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Impacts of Novel Fire and Herbivory Regimes on Snow-Water

Resources and Resilience of Aspen Forests

Jordan Daniel Maxwell

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

Impacts of Novel Fire and Herbivory Regimes on Snow-Water
Resources and Resilience of Aspen Forests

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Doctor of Philosophy

Human activities and expansion have created novel disturbance patterns across Earth's landscapes. Disturbance is an ecological interruption after which ecosystem recovery or transition into a new state can occur, affecting biodiversity, ecosystem functioning, and the availability of ecosystem services. Fire and herbivory are two of the most widespread forces of disturbance which shape ecosystems globally. In temperate forest ecosystems, fire affects forest composition, which influences the diversity and resilience of ecosystems (chapters 1 and 2) and forest canopy structure, which is important to snowpack accumulation and the availability of water resources (chapters 3 and 4). In chapter one, the effects of conifer competition, which occurs under fire suppression, and ungulate herbivory on aspen regeneration and recruitment were examined. It was found that conifer competition, and ungulate herbivory both drastically reduced successful aspen regeneration and recruitment and had a larger effect than climatic or topographical variables. In chapter two, this understanding was used to investigate mechanical and fire interventions by the National Forest Service in a mixed aspen conifer forest experiencing fire suppression and heavy ungulate herbivory. Untreated forests failed to recruit aspen suckers successfully due to conifer competition and ungulate browsing. Fire treatments were successful in restoring aspen habitat, but mechanical treatments failed due to heavy ungulate use, despite the treatment eliciting high sucker densities. In chapter three, fire severity was found to have important implications for snowpack accumulation and snow-water content in alpine forests. High burn severity, which is projected to become more common under future climatic conditions, led to deeper and denser snowpack possibly buffering the effects of water loss in a warmer climate. In chapter four, the interaction between topography and vegetation in burned forest conditions was evaluated. It was found that topographical aspect likely mediates the effect of vegetation on snowpack and may have an opposite effect on snow accumulation and melt on north vs south facing aspects. A synthesis of studies from different regions further supports the idea that this relationship between fire and snow is heavily dependent on latitude, elevation, and slope angle. Together, these findings demonstrate that the resilience and persistence of aspen forest ecosystems in changing disturbance regimes depend on complex interactions among disturbance type, disturbance severity, landscape position, and hydrology. These interactions should be integrated into management strategies to protect ecosystems and ensure ecosystem services for growing human populations in the western United States.

Keywords: disturbance ecology, succession, ecological function, snow, aspen, ungulate herbivory

ACKNOWLEDGEMENTS

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CHAPTER 1

Altered Fire and Herbivory Patterns:
Effects of Conifer Competition and Ungulate Herbivory on Aspen Forests

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ABSTRACT

Human activities are altering patterns of ungulate herbivory and wildfire regimes at a global scale with large potential impacts on plant community succession and ecosystem resilience. Aspen (*Populus tremuloides*) is a keystone species, which co-exists with conifer species across temperate forests in North America. Aspen sucker regeneration, which is the foundation of aspen-conifer forests succession, is often selected as a food source by multiple ungulate species. Using a region-wide exclosure network across a broad gradient of aspen-conifer overstory abundance, we empirically tested the effects of ungulate herbivory and conifer competition (that increases with fire suppression), on the regeneration and recruitment of aspen forests over a four-year period. We found that ungulate herbivory and increasing abundance of overstory conifers substantially reduced aspen regeneration and recruitment success. The average height of aspen suckers exposed to ungulate herbivory was 72% shorter than aspen suckers in fenced plots and resulted in 24% less recruitment. There was a 9% decrease in aspen recruitment with every 20% increase in overstory conifer density. Aspen suckers were most vulnerable to herbivory at 70 cm height, corresponding with the head height of ungulates, with the probability of herbivory decreasing under 50 cm or above 90 cm. Steep slope angles and higher winter precipitation increased aspen regeneration and recruitment success. Reduction in aspen recruitment in response to ungulate herbivory and competition by conifers may result in loss of biodiversity,

altered forest function, and loss of key ecosystem services because of the important role that aspen plays in facilitating forest succession and biodiversity.

INTRODUCTION

Plant community assembly, which occurs during secondary succession, is greatly influenced by patterns of disturbance as well as competitive and facilitative plant interactions (Augustine and McNaughton 1998; Goetz et al. 2007). Human activities are altering the intensity and timing of disturbance, which may alter patterns of plant community succession (Turner 2010). Two examples of changing disturbance regimes affecting forest ecosystems globally are ungulate herbivory and wildfire (Weisberg and Bugmann 2003; Bowman et al. 2009; Kauffman et al. 2010, Westerling 2016). Many studies have characterized the individual impacts of ungulate herbivory or changing fire regimes on forest structure (Kaye et al. 2005; Midoko-Iponga et al. 2005; Augustine and Derner 2014), however, fewer studies have characterized how these disturbances overlap and interact in influencing plant community regeneration and succession.

Ungulate herbivores play a pivotal role in the assembly and succession of plant communities (Augustine and McNaughton 1998). Ungulate movement and foraging behaviors vary in both space and time, making their effect on plant community development difficult to predict (Kauffman et al. 2010; Seager et al. 2013; Rhodes et al. 2017b). Introduction of domestic ungulates (Spear and Chown 2009) and changes in the abundance of native ungulate populations (Painter et al. 2015) have altered the intensity and timing of herbivory across earth's ecosystems (Romme et al. 1995; Weisberg and Bugmann 2003; Rhodes and St Clair 2018). Plants have several strategies to deal with ungulate herbivores including: tolerating herbivory through compensatory growth (strategy of tolerance), avoiding herbivory by quickly attaining heights

above the browse line (strategy of escape), or defense traits including thorns or secondary compounds to reduce herbivory (strategy of resistance) (Mauricio et al. 1997; Harding et al. 2009; Wan et al. 2014b)

Wildfire strongly influences patterns of plant community succession (Franklin et al. 2005, Johnstone et al. 2010; Smith et al. 2011) and plant-herbivore interactions (Wan et al. 2014a; Smith et al. 2016). Wildfires are also changing in frequency, size, and severity across earth's ecosystems (Bowman et al. 2009). Fire suppression by humans lengthens fire return intervals to which can lead to altered successional patterns in plant community development (Gallant et al. 2003; Calder and St Clair 2012; Adams 2013). Even small changes in disturbance patterns of fire and herbivory can "tip the scales" of competitive or facilitative relationships among plant species leading to large vegetative state changes (Augustine and McNaughton 1998; Adams 2013; Painter et al. 2015).

Aspen spp. (*Populus tremuloides* Michx. and *Populus tremula* L.) initiate secondary forest succession and plant community assembly following disturbance in multiple forest types of North America and Eurasia (Myking et al. 2011; Seager et al. 2013; St Clair et al. 2013). Aspen forests in North America provide an ideal study system to characterize the impacts of multiple and changing disturbance regimes on forest regeneration and succession because they are browsed by ungulate herbivores (Seager et al. 2013; Rhodes and Clair 2018), and coexist in a well-defined successional relationship with conifer species (Gallant et al. 2003; Calder et al. 2011). Aspen is typically among the first woody plants to regenerate following disturbance and its presence facilitates the germination and establishment of conifer species (Buck and St Clair 2014) that over time leads to conifer dominance in mid to late stages of forest succession (St. Clair et al. 2013). However, facilitation in the early life of conifers by aspen (Buck and St Clair

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2014), can lead to competitive exclusion of aspen by conifers leading to high aspen mortality in mid to late stages of forest succession when fire is suppressed (Calder and St Clair 2012). Studies of fire history suggest that fire suppression by humans (Gallant et al. 2003; Wagner et al. 2006) is lengthening fire return intervals in aspen forests of western North America resulting in increasing abundance of conifer in the forest overstory (Strand et al. 2009). Further complicating these challenges, aspen is heavily browsed by elk (*Cervus canadensis*), cattle (*Bos taurus*), deer (*Cervidae*), and sheep (*Ovis aries*) (Beck and Peek 2005), which can lead to excessive levels of herbivory pressure (Lindroth and St Clair 2013; Rhodes et al. 2017b).

Both climate and topography influence the health and persistence of aspen stands on the landscape (Rehfeldt et al. 2009; Worrall et al. 2015) and their competitive ability and resistance to herbivory (Rhodes et al. 2017a). Projected changes in climate are predicted to drive aspen both higher in elevation and north in latitude (Rehfeldt et al. 2009). We predict that abiotic stressors such as drought, which can be amplified by slope, aspect, or elevation, will likely play a role in the ability of aspen to regenerate and establish in the face of increasing pressure from conifer competition and ungulate herbivory.

