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Post-fire response of riparian vegetation in a heavily browsed environment

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ABSTRACT

Severe wildfires infrequently occur in large heterogeneous riparian valleys. Riparian areas may affect fire behavior and the pattern of burning due to saturated soils and patchy fuels that may have high moisture content in live and dead stems. We examined the effects of a severe fire on the dominant riparian vegetation: thin-leaf alder, river birch and willow, in a broad riparian valley in Rocky Mountain National Park, CO, USA. We mapped the canopy stem mortality and basal resprouting of 4507 first year post fire and 643 second year post fire individuals that had been the dominant woody canopy. To examine the effect of herbivory on resprouting willow stems, we established a paired experiment with 22 willows exclosed in cages to prevent browsing and 22 uncaged control plants. Aerial seed rain sticky traps were established on transects throughout the study area and pre-fire seed rain density was compared with post-fire seed rain densities.

Fire effects on willow were severe, with 91% of individuals having complete canopy loss. Fifty-one percent of thin-leaf alder individuals and 71% of river birch individuals also had complete canopy loss. Seventy-four percent of river birch, 45% of willow and 35% of thin-leaf alder resprouted from the base in the first summer post fire. In the second year post fire, 84% of river birch, 62% of thin-leaf alder and 55% of willow had resprouted. Willows inside exclosures had greater biomass at the end of the growing season compared with willows outside exclosures. Summer browsing resulted in significantly lower willow biomass compared with exclosed plants and the additive effect of summer and winter browsing resulted in control plants having 64% reduction in biomass. Post-fire aerial seed rain was 90% lower than pre-fire densities.

Fire dramatically altered the riparian vegetation. Willow seed rain was nearly eliminated because most stems were killed by fire. Resprouting woody riparian vegetation was prevalent however, ungulate browsing of the resprouting willow stems could limit the regrowth of a tall willow riparian overstory.

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1. Introduction

Fire is a critical and widespread disturbance in western North America, particularly in regions dominated by conifer forests. There is debate on whether fires in riparian areas burn more (Everett et al., 2003) or less severely in riparian areas compared with adjacent uplands (Olson and Agee, 2005; Skinner, 2003) and this is likely related to elevation, valley width and channel size (Van de Water and North, 2010). In addition, there is evidence that the overstory and understory burn severities are not coupled, where overstory vegetation may burn more severely, while understory vegetation burns less severely (Halofsky and Hibbs, 2008). The heterogeneity of riparian areas likely affect fire behavior and pattern of burning due to saturated soils and fuels with high moisture content (Dwire and Kauffman, 2003). Research on fire effects to riparian vegetation has focused on coniferous overstory dominated stream systems (Halofsky and Hibbs, 2009) or narrow valleys (Jackson and Sullivan, 2009). Fire may have different behavior in wide valleys with dense riparian shrub thickets and no coniferous overstory. Land use history, including grazing and invasive species management, can strongly influence fire properties in a riparian area (Busch and Smith, 1995; Dwire and Kauffman, 2003).

Riparian plant species are adapted to many types of disturbance, including flooding and debris flows (Naiman and Décamps, 1997), browsing (Bilyeu et al., 2008; Johnston et al., 2007), and periodic fire (Dwire and Kauffman, 2003; Pettit and

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Naiman, 2007). In the Rocky Mountains, riparian vegetation is typically dominated by species of willow (*Salix* spp.), river birch (*Betula fontinalis* Sargent), and thin-leaf alder (*Alnus incana* ssp. *tenuifolia* (Nutt.) Breitung). Willows can reproduce sexually from aerially dispersed seed and asexually from adventitious rooting of stem fragments (Karrenberg et al., 2002). After browsing or stem cutting, willows can resprout from the root crown (Baker et al., 2005). In addition, thin-leaf alder and river birch are known to resprout after disturbances (Dwire and Kauffman, 2003). Willow and river birch dominate many mountain stream riparian zones and produce aments on the previous year stems. Seed release is timed to occur just after peak stream flow when the availability of suitable germination sites is highest (Gage and Cooper, 2005; Karrenberg et al., 2002; Merritt and Wohl, 2002). Willow do not form a soil seed bank, while river birch and thin-leaf alder form short-lived seed banks (Karrenberg and Suter, 2003; Karrenberg et al., 2002). Resprouting may reestablish existing plants, but new colonization will not occur without a suitable seed source.

