlations among shrubs within plots. For each species in the burned plots, means for percentage of browsed stems and growth characteristics were compared between sampling dates using Tukey’s procedure and were considered significantly different if the adjusted probability of difference in least squares means was less than 0.05. Mean percentages of browsed stems in the burned and unburned plots were compared for each species using a paired t-test with a plot subject effect. Statistical analyses were performed using the SAS Mixed Procedure (SAS Institute, 2004).

**RESULTS**

In September 2002, mean percentage of browsed stems for shrubs in the burned plots ranged from zero to approximately 84 percent, depending on species (Table 2). For six of the 13 most common species, significantly higher browse levels were observed in September 2003 following combined grazing pressure from both native ungulates and cattle (Table 2). Browse levels were considerably lower for the new growth observed during the June 2003 sampling period. A comparison of mean percentage of browsed stems in the unburned plots (sampled July 2003) and burned plots (sampled June 2003) shows that browse levels were considerably lower for six species in the unburned plots (Table 2). However, browse levels were similar for black twinberry (Lonicer a involucrata), birch-leaved spiraea (Spiraea betulifolia), and russet buffalo berry (Shepherdia canadensis) in the burned and unburned plots and greater for common snowberry (Symphoricarpus canadensis) in the unburned plots in early to midsummer.

Two years following wildfire, mean heights for riparian shrubs ranged from approximately 0.2 m to more than 0.6 m, depending on species (Figure 2A). Although data were not collected in the first post-fire year, it was noted during reconnaissance that streamside shrubs had been completely burned in the Boulder Creek Fire. In the burned plots, all above ground biomass had been combusted, so the shrub stature variables sampled in September 2002 represented cumulative growth for two post-fire years (Figure 2). Mean shrub height was lower in September 2003 than in September 2002 for Booth’s willow (Salix boothii) (p < 0.01) (Figure 2A). Mean heights for serviceberry (Amelanchier alnifolia), black twinberry, russet buffalo berry, Drummond’s willow (Salix drummondiana),
### TABLE 1. Summary of Regenerative Postfire Responses and Palatability to Livestock and Native Ungulates for Riparian Shrub Species.

<table>
<thead>
<tr>
<th>Shrub Species Common Name</th>
<th>Species Regenerative Response to Fire</th>
<th>Nutritional Value</th>
<th>Palatability/References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood's Rose</td>
<td>Clonal; sprouts from rhizomes and surviving root crown.</td>
<td>Highly digestible spring and winter forage.</td>
<td>Palatability fair to good for cattle, poor for elk. May be important component of forage diet for native ungulates. References: Welch and Andrus (1977);Dittberner and Olson (1983); Fischer and Bradley (1987).</td>
</tr>
<tr>
<td>Serviceberry</td>
<td>Sprouts from surviving root crown; may also sprout from horizontal and vertical rhizomes but has not been observed following fire.</td>
<td>Palatability fair to good for cattle, poor for elk. May be important component of forage diet for native ungulates.</td>
<td>References: Sampson and Harvey (1982); Dittberner and Olson (1983); Fischer and Bradley (1987).</td>
</tr>
<tr>
<td>Booth's Willow</td>
<td>Sprouts from surviving root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Drummond's Willow</td>
<td>Sprouts from surviving root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Wolf's Willow</td>
<td>Sprouts from surviving root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Birch-Leaved Spirea</td>
<td>Clonal; sprouts from rhizomes, stem bases, and root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Black Bristly Currant</td>
<td>Sprouts from surviving root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Common Snowberry</td>
<td>Sprouts from surviving root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Russet Buffalo berry</td>
<td>Sprouts from surviving root crown or from buds on taproot.</td>
<td>Palatability considered poor; utilized primarily for livestock, fair to poor for native ungulates.</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Mountain Roswood</td>
<td>Sprouts from surviving root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Shrubby Cinquefoil</td>
<td>Sprouts from surviving root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
<tr>
<td>Snowbrush Ceanothus</td>
<td>Sprouts from surviving root crowns.</td>
<td>Palatability good for native ungulates, fair for cattle (will utilize if accessible).</td>
<td>References: Sampson and Jespersen (1963); Patten (1968); Houston (1982); Dittberner and Olson (1983); Fischer and Bradley (1987); Kovalchik et al. (1988); Carey (1995).</td>
</tr>
</tbody>
</table>
and Wolf’s willow (Salix wolffii) did not change significantly between fall sampling periods (Figure 2A). Mean crown area and volume remained about the same from September 2002 to September 2003 for four shrub species (Figure 2B, 2C). In contrast, serviceberry expanded significantly in crown area and volume (p < 0.01) over time (Figure 2B and 2C). Although Wolf’s willow showed an increase in crown area (p < 0.01) and volume (p = 0.02) from June 2003 to September 2003, the cumulative increase from September 2002 to September 2003 was not significant (Figure 2B and 2C).