Here we use a region-wide exclosure network established over a broad aspen-conifer successional gradient (variability in the overstory aspen: conifer ratio) across three national forests to evaluate the main and interactive effects of ungulate herbivory and increasing conifer abundance (as fire is suppressed). We also examine the influence of variation in physiographic conditions across our study sites to examine the effects of climate and topography on aspen regeneration and recruitment success. We hypothesized that: 1) aspen growth and recruitment would be reduced by ungulate herbivory through removal of apical meristems; 2) shorter aspen suckers would be more likely to be browsed by ungulates than taller aspen as they are more

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easily accessible; 3) aspen growth would be negatively correlated with conifer abundance likely due to resource competition; 4) physiographic conditions including aspect, slope, elevation, length of growing season, and winter precipitation would have modifying effects on aspen regeneration success by altering growing conditions or susceptibility to browsing by ungulates.

MATERIALS AND METHODS

Study Area

The study was established across nine different mountain ranges and three National Forests (Manti-LaSal, Fishlake and Dixie) in south and central Utah (Figure 1-1). Sites were selected across the study area using 1m remotely sensed NAIP (National Agricultural Imagery Program) imagery to locate transitions between aspen dominant and mixed aspen-conifer stands. Three hundred sites were randomly selected from aspen and mixed aspen-conifer forests across the three national forests. Seventy experimental blocks were selected from these 300 potential sites after on-ground observations were made of each site showing an aspen dominant stand adjacent to a mixed-aspen conifer stand. Elevation across the experimental plots ranged from 2400m to 3200m. Dominant overstory species present included quaking aspen (*Populus tremuloides*), douglas fir (*Psuedotsuga menzesii*), subalpine fir (*Abies lasiocarpa*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), blue spruce (*Picea pungens*), and Engelmann spruce (*Picea engelmannii*). Precipitation across our study sites ranged from 42 to 83 cm annually with 11 to 32 cm coming from December through March primarily as snow (Anon). Average annual temperatures ranged from 3.5°C to 7.3°C and average length of growing season defined by days with minimum temperatures above 0°C ranged from 141 days to 209 days a year.

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Experimental Design

Each of the 70 experimental blocks consisted of four plots, a fenced and unfenced plot in both an aspen dominant stand and an adjacent mixed aspen-conifer stand. All treatment plots within a block were located within 300 meters of each other and had similar elevation, aspect, and slope. The experimental blocks were established in May of 2013 (Figure 1-1). Fenced and unfenced plots (2.5 x 2.5 meters) were randomly assigned to include an area that was identified as having at least three aspen suckers less than 100 cm tall. Fencing for the ungulate exclusion plots was two meters tall and made from a wire mesh that prevented ungulate access.

Relative overstory density for aspen and conifer was determined as the percent of live stems greater than 10 cm DBH (diameter at breast height) using a point quarter method (Pollard 1971). Points were evenly spaced along a 50-meter transect which was placed in a random direction through each aspen and mixed aspen-conifer stand. Aspen and conifer species were the only trees present in any of the plots. In the fall of 2016, after four growing seasons, sites were again visited, and all regenerating aspen were measured and recorded for height, total number of leaders, and number of meristems removed by ungulate browsers. An aspen sucker was considered successfully recruited when it reached 150 cm or taller. Ungulate pellet groupings which consisted of cattle (*Bos taurus*), elk (*Cervis candensis*), mule deer (*Odocoileus hemionus*), and sheep (*Ovis aries*) were also collected and identified along the same 50 meter transects and used to help quantify ungulate use across the study sites.

Topographical and Climatic Data

Because of the large and diverse study area, several explanatory variables in addition to the fencing treatments and forest composition were acquired to help explain variation in aspen forest regeneration. These included: elevation, aspect, slope, length of growing season, average winter precipitation, and mean annual temperature. Elevation, aspect, and slope were calculated in ArcMap 10.3 using a 10x10-meter NED (National Elevation Dataset) acquired from the USGS (United States Geological Survey). Slope was calculated in degrees and aspect was calculated as a measure of northness by converting degree aspect to radians and taking the sine. This rendered a value ranging from 1 (0° north) to -1 (180° south) which was more compatible with a linear model. Length of growing season, mean winter precipitation, and mean annual temperature were determined using PRISM data from Oregon State University (Team 2004). Length of growing season was calculated using the number of days that minimum temperatures did not fall below 0°C. It was taken at a 4km resolution and averaged between the four years the study took place (2013-2016). Average winter precipitation was calculated by summing the monthly winter precipitation for the months of December–March and then averaging those values over the years 2012-2015. Mean annual temperatures were averaged between 2012 and 2015 for each plot.

Statistical Analysis

Linear mixed-effects models were used to test for differences in aspen sucker height, recruitment, and density using percent conifer overstory, fencing, topographical aspect and slope, length of growing season, winter precipitation, and elevation as fixed effects, and block as a random effect. Because of the experimental nature of this study, model selection was limited to one model including our hypotheses comparing the main effects of percent conifer and fencing

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along with all other variables mentioned above, and another model including the interaction between percent conifer and fencing along with all other variables. The optimal model between these two was selected using AICc. A mixed effects model allowed us to evaluate the influence of fixed effects while also accounting for spatial autocorrelation or non-independence between blocks (Dormann et al. 2007; Harrison et al. 2018). Data exploration was followed using the steps provided in Zuur et al. (2010) to examine whether model assumptions were met. The assumptions of normality and homogeneity of variance were evaluated graphically using residuals and were found to be satisfied. Mean annual temperature and length of growing season were collinear at 0.9. To prevent problems with multicollinearity, mean annual temperature was excluded in favor of length of growing season in the models. No other variables included in the models were correlated above a correlation coefficient of |0.6|. Pellet counts were excluded from the mixed effects models as they had no relevance to ungulate excluded plots. A one-way ANOVA test was used to test if ungulate pellet counts differed in number between treatments. To reduce the total number of parameters, all variables used in the mixed effects model were made continuous except for the two-level categorical value fenced or unfenced. In order to understand the effect of sucker height on removal of apical meristems, we used a general additive model of aspen browse as a function of aspen height. For this model we used individual aspen suckers across all unfenced plots totaling just over 5500 aspen suckers. All statistical analysis were performed using program R software (Team 2017) and packages: lme4 (Wood and Scheipl 2014), lmertest (Kuznetsova et al. 2015), and mertools (Knowles and Frederick 2016).

RESULTS

Aspen Sucker Height

The model including the interaction between fenced and percent conifer was excluded in favor of the general global model listed in Table 1-1 for sucker height, recruitment, and density. Ungulate herbivory over four growing seasons led to significant decreases in height of aspen suckers (Figure 1-2, Figure 1-3). Average height of aspen suckers exposed to ungulate herbivory was 72% shorter than aspen suckers in fenced plots (Figure 1-2, Table 1-1). Evaluation of aspen suckers with all leaders browsed show that suckers were most vulnerable to herbivory near 70 cm, and that the probability of browse decreased under 50 cm or above 90 cm (Figure 1-4).

Aspen sucker height and recruitment decreased linearly with increasing overstory conifer abundance (Figure 1-2). Average aspen sucker height was 6.6 cm shorter within a plot for every 20% increase in overstory conifer relative density (Figure 1-2; Table 1-1). Increased slope angles contributed to increased average aspen height with nearly 1 cm increase in growth for every degree of increase in slope angle (Table 1-1) ($p = 0.059$). The range of slope was 3°-28° showing a difference of nearly 25 cm growth between sites based on slope angle alone (Table 1-1). Winter precipitation was positively correlated with aspen sucker height (Table 1-1) ($p = 0.096$). No other topographic or climatic variables were significant below $\alpha = 0.1$ (Table 1-1).

The effects of both herbivory and conifer competition on average sucker height were additive and did not reveal any thresholds or interactions (Figure 1-2). Aspen regeneration success was greatest in pure aspen stands with ungulates excluded (Figure 1-3 panel a). Aspen regeneration was weakest in the presence of both herbivory and abundant overstory conifer with nearly one-third of such plots experiencing a decrease in average height after four growing seasons (Figure 1-3 panel d). A separate ANOVA analysis revealed that the average number of ungulate (cow,

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elk, deer, sheep) pellets between pure aspen stands and mixed aspen/conifer stands did not differ significantly (p = 0.66).