Riparian areas dominated by willows provide critical habitat for ungulates in the Rocky Mountains. Elk (*Cervus canadensis* Erxleben) eat willow stems and winter browsing can stimulate stem growth the following summer (Johnston et al., 2007; Marshall et al., 2013). Ungulate browsing in combination with other disturbances, such as beaver (*Castor canadensis* Linnaeus) harvesting (Baker et al., 2005) and sapsucker (*Sphyrapicus nuchalis* Baird) activity (Kaczynski et al., 2014) can result in the conversion of tall willow communities into short willow communities, detrimentally affecting passerine birds and beavers that rely on tall willows (Olechnowski and Debinski, 2008; Wolf et al., 2007). Burned willow stands may have abundant post fire resprouting (Halofsky and Hibbs, 2009), however these young stems may be browsed by ungulates, converting them into a short willow community (Dwire et al., 2006).

We examined the effects of a severe fire on riparian vegetation in a heavily browsed montane valley. We observed fire effects on the dominant shrub species and performed experiments to assess the limitations on willow recovery, addressing the following questions: 1. Does fire differentially affect the survival of thin-leaf alder, willow and river birch? 2. What is the effect of herbivory on post fire resprouting willow stems? 3. What are the effects of fire on willow seed dispersal?

2. Materials and methods

2.1. Study area

Rocky Mountain National Park (RMNP), Colorado, USA, is 108,000 ha in area between 2240 and 4345 m elevation. Our study occurred in Moraine Park, a 228 ha broad glacial valley averaging 2480 m in elevation. The Big Thompson River flows east in a series of channels through the valley and reconnect into a single thread channel at the eastern edge of the valley. Stream flow is snowmelt driven, with peak flow occurring in late May or early June. The nearest climate station is on the eastern edge of RMNP in Estes Park (2347 m). The average minimum temperature is 9.2 °C and occurs in January, and the average maximum temperature is 25.7 °C, occurring in July. The mean annual precipitation is 35 cm, with most falling as snow (Western Regional Climate Center, 2012).

The heterogeneous valley is comprised of wet and dry meadows and streamside riparian zones dominated by native and non-native grasses and sedges, herbaceous dicots, and shrubs. The most abundant shrubs are Geyer's willow (*Salix geyeriana* Andersson), mountain willow (*Salix monticola* Bebb), diamondleaf willow (*Salix planifolia* Pursh), thin-leaf alder (*A. incana* ssp. *tenuifolia*), and river birch (*B. fontinalis*). Pre-fire, dense, tall willows dominated the western portion of Moraine Park, while the central and eastern areas supported short, heavily browsed woody vegetation (Gage and Cooper, 2005). River birch was most common in the southern and western ends of the valley (Peinetti et al., 2002). Over the past two decades, tall willow stems have been reduced in height and the remaining dead stems were taller than live foliage producing large fuel loads. Sixty-seven percent of willow stems along a transect in Moraine Park were dead (Kaczynski, unpublished data). Ungulate browsing has reduced willow canopy cover, plant volume and seed rain density (Gage and Cooper, 2005). RMNP resource managers installed three large exclosures each greater than 8 hectares beginning in 2008 to exclude browsing and facilitate the persistence and recovery of browsed willows.