In early summer 2003, nearly three years post-fire, mean shrub heights in the burned plots were about one-third to one-half as tall as those in the unburned plots, depending on species (Figure 3A). Crown area and crown volume were many orders of magnitude smaller in the burned plots (Figure 3B and 3C). To present a comparison of crown area and crown volume between the burned and unburned plots, data are shown on a natural log scale to accommodate the range of data on the same graph. Shrub density was approximately 0.37 shrubs/m² in both the burned and unburned plots, and shrub species composition was generally similar, with Booth’s willow being the most abundant species in the riparian communities of both drainages (Table 2). Differences included the lack of Wood’s rose (Rosa woodsii) but considerably more abundant common snowberry in Upper Little Granite Creek. Snowbrush ceanothus (Ceanothus velutinus) occurred as seedlings in the Boulder Creek burned plots and was not present in the unburned plots.

Although most sampled shrubs either decreased or remained constant in size in the burned plots, the occurrence of new shrubs, mostly clonal species, that appeared between the sampling periods was recorded. In September 2002, a total of 332 shrubs were located and measured in the sampled transects along Boulder Creek. In June 2003, 49 plants were added, mostly Wood’s rose (n = 22) and black bristly currant (Ribes lacustre) (n = 8). In September 2003, 58 plants were added, including Booth’s willow (n = 9), more Wood’s rose (n = 12), and mountain boxwood (Paxistima myrsinites) (n = 13). Based on counts of burned shrub stumps that occurred within the plots but did not resprout, it was estimated that approximately 10 percent of the streamside shrubs were killed in the Boulder Creek Fire.