Aspen Sucker Recruitment

The exclusion of herbivores over four growing seasons also led to an increased number of aspen suckers recruited (>1.5m; Figure 1-2). Plots with ungulates excluded had 24% more aspen suckers reaching 150 cm or greater in height during the study period than plots with ungulates present (Table 1-1).

Lower overstory conifer abundance also increased aspen recruitment (Figure 1-2) with a 9% increase in aspen recruitment for every 20% decrease in overstory conifer density (Table 1-1). Browse data collected from over 5500 suckers when treatments were put into place in the spring of 2013 showed that aspen were much less likely to be browsed after reaching 150 cm in height (Figure 1-4). Steeper slopes increased aspen recruitment (p = <0.01) (Table 1-1). Physiographic conditions including aspect, length of growing season, winter precipitation, and elevation were not significant in predicting aspen recruitment (Table 1-1).

Aspen Sucker Density

While the model for sucker density accounted for 54% of the variation there were no strong predictors of aspen suckering density. Neither the presence of herbivory nor proportion of conifers in the overstory were reliable predictors of aspen sucker density (Figure 1-2; Table 1-1). Aspect, slope, length of growing season, winter precipitation, and elevation were not significant in predicting aspen sucker density (Table 1-1).

DISCUSSION

Human driven changes in ungulate populations and fire regimes are creating novel disturbance patterns that can alter plant community development and succession (Weisberg and Bugmann 2003; Calder et al. 2011; St Clair et al. 2013). This study documents that concomitant increases in conifer abundance, that occur under longer fire return intervals and greater ungulate browse pressure, alter patterns of aspen forest regeneration and recruitment. Our first hypothesis that aspen growth and recruitment would be hindered by ungulate herbivory was strongly supported (Figure 1-2; Table 1-1). Our second hypothesis that shorter aspen suckers would be more likely to be browsed by ungulates than taller aspen as they are more easily accessible was only partially supported with intermediate suckers being browsed more heavily than either short or tall suckers (Figure 1-4). There was strong evidence for our third hypothesis that aspen growth would be negatively correlated with greater conifer abundance, and that it is likely driven by resource competition (Calder et al. 2011). The negative effects of ungulate herbivory and conifer abundance on aspen growth and recruitment were additive, indicating there was not a strong interaction between them (Figure 1-2) (Hanley 1982; Augustine and McNaughton 1998; Launchbaugh and Howery 2005). Our fourth hypothesis that physiographic conditions would have modifying impacts on aspen regeneration and recruitment success was only partially supported, with slope and winter precipitation being the only physiographic variables that significantly impacted aspen success (Table 1-1).

Ungulate Effects on Aspen Regeneration and Recruitment

Aspen regeneration responses to the experimental exclusion of ungulates in this study were consistent with previous findings showing a significant decrease in sucker growth and

regeneration success due to ungulate herbivory (Smith et al. 2016; Rhodes et al. 2017b). Our data demonstrate that in the presence of ungulates nearly 20% of plots in aspen stands and 30% of plots in mixed-aspen conifer stands had negative growth rates over the four growing seasons (Figure 1-3). Negative growth rates of aspen in the presence of ungulate herbivory suggests that herbivory can significantly alter forest development and succession (Figure 1-3). While aspen regeneration during post-fire conditions has been investigated (Smith et al. 2016) this study reflects natural regeneration and recruitment in intermediate to late stages of aspen-conifer forests succession, which is the most common condition that aspen forests exist. During this mid-successional condition, vertical growth rates of suckers decrease and the amount of time suckers are exposed to ungulate herbivory is increased (Figure 1-3) (Smith et al. 2016). While meristem removal by ungulates reduced vertical growth rates, it has also shown to increase allocation of resources to defense chemistry expression (Rhodes et al. 2017a), which would further slow vertical escape (Lindroth and St Clair 2013). Ungulate herbivory can increase aspen suckering (Frey et al. 2003), reduce sucker density (Bork and others 2013), or as we see in this study have no impact on aspen density (Table 1-1). It is possible that an observation period longer than four growing seasons would show a clearer effect of ungulate browsing on sucker density.

Aspen suckers were most vulnerable to browsing by ungulates around 70 cm in height with the probability of being browsed decreasing below 50 cm and above 90 cm (Figure 1-4). We believe this pattern may be related to energy conservation; aspen suckers below 50 cm and above 90 cm would require most ungulates to either reach higher or stretch lower to browse, thus increasing energy output of foraging (Hanley 1982; Augustine and McNaughton 1998). This data, which was collected with over 5500 aspen suckers, helps to discover thresholds of aspen

recruitment at which aspens are tall enough that herbivory events that would remove apical meristems decreases (Figure 1-4).

Vertical growth of aspen decreased with increasing conifer abundance and ungulate herbivory, but there was no significant interaction between the two, indicating that the fencing (herbivory) effect remained consistent (parallel trend lines) as overstory conifer abundance increased (Figure 1-2). Furthermore, pellet counts did not differ significantly in aspen versus mixed stands in this study, suggesting ungulates spent similar amounts of time in both aspen and mixed treatments. These findings are consistent with another study showing that the impacts of ungulate herbivory on aspen growth did not differ strongly between aspen dominant and mixed aspen-conifer stands (Rogers and Mittanck 2014). Other studies have shown that ungulates prefer to browse in aspen stands due to higher biomass and nutrition of understory species (Beck and Peek 2005). Both aspen and conifer forests provide different opportunities for ungulates to maximize energy and nutritional acquisition, regulate temperature, avoid predation, and forage on species other than aspen (Hanley 1982; Gervasi et al. 2013; Long et al. 2014). More research is needed to better identify how overstory stand composition influences ungulate behavior and subsequently impacts on aspen regeneration.

Aspen Regeneration and Conifer Competition

Results showed a significant decrease in aspen height and recruitment with increased percentages of overstory conifer abundance, which occurs as forest succession progresses in the absence of disturbance (Figure 1-2). Calder et al. (2011), demonstrated two mechanisms for competition between aspen and conifer in late successional mixed-aspen conifer forests: 1) conifers greatly reduce light availability and thus photosynthetic rates for growing aspen suckers

which are generally shade intolerant; and 2) soils exposed to sustained conifer dominance showed significant decreases in macronutrients and organic matter which was correlated with reductions in growth, photosynthetic rates and defense chemistry expression. Long-term changes in soil chemistry under prolonged conifer dominance have been documented by Buck and St. Clair (2012). While the effects of overstory conifer dominance also appeared to be additive, these changes in soil chemistry under sustained conifer dominance or active fire suppression, over time, could create a "tipping point" that favors conifers and discourages aspen regeneration even after fire returns (Gallant et al. 2003, Smith and Smith 2005, Smith et al. 2011, Adams 2013).

   Decreases in photosynthetic rates of aspen suckers under a conifer dominated canopy may also decrease aspen's capacity to tolerate, resist, or escape herbivory. Aspens produce secondary compounds including phenolic glycosides and condensed tannins to deter insect or ungulate herbivores (Wooley et al. 2008) and protect against microbial pathogens (Holeski et al. 2009). Calder (2011) also showed that decreased photosynthetic rates from light reduction and changes in soil chemistry due to high overstory conifer abundance significantly reduced the growth and production of secondary defense compounds. Lower levels of secondary defense compounds would increase aspens palatability and vulnerability to chronic levels of ungulate herbivory (lower resistance) (Wooley et al. 2008), while decreased photosynthetic rates in conifer dominated forests would slow growth rates leading to longer exposure to ungulate herbivory (Villalba et al. 2014). When herbivory is chronic, aspen root systems are in danger of depleting carbohydrates, which reduces aspen defenses and increase stand mortality (Lindroth and St Clair 2013).

Climate and Physiographic Effects

Climate extremes are one of the main drivers of aspen decline in the western United States (Rehfeldt et al. 2009; Worrall et al. 2012). However, in this study climatic conditions had a surprisingly small effect on aspen height, recruitment, and density (Table 1-1). Winter precipitation would be expected to increase aspen regeneration as increased snowpack can lead to increased soil moisture (Mysterud and Austrheim 2014). Other studies have shown winter precipitation to be an important predictor of aspen height and recruitment with similar precipitation ranges (10-31 cm) from December-February (Rhodes et al. 2017b), but it was only a moderate predictor of aspen growth in this study (Table 1-1). The length of growing season also did not show any influence on successful aspen regeneration in this study (Table 1-1). While few studies have directly observed the effect of growing season length on aspen regeneration, longer growing seasons are known to increase photosynthetic periods and reduce mortality rates due to late spring frost (Frey et al. 2004) and increase net primary production at high elevations (Berdanier and Klein 2011).