Most fires in RMNP have occurred in late summer and fall (Sibold et al., 2006). The Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) woodlands surrounding Moraine Park last burned approximately 140 years ago, but the fire was predominantly of low severity (Ehle and Baker, 2003). It is uncertain when the riparian vegetation in Moraine Park last burned prior to this fire. October 9, 2012 was unseasonably warm and dry when a lightning strike started the Fern Lake fire (Williamson, unpublished report on Fern Lake fire). For several weeks the fire burned in remote upland conifer forests dominated by lodgepole pine (*Pinus contorta* Douglas), Engelmann spruce (*Picea engelmannii* Parry ex Engl.) and subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) west of Moraine Park. On December 1, wind velocities reached 113 km/h and drove the fire rapidly to the east where it burned through Moraine Park, which was snow free. The fire grew to 1341 ha and RMNP firefighters ignited a back burn at the east end of Moraine Park to prevent the fire from threatening the town of Estes Park (Williamson, unpublished report on Fern Lake fire).

A burned area reflectance classification (BARC) of post fire vegetation condition was made by the Remote Sensing Applications Center of the US Forest Service. BARC maps are created by comparing reflectance values from LandSat short wave infrared bands 7 and 4 of pre-fire and post-fire remotely sensed imagery (Key and Benson, 2006). Larger changes in reflectance indicate a more severe burn. The data are used to identify four classes of burn severity: high, moderate, low and unburned. We used the BARC map to gain an understanding of the severity of the burn through the riparian area. We compared the post-fire response of woody plants in each of the burn severity classes.

2.2. Post fire response of riparian woody plant species

In August 2013, eight months post fire, we identified and mapped 4507 woody riparian plants throughout the entire burned area (~200 ha) of Moraine Park using a Trimble GeoXT GPS unit. This sample represents approximately 75% of the woody shrubs and included 2461 river birch, 555 thin-leaf alder, and 1491 willow. At locations with high plant density, one random individual was sampled. Plants were sampled inside and outside of exclosures. We identified and recorded the species for each individual (when sufficient stem and bark remained for identification), percent of canopy killed and the presence of resprouting stems. If all stems were dead, the plant was recorded as 100% canopy loss. A total of 658 individuals were unidentifiable because the bark was completely burned off and basal resprouts were not produced. We assigned species identities to unknown individuals using a pre-fire vegetation map of Moraine Park created by Peinetti et al. (2002). In addition, we mapped a random subset of these burned individuals ($N = 643$) throughout the same study area in summer 2014, the second season post fire. We collected data on species of willow if possible, whether the plant was browsed, and if resprouting stems were still present on 354 river birch, 93 thin-leaf alder and 189 willow individuals in summer 2014. The mapped shrubs and trees were overlaid on the BARC burn severity map.

We examined the spatial relationships of live vs. dead and resprouting vs. non-resprouting plants one season post fire using Ripley's *K* function to determine if plants with similar responses were clustered. Ripley's *K* is a second order analysis that examines the variance of pairs of points at different distances from one another (Haase, 1995). This analysis considers all combinations of pairs of points and compares the number of observed pairs at all distances to a random spatial distribution of points (Haase, 1995). We accounted for boundary effects using a weighted edge correction method (Haase, 1995). Analyses were done in ArcGIS 10.1 (ESRI Redlands, CA). We used logistic regression to examine the relationship of live vs. dead and resprouting vs. non-resprouting plants with respect to burn severity class. Logistic regressions were computed using a generalized linear model framework in R v3.0.2 (R Core Development Team). We used likelihood ratio testing to compare the fitted model to the null model and compared misclassification rate between the null (majority classification) and fitted model to determine goodness of fit.

2.3. Effect of ungulate browsing on willow resprouts

We used an experimental approach to examine the effect of ungulate browsing on post-fire willow basal resprouting. We established 22, 0.6 m^3 cylindrical exclosures made from 2.5 cm chickenwire, each surrounding one burned willow, and compared the number of resprouting stems, growing season stem length, summer and winter browsing, and overall biomass with 22 paired uncaged, control willows. All willows were randomly selected and at the onset of the experiment were charred stumps lacking live stems. We installed two motion sensor infrared cameras to identify large ungulate browsers in the vicinity of our study plants.