<table>
<thead>
<tr>
<th>Shrub Species</th>
<th>Common Name</th>
<th>n</th>
<th>September 2002</th>
<th>June 2003</th>
<th>September 2003</th>
<th>n</th>
<th>July 2003</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rosa woodsii</td>
<td>Wood’s Rose</td>
<td>42</td>
<td>84 ± 7b</td>
<td>12 ± 5a</td>
<td>73 ± 4b</td>
<td>0</td>
<td>ND</td>
</tr>
<tr>
<td>Amelanchier alnifolia</td>
<td>Serviceberry</td>
<td>35</td>
<td>63 ± 6b</td>
<td>35 ± 6a,E</td>
<td>58 ± 5b</td>
<td>17</td>
<td>9 ± 4D</td>
</tr>
<tr>
<td>Salix boothii</td>
<td>Booth’s Willow</td>
<td>81</td>
<td>45 ± 4ab</td>
<td>38 ± 4a,E</td>
<td>49 ± 4b</td>
<td>64</td>
<td>12 ± 2D</td>
</tr>
<tr>
<td>Salix drummondiana</td>
<td>Drummond’s Willow</td>
<td>32</td>
<td>43 ± 6ab</td>
<td>39 ± a,E</td>
<td>58 ± 6b</td>
<td>26</td>
<td>7 ± 2D</td>
</tr>
<tr>
<td>Salix wolffii</td>
<td>Wolf’s Willow</td>
<td>10</td>
<td>35 ± 12a</td>
<td>24 ± 9a,E</td>
<td>20 ± 7a</td>
<td>20</td>
<td>7 ± 3D</td>
</tr>
<tr>
<td>Lonicera involucrata</td>
<td>Black Twinberry</td>
<td>17</td>
<td>36 ± 8b</td>
<td>7 ± 4a,D</td>
<td>86 ± 5c</td>
<td>33</td>
<td>8 ± 3D</td>
</tr>
<tr>
<td>Spiraea betulifolia</td>
<td>Birch-Leaved Spiraea</td>
<td>10</td>
<td>43 ± 9b</td>
<td>12 ± 3a,D</td>
<td>59 ± 7b</td>
<td>8</td>
<td>10 ± 6D</td>
</tr>
<tr>
<td>Ribes lacustre</td>
<td>Black Bristly Currant</td>
<td>43</td>
<td>15 ± 4a</td>
<td>14 ± 3a,E</td>
<td>38 ± 6b</td>
<td>25</td>
<td>3 ± 2D</td>
</tr>
<tr>
<td>Symphoricarpus alba</td>
<td>Common Snowberry</td>
<td>16</td>
<td>7 ± 5a</td>
<td>3 ± 3a,D</td>
<td>19 ± 6b</td>
<td>35</td>
<td>10 ± 3E</td>
</tr>
<tr>
<td>Shepherdia canadensis</td>
<td>Russet Buffalo berry</td>
<td>16</td>
<td>5 ± 2a</td>
<td>6 ± 4a,D</td>
<td>17 ± 7b</td>
<td>11</td>
<td>7 ± 3D</td>
</tr>
<tr>
<td>Paxistima myrsinites</td>
<td>Mountain Boxwood</td>
<td>30</td>
<td>3 ± 2b</td>
<td>8 ± 8c</td>
<td>0.5 ± 0.4a</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Potentilla fruticosa</td>
<td>Shrubby Cinquefoil</td>
<td>8</td>
<td>3 ± 3b</td>
<td>0.3 ± 0.3a</td>
<td>6 ± 6c</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Ceanothus velutinus</td>
<td>Snowbrush Ceanothus</td>
<td>10</td>
<td>0a</td>
<td>3 ± 3b</td>
<td>0.3 ± 13c</td>
<td>0</td>
<td>ND</td>
</tr>
</tbody>
</table>

Notes: Shubs were subject to browse by native ungulates in 2002 and 2003; in addition, cattle utilized shrubs along Upper Little Granite Creek in 2002 and along Boulder Creek in 2003. For each species in Boulder Creek, different lower case superscripts indicate significant differences according to Tukey’s procedures (α = 0.05). For some species, different upper case superscripts indicate significant differences (paired t-test, α = 0.05) in percentage of browsed stems for shrubs along Boulder Creek in June 2003 compared to Upper Little Granite Creek in July 2003. ND (no data) indicates that this species did not occur in the unburned plots.
DISCUSSION

Results indicate that growth of riparian shrubs can be limited by herbivory in the first few years following wildland fire. In the burned plots, native ungulates browsed several riparian shrubs heavily following the 2000 Boulder Creek Fire (Table 2). The most consistently browsed species were Wood's rose, serviceberry, and the three willows, which appeared to receive high relative use in winter and spring as well as through the summers of 2002 and 2003. Limited information is available on the palatability of black twinberry (Table 1); however, it was browsed heavily during summer 2003 in the burned plots (Table 2). Although birch-leaved spiraea is considered to be marginally palatable to livestock and native ungulates, it was moderately browsed (~40 to 60 percent) during the summer season in the burned plots. Utilization of these species may be increased due to higher post-fire accessibility or nutritional value. However, less palatable species, including russet buffalo berry, mountain boxwood, and shrubby cinquefoil (Potentialla fruticosa), were minimally browsed (Tables 1 and 2).

Willow species are known to be extensively utilized by elk in western Wyoming (Patten, 1968; Houston, 1982), although forage preference and browsing patterns vary seasonally (Singer et al., 1994; Allardredge et al., 2002). Willows and other shrubs may

Figure 2. Height, Crown Area, and Crown Volume (mean ± 1 standard error) for Three Sampling Periods (September 2002, June 2003, September 2003) for Six Common Riparian Shrub Species Occurring Along Boulder Creek, Wyoming. For each species, different letters denote significant differences in means; ND denotes no difference.