Slope was the most important topographical variable in predicting aspen recruitment potential (Table 1-1). The 3° to 28° range of slope between sites showed a difference of nearly 25 cm growth between sites based on slope angle alone (Table 1-1). Other studies have also shown increased aspen regeneration and recruitment on steep slopes and suspect that increased slope angles help to deter ungulates by increasing foraging costs (Hanley 1982; Rogers and Mittanck 2014; Rhodes et al. 2017b). This study gives additional evidence that steep slopes may reduce herbivory rates and provide a refuge where aspen are more likely to recruit successfully (Table 1-1). Winter precipitation had a weak positive effect on aspen sucker growth. Other physiographic variables tested in our study showed minimal effects on aspen regeneration

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success (Tables 1-1) despite other studies showing that elevation, aspect, or length of growing season can influence aspen regeneration success (Binkley 2008; Worrall et al. 2013; Rogers and Mittanck 2014, Rhodes et al. 2017b). This may suggest that herbivory and conifer abundance had particularly dominant effects on aspen regeneration success in our study system.

Conclusions and Implications

Because aspen is a keystone species supporting much of the biodiversity in less diverse conifer dominated systems (Hollenbeck and Ripple 2007), the loss of aspen vigor and recruitment success will likely have detrimental effects upon species that it supports as well as implications for ecosystem resilience (Seager et al. 2013; Tilman et al. 2014). Other ecosystem services which aspen provide, such as increased water yields (LaMalfa and Ryle 2008) and soil productivity (Buck and St Clair 2012), will also likely be negatively affected. Because aspen plays a fundamentally important role in facilitating conifer species (Calder and St Clair 2012, Buck and St Clair 2014) that drives mixed aspen conifer forest succession, the loss of aspen due to competitive exclusion by conifers with fire suppression (Smith et al. 2011; Calder and St Clair 2012) or chronic ungulate browsing (Rhodes et al. 2017a; Rhodes and Clair 2018) can result in forest regeneration failure (St Clair et al. 2013; Rhodes and Clair 2018).

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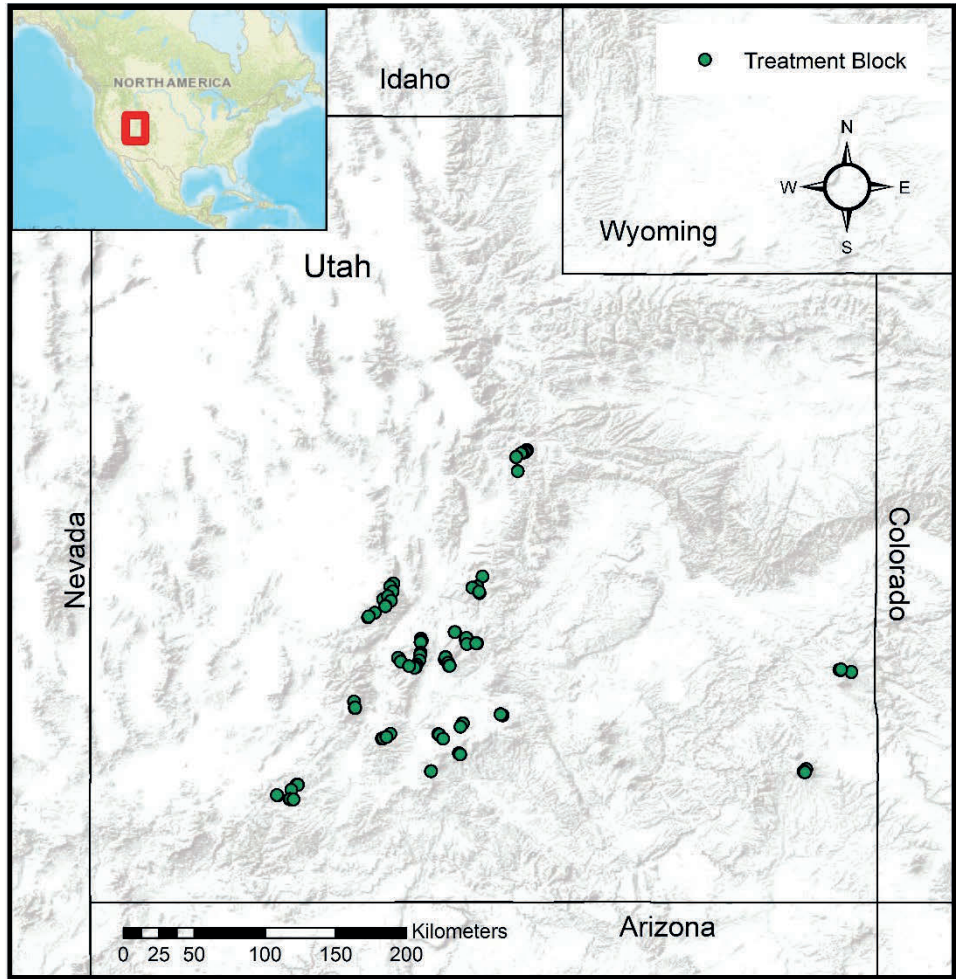
Figure 1-1: Site locations for seventy treatment blocks across south and central Utah.
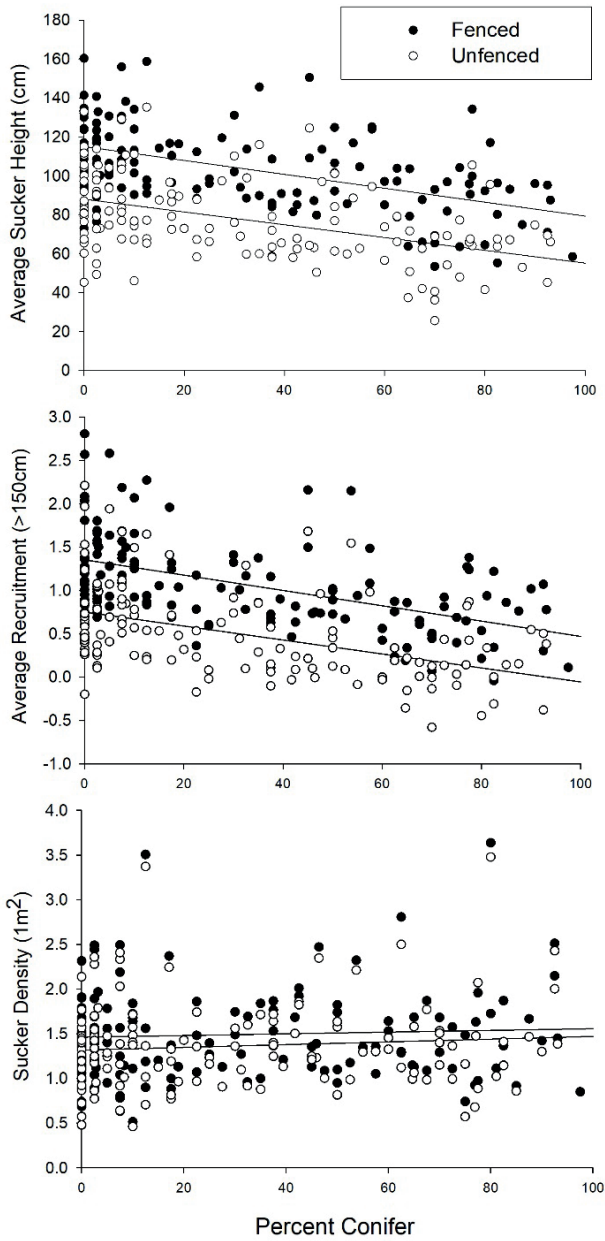
Figure 1-2: Bivariate scatterplots showing predicted height, recruitment and density of aspen suckers in both fenced and unfenced plots across gradients of overstory conifer abundance.
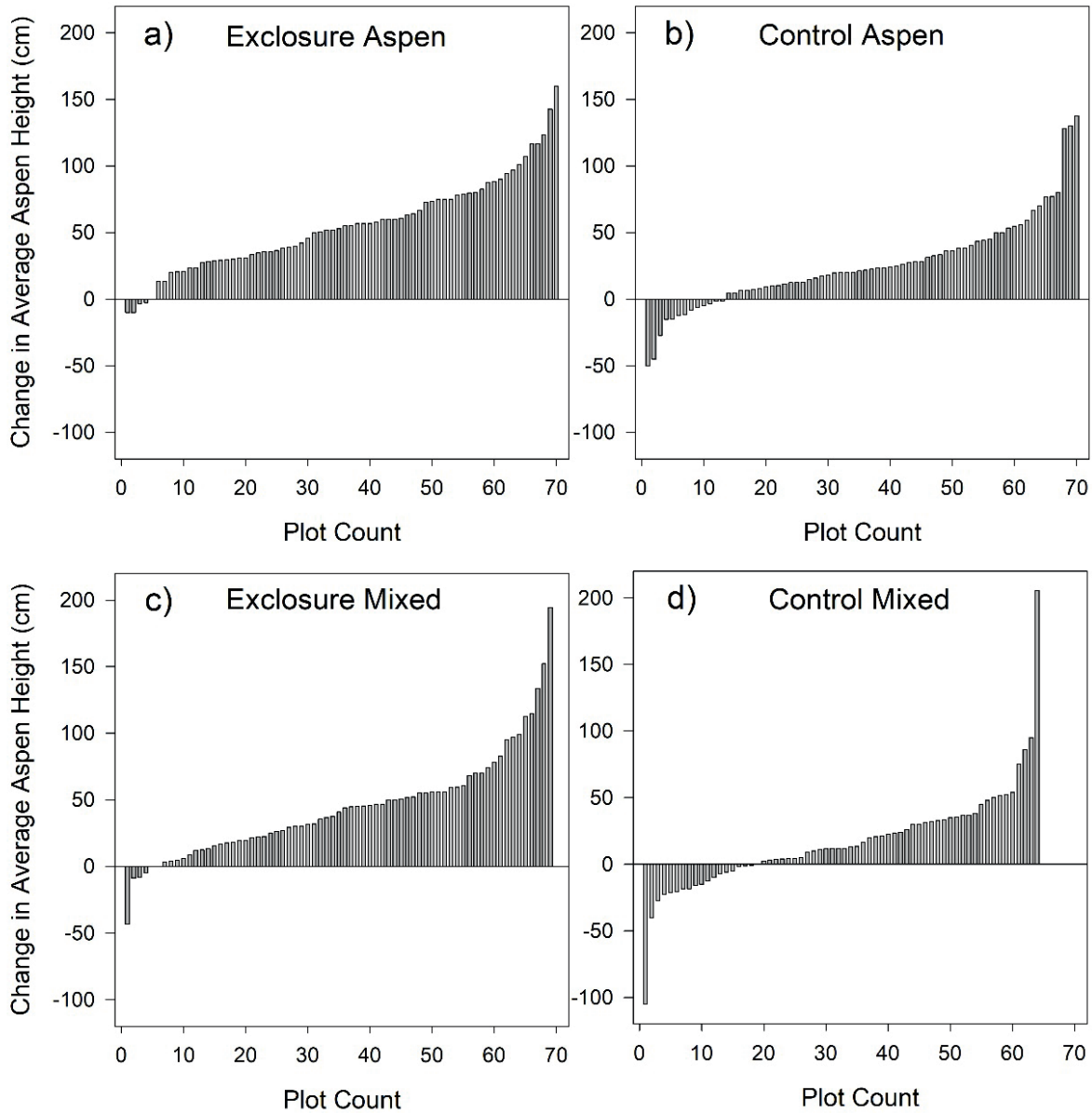
Figure 1-3: Raw data showing the difference in average aspen sucker height per plot after four growing seasons (spring 2013-fall 2016) grouped by treatment type. Here we see both the main and interactive effects of herbivory and conifer competition on aspen growth. We see the strongest aspen regeneration in exclosed aspen plots (top left) and the weakest aspen regeneration in plots with both herbivory and conifer competition present (bottom right). When both conifers and herbivory were present, nearly 1/3 of plots had negative growth rates.
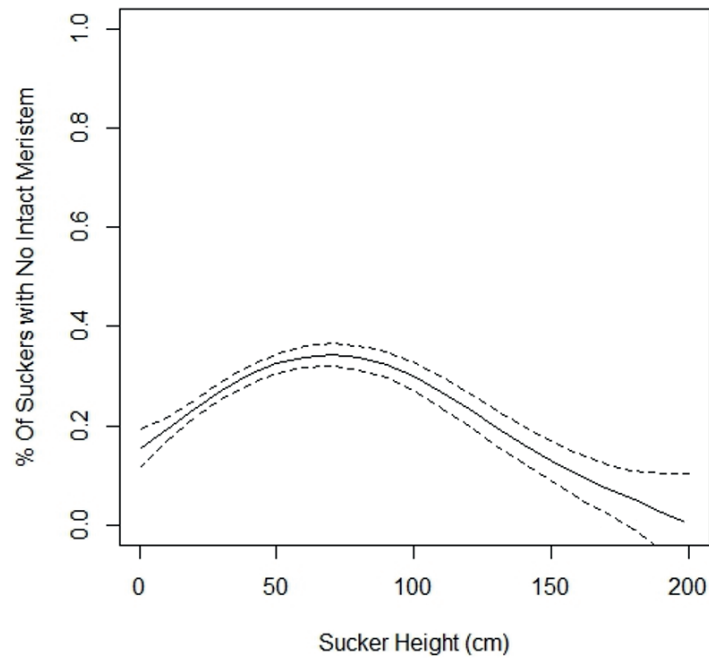
Figure 1-4: Mean percent of aspen suckers browsed with no intact leaders showing preference of sucker height for ungulate herbivores at intermediates heights. Error lines show the standard error of the proportion of suckers with all leaders browsed.