We quantified the production and the impact of both summer and winter browsing on the 44 experimental plants using methods of Bilyeu et al. (2007). Production and summer browsing were assessed in late August, 2013 and winter browsing was assessed in late March, 2014. Due to flooding in September, 2013, three cages were displaced and plants subjected to winter browsing. This resulted in an adjusted sample size for analyses of 19 unbrowsed and 22 browsed plants. We measured the height of the tallest resprouting stem on each plant and counted the total number of stems per plant. We also measured the diameter and length of a subset of stems on each plant following methods from Bilyeu et al. (2007). We built regression models relating stem length, diameter and biomass that we used to estimate biomass remaining and biomass removed by browsing on each plant (Bilyeu et al., 2007). In March, 2014 we could not differentiate stems browsed in the summer from stems browsed in the winter, so we measured all browsed stems. To calculate winter biomass browsed, we subtracted the biomass browsed in summer from the biomass browsed calculated after the March, 2014 sampling. Summer biomass remaining, summer biomass removed by browsers, winter biomass removed by browsers, height, and the number of resprouting stems were compared between caged and control plants using ANOVA with a random effect for plant. We calculated unbiased effect sizes using ω^2 and adjusted for unequal sample sizes post-winter browsing using Tukey's HSD. We used the lme4 (Bates et al., 2010) and lmerTest (Kuznetsova et al., 2013) packages in R v.3.02 (R Core Development Team) for all analyses.

2.4. Willow seed production

We measured aerial seed rain using 900 cm^2 sticky traps attached to t-posts approximately one meter above and parallel to the ground surface. Thirty seed rain traps were installed along transects established by Gage and Cooper (2005) in Moraine Park. Traps had adhesive Tanglefoot™ applied weekly. Seeds were counted weekly from late May through mid-July, 2013 to capture the entire seed rain period. Due to sampling limitations, we could not reestablish all seed rain traps from 2000, therefore interpolation allowed us to compare areas which did not have traps in 2013 to areas in 2000. The inverse distance weighted metric in ArcGIS 10.1 (ESRI Redlands, CA) was used to interpolate seed rain values between traps. Using the interpolated surface, aerial seed rain in 2013 was compared with seed rain in 2000 (Gage and Cooper, 2005).

3. Results

3.1. Burned shrub response

Ninety-one percent of the burned area in Moraine Park was classified as low severity or unburned/very low severity according to the Fern Lake BARC map (Table 1). Of the 4507 shrub individuals mapped 4300 had burned. Ninety-one percent of willow, 71% of river birch, and 51% of thin-leaf alder individuals had 100% canopy loss regardless of burn severity class (Fig. 1). Seventy-four percent of river birch individuals resprouted from the base during the first post-fire summer, compared with 45% of willow and 35% of thin-leaf alder.

There was an increase in the proportion of plants that resprouted in the second year post fire: 84% of river birch, 62% of thin-leaf alder and 55% of willow. We could identify 55% of willow individuals as seven species: *S. planifolia*, *Salix bebbiana*, *S. monticola*, *Salix drummondiana*, *S. geyeriana*, *Salix ligulifolia*, and *Salix lasiandra*. Forty-five percent of willow could not be identified to species due to lack of resprouting stems or extensive stem browsing. Browsing of resprouting stems in Moraine Park the second year post fire occurred on 1% of thin-leaf alder, 5% of river birch and 35% of willow. Browsing was highest on *S. bebbiana*, with 50% of plants exhibiting browsing of current year stems.

Individuals with similar responses to the fire were clustered at both small (<100 m) and large (>800 m) spatial scales. Live plants were clustered with live plants and plants exhibiting 100% canopy loss were clustered with other similar plants (Fig. 2).

The logistic model using burn severity class to predict whether a plant was alive or sustained 100% canopy loss was significantly different than the null model (chi square: 63.181, $p < 0.001$, $df = 4$), but did not reduce the misclassification rate (null: 24%, fitted: 24%). Burn severity class was a significant predictor for resprouting (chi square: 14.547, $p = 0.005$, $df = 4$), with higher probability of resprouting for plants in areas with a lower burn severity class. The model reduced the misclassification rate (null: 60%, fitted: 40%).