Species codes are: AMAL = Amelanchier alnifolia, LOIN = Lonicera involucrata, SHCA = Shepherdia canadensis, SABO = Salix boothii, SADR = Salix drummondiana, SAWO = Salix wolffi.
also provide a principal source of browse to cattle in late summer when other forage is depleted or has declined in nutritional value (Kauffman et al., 1983; Uresk and Painter, 1985). In unburned environments, high levels of herbivory by native ungulates can reduce growth and limit reproduction of *Salix* spp. (Kay and Chadde, 1992; Case and Kauffman, 1997), while the combined effects of ungulate and livestock herbivory can retard willow growth for years (Brookshire et al., 2002). Following fire, resprouting shrubs are exposed, highly visible, and stressed and thus especially vulnerable to tissue loss through herbivory (Mills, 1986; Moreno and Oechel, 1991).

Shoot growth for some willow species depends largely on the resources accumulated during the previous growing season (Wijk, 1986). Reduction in height growth by ungulate browsing can damage and potentially kill individual willow stems (Kovalchik, 1992). In a study of simulated beaver herbivory, Kindschy (1989) found that less than half of heavily browsed willow stems survived into the following year, even with subsequent protection from browsing.

---

**Figure 3.** Height, Crown Area, and Crown Volume (mean ± 1 standard error) for Six Common Riparian Shrub Species Occurring Along Boulder Creek (burned August 2000, sampled June 2003) and Upper Little Granite (unburned, sampled July 2003). Shrub height is shown on a linear scale (m), while crown area (m²) and crown volume (m³) are shown on a natural logarithmic scale.

Species codes are: AMAL = *Amelanchier alnifolia*, LOIN = *Lonicera involucrata*, SHCA = *Shepherdia canadensis*, SABO = *Salix boothii*, SADR = *Salix drummondiana*, SAWO = *Salix wolfii*.
Of the surviving stems, the following year’s regrowth was half that of unbrowsed stems. Therefore, it may take several years for heavily browsed willow stems to recover from browsing by domestic or wild ungulates. In this study, the amount of browsing on each stem or leader was not estimated, only whether a leader was browsed or not, so browse levels may have been overestimated or underestimated. However, for the species with greater than 50 percent of browsed stems, continued herbivory pressure may decrease plant survival rates (Table 2). Whereas additional time will be required before meaningful growth rates for species sampled in the Boulder Creek basin can be calculated, arrested growth (Figure 2) and high percentages of browsed stems (Table 2) suggest that decades may be required to achieve the crown area and volume of unburned shrubs (Figure 3).

Since no plots were excluded from grazers, assessment of the influence of cattle herbivory on shrubs in the burned plots was limited to comparing data for the two September sampling periods, September 2002 (native ungulates only) and September 2003 (native ungulates and cattle). Consideration of these results indicates that the percentage of browsed stems was higher in September 2003 than in September 2002 for six of the 13 most common species (Table 2) and that one willow species, Booth’s willow, had significantly lower average height in September 2003. Of the three willow species sampled in this study, Wolf’s willow was browsed the least (Table 2), and although this species did not increase in height, slight increases in crown area and volume were observed (Figure 3). Although the crown area and crown volume for serviceberry were higher in September 2003 after the introduction of cattle, this species may have adjusted to high browse levels by spreading laterally, that is, by expanding in crown area while its height remained unchanged (Figure 2). In west-central Montana, serviceberry showed considerable damage from deer browse following wildland fire (Crane et al., 1983). Other species did not increase in either height or crown area, suggesting that growth had been suppressed. It was assumed that the shrub heights observed in fall 2002 (~ 20 to 60 cm in height) represented two years of post-fire regrowth. However, during the third post-fire year September 2002 to September 2003, the stature of many of the sampled plants remained constant or declined, representing a cessation in growth, likely due to the combined herbivory pressure of native ungulates and cattle. For less palatable species such as russet buffalo berry, which was minimally browsed (Table 2) but did not increase in height, crown area, or crown volume (Figure 2), other factors may be limiting post-fire regrowth.