Table 1-1: Fixed effects in the linear mixed effects model for the height, recruitment, and density of aspen suckers after four growing seasons. Block was included in each model as a random effect. Models are illustrated graphically in Figure 1-2. (** = p-value < 0.1).

Fixed Effects	Beta Estimate ± SE	Statistic	p - value	Full model
Average Sucker Height (cm)		*T-value*		R^2
Percent Conifer	-0.33 ± 0.1	-3.4	<0.0001**	**0.41**
Fenced	26.6 ± 5.4	-4.9	<0.0001**	
South Aspect	2.7 ± 5.4	0.5	0.62	
Slope	1.04 ± 0.55	1.9	0.059*	
Length of Growing Season	0.30 ± 0.022	1.4	0.17	
Winter Precipitation	1.4 ± 0.8	1.7	0.096*	
Elevation	-0.02 ± 0.02	-0.7	0.51	
Recruitment (>150cm)				
Percent Conifer	-0.008 ± 0.003	-3.1	0.002**	**0.37**
Fenced	0.59 ± 0.14	-4.1	<0.0001**	
South Aspect	-0.02 ± 0.1	-0.1	0.89	
Slope	0.04 ± 0.01	3.0	0.003**	
Length of Growing Season	-0.003 ± 0.006	-0.4	0.67	
Winter Precipitation	0.03 ± 0.02	1.3	0.2	
Elevation	-0.0004 ± 0.0007	1.3	0.2	
Density (suckers/m^2)				
Percent Conifer	0.004 ± 0.006	0.6	0.97	**0.54**
Fenced	0.58 ± 0.36	-1.6	0.52	
South Aspect	-0.55 ± 0.41	-1.3	0.11	
Slope	-0.03 ± 0.04	-0.8	0.19	
Length of Growing Season	-0.02 ± 0.02	-1.2	0.22	
Winter Precipitation	0.1 ± 0.07	1.5	0.14	
Elevation	0.003 ± 0.002	1.3	0.18	

CHAPTER 2

Can Mechanical Thinning of Forests Provide the Same Ecosystem Benefits as Fire?

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ABSTRACT

Disturbances such as fire and herbivory strongly influence plant community composition, succession, and function; however, novel disturbance regimes related to human activities are changing the timing, extent, and severity of these disturbances. Billions of dollars are spent annually on management interventions designed to restore ecosystem functionality, often with little knowledge about their effectiveness. We investigate the effects of prescribed fire and mechanical thinning of overstory trees, aimed at increasing resilience and restoring competitive balance to mixed aspen-conifer forests that have experienced long periods without fire, and excessive ungulate herbivory pressure that can result in forest regeneration failure. We found that untreated aspen-conifer stands were not recruiting aspen for overstory replacement due to high conifer abundance and chronic ungulate herbivory. Prescribed fire released aspen from conifer competition and increased stand tolerance and resistance to ungulate herbivory by stimulating synchronous aspen regeneration, growth, and defense chemistry expression. Mechanical treatments also stimulated a strong regeneration response, but this benefit was counteracted by increased ungulate activity. Specifically, deer and cattle were attracted to mechanically thinned stands which increased herbivory pressure and resulted in growth trends indicative of forest recruitment failure. These results suggest that: 1) where and when possible, fire be given high priority as a restoration treatment option for late-succession aspen-conifer forest stands, and that

treatments be sufficiently large for the aspen regeneration response to saturate anticipated herbivore response; 2) if mechanical treatments are used where ungulate herbivory may pose a threat to aspen recruitment, then project plans must include resources for sufficient monitoring to detect excessive ungulate herbivory pressure and to deploy protective measures needed to prevent regeneration failure.