3.2. Effect of ungulate browsing on resprouting willow stems

Resprouting willow stems inside exclosures grew to an average of 88 cm (*se* = 3 cm), and were 57% taller than control stems

Table 1
Percent of burned area in Moraine Park, Rocky Mountain National Park, as determined from the burned area reflectance classification (BARC) map of burn severity. In addition, % of individuals in each severity class that had 100% loss of canopy and % of burned individuals that resprouted.

Burn severity level	% of burn	% individuals with total canopy loss	% burned individuals resprouting
Unburned/very low severity	42.6	69	63
Low severity	47.8	79	64
Moderate severity	9.3	84	53
High severity	<1	92	67

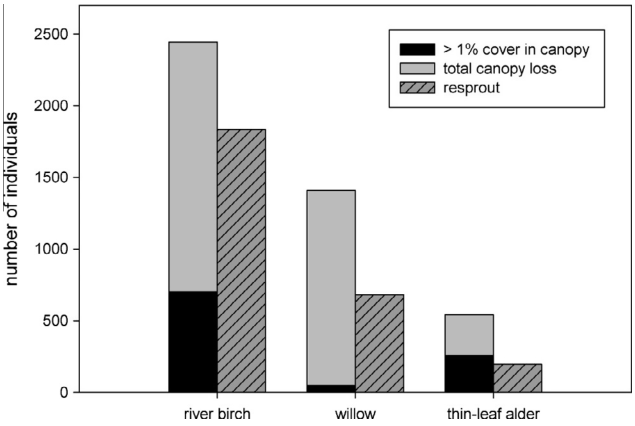

Fig. 1. Number of burned individuals with total canopy loss (100% canopy loss) and those with >1% canopy cover remaining. These are paired with the number of individuals resprouting. River birch = *Betula fontinalis*; willow = *Salix* spp.; thin-leaf alder = *Alnus incana* ssp. *tenuifolia*.

outside exclosures, which averaged 56 cm tall ($se = 4$ cm; $t = 22.997$, $p < 0.001$) (Fig. 3). Stems inside exclosures had 58% greater volume (inside: 0.41 m^3, $se = 0.05$) than stems outside that averaged 0.26 m^3 ($se = 0.07$; $t = 2.035$, $p = 0.0314$), and less biomass removed during the 2013 growing season, averaging 5 g ($se = 1.53$) compared with 14 g ($se = 3.84$) removed on control plants. Exclosed plants had 76% more biomass at the end of the 2013 growing season (averaging 66 g, $se = 9.1$) than control plants (37 g, $se = 9.5$; $t = 2.845$, $\omega^2 = 0.08$, $p = 0.0097$). Control plants had more stems than exclosed plants, but the difference was not significant ($t = 1.282$, $p = 0.214$). Our camera data indicated that the primary browsers of resprouting willow stems were elk, however deer (*Odocoileus hemionus* Rafinesque) were also present.

In spring 2014 exclosed willow stems averaged 85 cm long ($se = 3.4$ cm) and were significantly taller than control stems that averaged 47 cm ($se = 3.5$ cm; $t = 23.77$, $p < 0.001$) (Fig. 3). Unexclosed control stems lost an average of nine cm of length due to winter browsing, but were not significantly shorter than at the end of the growing season ($t = -1.79$, $p = 0.08$). Control plants had 24 times more biomass removed per plant in winter than exclosed plants, some of which were browsed because their stems grew out of the cages ($t = 2.94$, $\omega^2 = 0.15$, $p = 0.005$). The cumulative effects of summer and winter browsing resulted in exclosed plants retaining 93% of their biomass, while control plants retained 46%.