Most of the species sampled resprouted from root crowns that survived the Boulder Creek Fire (Table 1). However, as noted above, approximately 10 percent of the shrubs that occurred in the sampled transects had not resprouted by 2003, the third post-fire year. It is possible that these plants were killed by the fire; however, future sampling may show that some individuals require more than three years to recover from top kill caused by fire. For clonal species (Table 1), the cover and number of stems increased considerably in 2003 (Dwire, 2002, 2003, unpublished data). The clonal regeneration of snowberry and birch-leaved spiraea following fire has also been observed in Montana and Idaho (Crane et al., 1983; Stickney, 1986). Although each of the clonal species was browsed at a different level (Table 2), in general they may have been less vulnerable to herbivory than individual plants resprouting from root crowns because of their clonal nature. To date, the only shrub species that regenerated by seed was snowbrush ceanothus. Seedlings were present in several burned plots, suggesting that this fire adapted species was present in the seed bank and regenerated from seed stimulated by fire to germinate (Ruha et al., 1996; Miller, 2000). Interestingly, no resprouting snowbrush ceanothus shrubs were found in the burned plots, and this species did not occur in the unburned plots. Snowbrush ceanothus is a minor component of the shrub community in the study area, and the seed source is uncertain. However, Ceanothus spp. have been reported to germinate from seeds buried in the soil for as long as 200 to 250 years (Conard et al., 1985).

There are limitations of sampling in only one burned watershed, most notably that post-fire recovery of riparian shrubs may proceed differently in other locations. Also, since the burned plots were not protected from either native ungulate or cattle grazing, the assumption that differences in growth responses between the sampling periods (September 2002 and September 2003) were due to the addition of cattle grazing could be questioned. However, the combination of browse and growth data strongly suggests that herbivory limited early post-fire recovery of several riparian shrub species in the study area. Because snowpack and growing season rainfall were similar for the two years of the study, it is likely that growing conditions were also comparable between years.

Ecological functions provided by riparian vegetation — including stream shading, provision of avian nesting habitat, beneficial effects to bank stability and channel form, and organic matter inputs to adjacent streams — will not be resumed until the crown area and volume of riparian shrubs increases. Several studies have shown that browsing by native ungulates can curtail shrub growth following fire (Howe,
1981; Mills, 1986; Moreno and Oechel, 1991). For several riparian species in the Boulder Creek watershed, the addition of cattle likely contributed to higher percentages of browsed stems and arrested growth in the third growing season following wildland fire. Further, the number of resprouting riparian shrubs continued to increase with time in the sampled transects, indicating that some plants required several post-fire years to regenerate. In order to expedite the recovery of stream and riparian habitat, it is suggested that livestock be excluded from recently burned areas until key riparian shrub species achieve a target height or other designated growth characteristic (Kauffman et al., 1997; Beschta et al., 2004).

ACKNOWLEDGMENTS

The authors appreciate the careful reviews provided by Rudy King, Carolyn Hull Seig, and Marc Coles-Ritchie and comments on previous drafts by Robert Beschta, Richard Shulz, and Richard Lowrance. The authors are grateful to the U.S. Department of Agriculture Forest Service, Bridger-Teton National Forest – particularly Wes Smith – for providing field housing and general logistical support. The authors thank Dustin Burger, Audra McGinnis, Karla Clark, Jessica Baker, Zach Crosby, Doug Woody, and Todd Creamer for assistance in the field, and Dusti Lawson for assistance with literature searches. Thanks to Rudy King for statistical advice and assistance and to Joyce VanDeWater for drafting the study area map. Funding was provided by the National Fire Plan awarded to Catherine Parks, Pacific Northwest Research Station, LaGrande, Oregon, the Bridger-Teton National Forest, and the Rocky Mountain Research Station RWU-4352.

LITERATURE CITED


Influence of Herbivory on Regrowth of Riparian Shrub Following a Wildland Fire