INTRODUCTION

As a keystone process, wildfire has strong direct and indirect influences on the composition, structure, and successional patterns of biological communities which in turn drive ecosystem function and biodiversity (Pausas and Keeley 2009; Bowman and others 2011). Novel fire regimes due to climate change, plant invasions, human ignitions or fire suppression, can destabilize ecosystem function and result in losses of ecosystem services (Carroll and others 2007; Hammer and others 2009; Gill and others 2013; Moritz and others 2014; DeFries and Nagendra 2017). Fire suppression and other management activities have resulted in uncharacteristically long fire-free intervals and increased fuel loads for many forest and shrubland ecosystems around the world (Gallant and others 2003). These vegetation changes have resulted in larger fires with higher burn severity in recent decades (Bowman et al. 2009, Jolley et al. 2015). Increasing temperatures due to climate change have also lengthened the fire season and are contributing to increases in fire frequency, severity, and size with often unpredictable effects on successional trajectories or ecosystem resilience (Abatzoglou et al. 2016; Westerling 2016).

Ungulate herbivory regimes are also changing globally due to human influence (Spear and Chown 2009) and are known to have strong interactions with changing wildfire regimes

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(Augustine and McNaughton 1998; Anderson et al. 2007; Wan et al. 2014a). The introduction of domestic ungulates and the management of native ungulates has generally increased population density and sizes globally (MacDougall 2008), increasing herbivore pressure on plant communities (Cote and others 2004). Ungulate behavior is also changing due to the extirpation of apex predators (Kauffman and others 2010), habitat fragmentation (Mysterud 2010), hunting, and agriculture (MacDougall 2008). Forage nutrition and chemistry often affects the spatial distribution of ungulates and their browsing patterns (Seagle and McNaughton 1992; Augustine and McNaughton 1998). In order to deal with herbivory, plants have developed several strategies including: pulsed growth that overwhelms or saturates herbivore populations and compensates for removal of plant tissue (strategy of tolerance), mechanical or chemical defenses used to deter herbivory or decrease palatability (strategy of resistance), or reducing exposure to herbivory by quickly growing beyond the reach of herbivores (strategy of escape) (Augustine and McNaughton 1998).

Human-driven interruptions in natural fire and herbivory regimes have been recognized globally and extensive management efforts are being made to restore natural fire cycles (Stephens and others 2009; Gill and others 2013) as well as to properly manage native and non-native ungulate populations (Veblen and Young 2010). Forest treatments have consisted mostly of prescribed fires but have also included fuel reductions, or mechanical thinning of stands, to help regulate fire severity and direct fire away from human infrastructure and assets (Stephens and others 2009; Prichard and others 2010). Mechanical treatments that remove undesirable trees or restore successional balance among species have several potential advantages over fire in that they can be more precisely applied and risk of damage to human infrastructure and poor air quality due to smoke is reduced or eliminated (Fraser and others 2003; Stephens and others

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2009). Regulation of the timing and intensity of livestock grazing and control of native ungulates through culling, reintroduction of predators, or behavior modification have also been implemented, though herbivory is difficult to control, particularly in native ungulates, as it varies both spatially and temporally (Long and others 2014). As humans continue to modify the environment it is essential that research continues to address both the individual and interactive effects of changing disturbance regimes to inform management decisions.

Mixed aspen-conifer forests in western North America have experienced large changes in fire regimes (Westerling and others 2006), are used heavily by both native and non-native ungulates, and are widely distributed across the northern hemisphere (Chen and Popadiouk 2002). Quaking aspen (*Populus tremuloides*) is an ecologically important tree supporting much of the biodiversity in these systems and facilitating the establishment of conifer seedlings (Calder and St Clair 2012). Under natural fire regimes, mixed aspen-conifer forests are reset by 70-150 year fire cycles (Heyerdahl and others 2011) that allow both aspen and conifer stands to coexist (Chen and Popadiouk 2002; Calder and St Clair 2012). Fire stimulates dense aspen root suckering by removing apical dominance through mortality of overstory trees which increases auxin production and promotes vertical growth of suckers (Brown and Debyle 1987; Nilsson and others 2008). After fire, aspen which recruit into the overstory eventually facilitate the establishment of conifer seedings that over time results in conifer dominance until fire returns (Buck and St Clair 2014). However, fire suppression and other management activities have lengthened fire return intervals, resulting in competitive exclusion by conifers and mortality of aspen (Smith et al. 2011, Calder and St Clair 2012,). Another limitation to successful forest regeneration and recruitment is heavy ungulate herbivory that can prevent forest regeneration and recruitment (Rogers and Mittanck 2014; Rhodes et al. 2017; Rhodes et al. 2018). Aspen use

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a combination of the strategies of tolerance, resistance and vertical escape to mitigate the impacts

of herbivory (Lindroth and St. Clair 2013) including expressing defense compounds (phenolic

glycosides) to deter ungulate herbivores (Wooley et al. 2008)

In this context, we tested the effect of two management interventions (prescribed fire and

mechanical stand thinning treatments) on mixed aspen-conifer forest experiencing late

successional conifer dominance from fire suppression and heavy herbivory pressure. These

treatments were aimed to increase forest ecosystem resilience through aspen regeneration and

recruitment success. We hypothesized that: 1) aspen regeneration and recruitment will fail in

untreated stands due to high conifer abundance heavy ungulate herbivory pressure; 2) fire and

mechanical treatments will increase aspen regeneration by reducing conifer competition,

increasing light availability, and suppressing apical dominance; 3) effects of herbivory pressure

will be reduced in fire and mechanical treatments due to increased tolerance, resistance (defense

chemistry), and vertical escape of aspen suckers as competition from conifers is eliminated and

light availability increases (Calder et al. 2011 and Wan et al. 2014a); 4) changes in forage

availability due to fire and mechanical treatments will have modifying influences on patterns of

ungulate herbivory.

MATERIALS AND METHODS

Study Area

Study plots were located on Monroe Mountain in south central Utah (Figure 2-1) (Lat: 38.47

Long: 112.03). This mountain range is used heavily as rangeland for cattle, for trophy elk and

deer hunting, includes several cabin subdivisions and is a popular location for campers and other

recreationists. Vegetation on the landscape consists mostly of subalpine fir (*Abies lasiocarpa*),

douglas fir (*Pseudotsuga menziesii*), blue spruce (*Picea pungens*), engelmann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*). Large ungulate species present include rocky mountain elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and cattle (*Bos taurus*). Annual precipitation for the area is 91 cm with approximately 50% coming as snowpack in the months of November-March. Average annual temperature is 6.4°C, ranging from an average of -3.2°C in January, to 16.3°C in August.

Fire Treatment

Fire treatments were applied in large forest stands by professional firefighting crews employed by the U.S. Forest Service using drip and heli-torches. Fire treatments yielded high severity effects across all sites with 100% canopy tree mortality. Total treatment area was 279 hectares in 2016 and 141 hectares in 2017. All forests treated and monitored in this study were classified as mixed aspen-conifer forest (Figure 2-1).

Mechanical Treatment

Mechanical treatments were completed using a feller buncher attached to a large skid steer. The objective of this treatment was to remove 100% of the conifer species from forest patches. During the removal of conifer species, anywhere from 20 to 80% of the overstory aspen canopy was also removed to stimulate suckering (Fraser and others 2003). Approximately 92 hectares were treated mechanically in July of 2016 and 130 hectares in July of 2017 (Figure 2-1).

Aspen Regeneration, Vegetation Cover, and Ungulate Quantification

A total of thirty-nine 100 x 2 meter transects were placed in the study landscape including fifteen transects in fire treated forest, sixteen transects in mechanically treated forest, and eight transects in untreated forests (Figure 2-1). Fire and mechanical treatments took place over the summers of 2016 and 2017 and all measurements were taken at the end of the 2018 summer season, showing the effects two- and three-years post treatment.