3.3. Willow seed production

The maximum seed rain density in the study area was 33 seeds/m^2 in the unburned, eastern side of the valley (Fig. 4). In 2000 measured seed rain density was as high as 7500 seeds/m^2 (Gage and Cooper, 2005). In 2013 zero willow seeds were captured on many

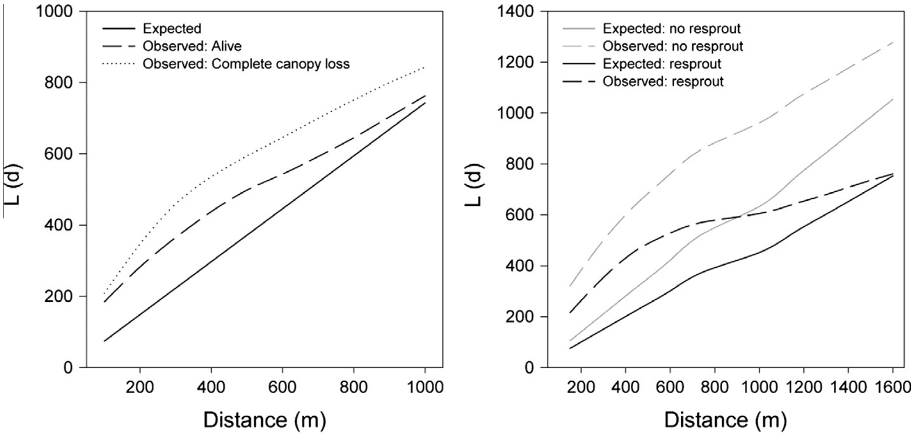

Fig. 2. Ripley's K function graphs. The *y*-axis, $L(d)$, takes into account the size of the study area and the number of point pairs at any given distance (d). Solid lines depict the expected value at any distance given a random distribution of points. Dashed lines are what we observed. In both data sets, the $L(d)$ we observed was greater than expected, resulting in clustered patterns of individuals.

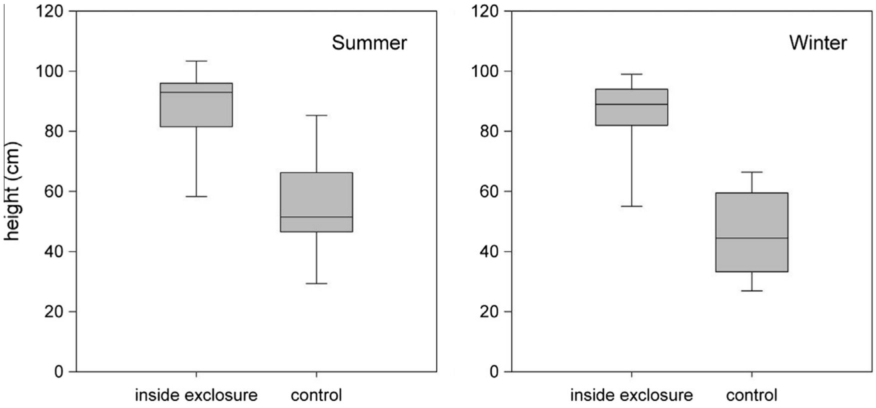

Fig. 3. Comparison of heights (in cm) between exclosed and control treatments. Summer heights were measured at the end of the growing season and winter heights were measured in early spring.

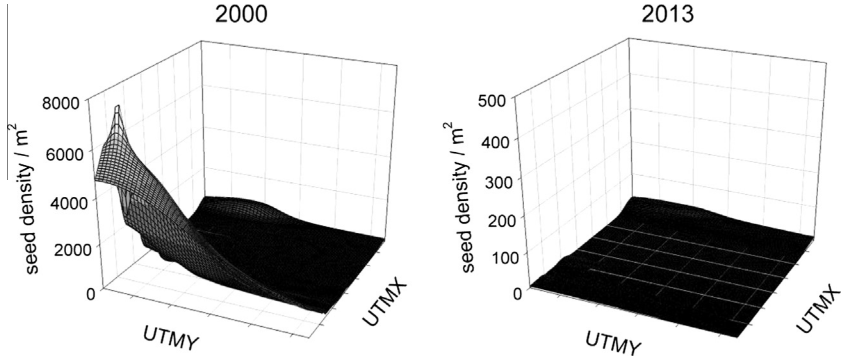

Fig. 4. Comparison of willow seed density per m^2 between 2000 and 2013 across Moraine Park. Scales on z axis (seed density/m^2) are different for the two years.