Each sucker along the 100 x 2 meter transect was measured for height and inspected for number of meristems browsed. Overstory tree density was characterized using the point quarter method every 10 meters along the same 100 x 2 meter transect (Pollard 1971). Vegetation cover estimates were completed by using the pin drop method (Pilliod and Arkle 2013) where a pin was dropped approximately each meter along the transect and each plant touching the pin was identified to species. Plants were later categorized into functional type (grass, forb, shrub). Ungulate fecal groupings within the 100 x 2 meter transect were identified to species and counted. Pellet groupings from elk and deer were included as one when there were 3 or more pellets which appeared to be from the same defecation (Rogers and Mittanck 2014).

Defense Chemistry and Nutritional Analysis

Defense chemistry of aspen suckers was determined by removing the youngest fully expanded leaves on the two closest suckers to the transect line every five meters. Leaves were immediately placed on dry ice, taken to a lab where they were freeze dried to preserve chemical integrity and ground using a mixer mill with a #10 mesh screen (Wiley Mill, Thomas Scientific, Swedesboro, NJ, USA). To extract phenolic glycosides, 40mg of ground leaf tissue was vortexed with 0.66 ml of methanol for 1.5 minutes and centrifuged at 16.1g for 1min. Supernatant was then pipetted into a separate 2 ml vial. This procedure was repeated two more times. Samples

were processed using high-performance liquid chromatography (Agilent 110 Series, Santa Clara, CA, USA) with a Luna 2, C18 column (150 x 4.6 mm, 5μm) at a flow rate of 1 mlmin^{-1} to quantify phenolic glycoside concentrations. A UV lamp at 280nm wavelength was then used along with purified salicortin and tremulacin standards to detect compound peaks.

Leaf carbon and nitrogen were determined using the combustion method using a nitrogen analyzer (TruSpec, CN Determinator, LECO Corporation, St. Joseph, MI).

Statistical Analysis and Model Selection

Differences in aspen sucker height, density, and browse were tested using linear models with treatment type, years since treatment, total ungulate pellets, total phenolic glycosides, and vegetation cover, as explanatory variables. Ten models are selected for each response variable (aspen sucker height, density, and browse) based on hypotheses generated from existing literature and selected for using AICc (Corrected Akaike's Information Criterion). As treatment type and time since treatment were primary variables of interest and parameters were limited, treatment type and time since treatment are first excluded and ten models including other explanatory variables were selected using AIC. Treatment type and time since treatment are then tested with and without the optimal model using AIC and the model with the lowest AIC was taken as the final optimal model. For variables of interest that were not included in the final optimal model, a one-way ANOVA and Tukey post-hoc test was used to determine differences between treatment types.

All covariates are made continuous except for treatment type which had three levels: burned, mechanical, and untreated. Variables are examined for multicollinearity and variables containing a correlation coefficient of greater than 0.6 are excluded from the same model. Data is evaluated

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for spatial autocorrelation first graphically using semi-variograms, and secondly by using AIC to test the fit between a spatially correlated model and independent model. There was no evidence of spatial autocorrelation and AIC selected the independent model for aspen height, density, and browse. All statistical analysis were performed using program R software (Team 2017) and the package nlme (Pinheiro and others 2017)

RESULTS

Regeneration: Density, Height, and Herbivory Pressure (meristem removal)

Aspen sucker density was 13x greater in mechanically thinned stands than in untreated stands ($p = 0.06$) and 20x greater in fire treated stands than in untreated stands ($p = 0.002$) (Figure 2-2). Mechanically thinned and fire treated stands were not significantly different in aspen sucker density ($p = 0.12$) (Table 2-1). The percent (%) of meristems browsed was highest in untreated stands (73%) and mechanically thinned stands (68%) and was significantly lower in burned stands (31%) ($p = <0.001$) (Figure 2-3). Suckers were significantly taller in burned than in mechanically thinned or untreated stands ($p = <0.001$) and was the only treatment to show an increase in height between two- and three-years post treatment ($p = <0.001$) (Table 2-1; Figure 2-4).

Ungulate Fecal Counts

Total ungulate fecal counts were on average highest in mechanically thinned stands but were not significantly different than untreated ($p = 0.19$) or burned ($p = 0.11$) stands (Figure 2-4). Cattle ($p = 0.01$) and deer ($p = 0.04$) fecal counts were nearly 4x greater in mechanically thinned treatments than in burned treatments and over 2x greater than in untreated stands (cattle $p = 0.13$; deer $p = 0.33$) (Figure 2-5).

Forage Availability and Leaf Chemistry

Total vegetation cover was significantly lower in burned stands (25%) than in untreated stands (46%) or mechanically thinned treatments (42%) (Figure 2-6). Grass cover was higher in mechanical stands than burned stands ($p = 0.02$) and shrub cover was higher in untreated stands than in burned stands ($p = 0.003$) (Figure 2-5). Aspen foliage in mechanically thinned and burned had lower C:N ratios than untreated stands ($p = 0.003$) (Figure 2-7). Mechanically thinned and burned stands also had higher foliar phenolic glycoside levels than untreated stands ($p = 0.02$) (Figure 2-6).

DISCUSSION

Human-mediated changes to natural fire and herbivory regimes are creating novel disturbance patterns in forest ecosystems, with uncertain successional trajectories and impacts on forest resilience (MacDougall 2013). This study documents that both fire and mechanical interventions, done after long periods of fire suppression, can have positive effects on forest regeneration but that they are not equal in protecting against ungulate herbivory. Our first hypothesis that untreated forest would fail to regenerate and recruit aspen into the overstory due to conifer dominance and heavy ungulate herbivory pressure was strongly supported (Figure 2-2 and 2-3). Our second hypothesis that fire and mechanical treatments would have positive effects on aspen regeneration was also strongly supported as both treatments significantly triggered increases in suckering density. Our third hypothesis that fire and mechanical treatments would mitigate the effects of herbivory pressure was supported for fire treated stands but not for mechanically thinned stands. Our fourth hypothesis that changes in forage availability due to fire and mechanical thinning treatments would have modifying influences on ungulate herbivory of aspen was not strongly supported although it is possible that greater forage availability

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particularly grasses in mechanically thinned stands may have attracted cattle and deer that contributed to excessive browsing and recruitment failure (Figures 2-4 and 2-5).

Impacts of Conifer Competition and Heavy Ungulate Browse Pressure on Forest Regeneration Without Intervention

Untreated forests in this study had low aspen sucker density (Figure 2-2), high herbivory pressure (Figure 2-3) and no evidence of recruitment (Figure 2-4). Previous studies have established that aspen stands with more than 30% of meristem removal have impaired recruitment, while meristem removal above 60% causes recruitment failure (Rhodes and others 2018). Aspen suckers in untreated stands had an average of 73% of meristems removed (Figure 2-3), suggesting that aspen in these forest ecosystems are likely at a "tipping point" that if left in their current state will result in aspen stand failure and associated losses of biodiversity, resilience, and ecosystem function (Adams 2013; MacDougall and others 2013).

Light limitation in the presence of tall conifers, which occurs during fire suppression (Calder and St Clair 2012), is likely responsible for the reductions in growth, defense chemistry production, and high carbon to nitrogen ratios seen in aspen suckers in untreated stands (Figures 2-2, 2-3, and 2-6). Previous studies have demonstrated that high light environment increases photosynthetic rates and defense chemistry production in aspen (Calder and others 2011; Wan and others 2014b). Competition for soil resources between aspen and conifer also may reduce aspen growth. Calder (2011) demonstrated that soils exposed to sustained conifer dominance had lower macronutrients and organic matter and were correlated with reductions in aspen growth, photosynthetic rates, and defense compound production. These changes to soils occur slowly, but

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if conifer dominance is sustained, can limit regeneration success (Gallant and others 2003; Smith and others 2011)

Reduced aspen vigor in the presence of conifers makes aspen suckers less tolerant to herbivory by increasing the time that suckers are exposed to herbivores, increasing vulnerability to browsing, as well as increased palatability of aspen suckers by due to reduction in chemical defenses (Augustine and McNaughton 1998; Lindroth and St Clair 2013) High browse has been shown to increase suckering density of aspen (Rhodes and others 2019) though we did not observe this in untreated stands, possibly due to suppressed aspen root system vigor.