traps, and across the study area more than 90% of the landscape had less than 10% of the 2000 seed rain density (Fig. 4). In 2000, the western part of Moraine Park was the primary seed source for the area (Gage and Cooper, 2005). This area produced relatively few seeds in 2013 because it was largely burned. The central part of Moraine Park produced very few seeds in both 2000 and 2013 (Fig. 4).

4. Discussion and conclusions

Fire significantly altered woody riparian vegetation. The pattern of burning in the Moraine Park ecosystem created clusters of plants with above-ground survival and others with 100% canopy death. In the first growing season, 74% percent of river birch plants resprouted, compared with 45% of willow and 35% of thin-leaf alder. Willow seed rain density was reduced by more than 90% across the study area. Ungulate browsing removed approximately 50% of first summer resprouting stem biomass. Cumulative effects of summer and winter browsing resulted in a 64% reduction in biomass. All of these factors will affect the long term recovery of willows.

4.1. Regeneration of woody plants

Many species of willow resprout after fire (Dwire et al., 2006; Halofsky and Hibbs, 2009; Kobziar and McBride, 2006; MacCracken et al., 1990), however little is known about the response of river birch and thin-leaf alder to burning. We found in our second year sampling that at least 50% of river birch, willow and thin-leaf alder individuals resprouted. In addition to the high percentage of willows that sprouted from the root crown, Kobziar and McBride (2006) found that post-fire in the Sierra Nevada, CA there was high seedling recruitment. After the 1988 Yellowstone National Park fires, willow seedlings established on bare soil farther from the stream channels than was expected (Wolf et al., 2007). Patches of bare soil were abundant throughout Moraine Park and might have been suitable substrate for seedling establishment, however the extremely low seed rain density likely limited establishment.

First year unexclosed resprouting willow stems were 32 cm shorter with significantly less biomass than exclosed plants due to summer browsing. The additive effect of summer and winter browsing resulted in unexclosed plants having more than 50% of their biomass removed. The influence of winter browsing by elk on Rocky Mountain region willow communities is well known (Alstad et al., 1999; Peinetti et al., 2002; Zeigenfuss et al., 2002) and here we demonstrate that summer browsing by elk independently has a large impact on willow growth. Our second year data demonstrated that throughout the study area willows were disproportionately affected by summer browsing compared with alder and river birch.

In heavily browsed portions of Moraine Park little willow seed production occurred, with most seeds from a single large stand of tall willows on the western edge of the valley (Gage and Cooper, 2005). However, the fire studied here resulted in the majority of willows sustaining 100% canopy loss. Willow stems taller than three meters can escape browsing (Keigley et al., 2002) and are more likely to produce seeds. Burned willows whose only stems are basal resprouts are easily browsed by elk. Dwire et al. (2006) demonstrated that three years after a fire in Wyoming, four of the six common willow species did not show an increase in crown area or crown volume, due to browsing by both wild and domestic ungulates.

4.2. Conclusions and implications for management

This study, addressing one fire, is applicable to many riparian sites throughout the Rocky Mountains and western United States. The dominant tall shrub vegetation studied in Moraine Park is common in river valleys throughout western North America. Fire is an uncommon disturbance in these large mountain valleys, but where wild or domestic ungulate browsing is intense long-term changes in riparian communities may result. Browsing may be at a higher intensity in Rocky Mountain National Park compared to other regions, but recognizing the role browsing plays post-fire is important for management. Ungulate exclosures can protect a proportion of resprouting stems and newly established seedlings from browsing. This will allow greater seed production as stems mature. However, in areas with high browsing pressure, vegetation outside of the exclosures will be maintained at a short stature reducing habitat value for many wildlife species including birds and beaver.

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