Prescribed Fire Effects

Aspen suckers in burned stands showed annual progression towards recruitment into the overstory (Figure 2-2), under similar herbivory pressure as untreated stands (Figure 2-4), showing that fire likely increases the ability of these ecosystems to tolerate and resist herbivory (Wan and others 2014b). Faster and more dense growth in fire treated stands increases survival for aspen suckers through vertical escape from herbivory, compensatory growth if suckers are browsed, and saturation of ungulate consumption due to higher regeneration density and faster growth (Augustine and McNaughton 1998; Wan and others 2014b). Fires likely elicited such a strong growth response from aspen suckers by removing all apical dominance of overstory aspen in addition to overstory conifer, thus increasing auxin production (Nilsson and others 2008) and the ability of suckers to compensate for browse damage and quickly escape herbivory through vertical growth.

Faster Growth and Higher Densities of Aspen in Fire-Treated Stands

Light limitation in the presence of large conifers, due to fire suppression (Calder and St Clair 2012), is likely responsible for the reductions in growth, defense chemistry production, and high carbon to nitrogen ratios seen in aspen suckers in untreated stands (Figures 2-2, 2-3, and 2-6). Previous studies have demonstrated that high light environment increases photosynthetic rates and defense chemistry production in aspen (Calder and others 2011; Wan and others 2014b). Competition for soil resources between aspen and conifer also may reduce aspen growth. Calder (2011) demonstrated that soils exposed to sustained conifer dominance had lower macronutrients and organic matter and were correlated with reductions in aspen growth, photosynthetic rates, and defense compound production. These changes to soils occur slowly, but if conifer dominance is sustained, can limit regeneration success (Gallant and others 2003; Smith and others 2011)

Mechanically Thinning Treatment Effects

Mechanical treatments were unique in that they stimulated dense aspen suckering (Figure 2-3), yet suckers did not reach recruitment heights nor show progression in height from year to year (Figure 2-2). As addressed above in the case of fire, apical dominance of adult aspen which remained standing in mechanically treatments, likely slowed growth rates, increasing the time that suckers were exposed to herbivores and reducing the ability of suckers to tolerate browse through compensatory growth and escape (Figure 2-2) (Augustine and McNaughton 1998; Wan and others 2014b). High phenolic glycoside production which has been shown to deter ungulate herbivory in some cases (Villalba and others 2014) did not deter ungulate herbivores from heavily browsing aspen suckers in mechanical treatments, particularly deer and cattle (Figures 2-3 and 2-6).

High aspen suckering densities and high browse levels (Figure 2-3) along with higher average pellet counts in mechanical treatments (Figure 2-4) also give compelling evidence that ungulates were possibly attracted to mechanically treated areas for unknown reasons and that herbivory pressure was higher than in burned or untreated stands.

Large fire size has been shown to increase aspen recruitment success because of the ability of large treatments to saturate the effect of ungulate herbivores compared to small treatment sizes (Wan and others 2014a). For this reason, it is likely that larger mechanically thinned treatments would be better at successfully recruiting aspen suckers into the overstory, even with reduced growth rates. Disturbance severity, also likely would increase the probability of aspen recruitment success (Wan and others 2014b). Aspen has been documented as successfully regenerating and recruiting after clear cutting in some cases (Bartos and Mueggler 1982) though other cases have shown complete loss of aspen stands after a clear cut (Lindroth and St Clair 2013). Ungulate herbivory pressure likely plays a large role in the success or failure of aspen stands in these cases.

Conclusions and Recommendations

Forests in this study appear to be at a "tipping point" where under current conditions of conifer competition (fire suppression) and heavy ungulate herbivory, forests will fail to recruit aspen into the overstory if left untreated (Adams 2013). As aspen supports hundreds of species decreases in aspen vigor or complete loss will likely result in heavy losses in biodiversity and have large implications for future ecosystem resilience. Fire disturbance increased the ability of these forests to tolerate herbivory pressure, demonstrating that ecosystem level approaches to restoration involving disturbance interactions are advantageous.

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We recommend that: 1) where and when possible, fire be given high priority as a restoration treatment option for late-succession aspen-conifer forest stands, and that treatments be sufficiently large for the aspen regeneration response to saturate anticipated herbivore response; 2) if mechanical treatments are used where ungulate herbivory may pose a threat to aspen recruitment, then project plans must include resources for sufficient monitoring to detect excessive ungulate herbivory pressure and to deploy protective measures needed to prevent regeneration failure.

We also point out that as the timing, intensity, and extent of both fire, herbivory, and other disturbances continues to be altered across the earth, it is necessary for the preservation of diversity and resilience of ecosystems, to reassess the influence of interacting disturbances in shaping plant communities globally.

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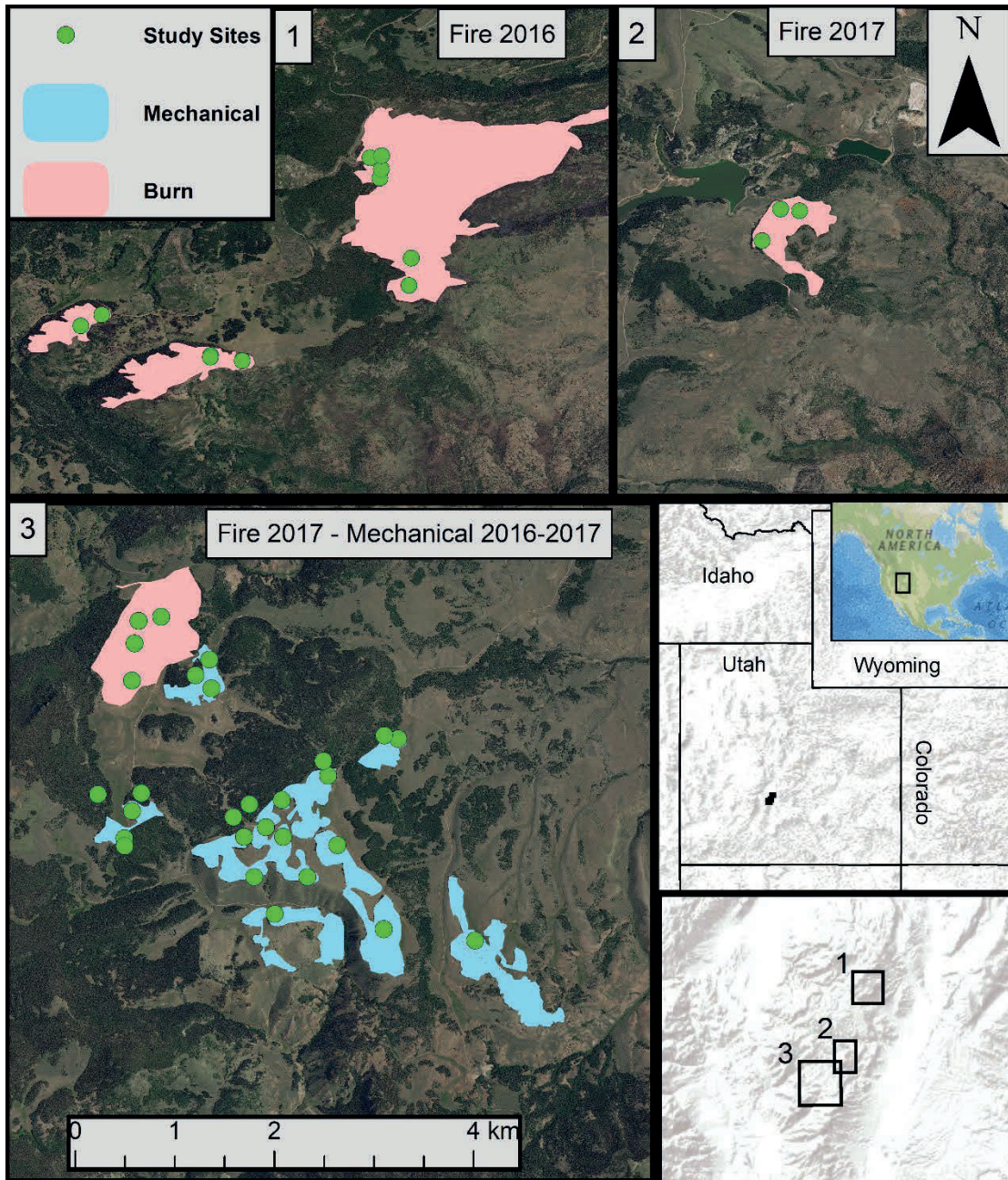
Figure 2-1: Study area including burn, mechanical, and untreated treatments with transect start points shown as circles. Sites are nested within groups (not each treatment is represented in each group) and not crossed.
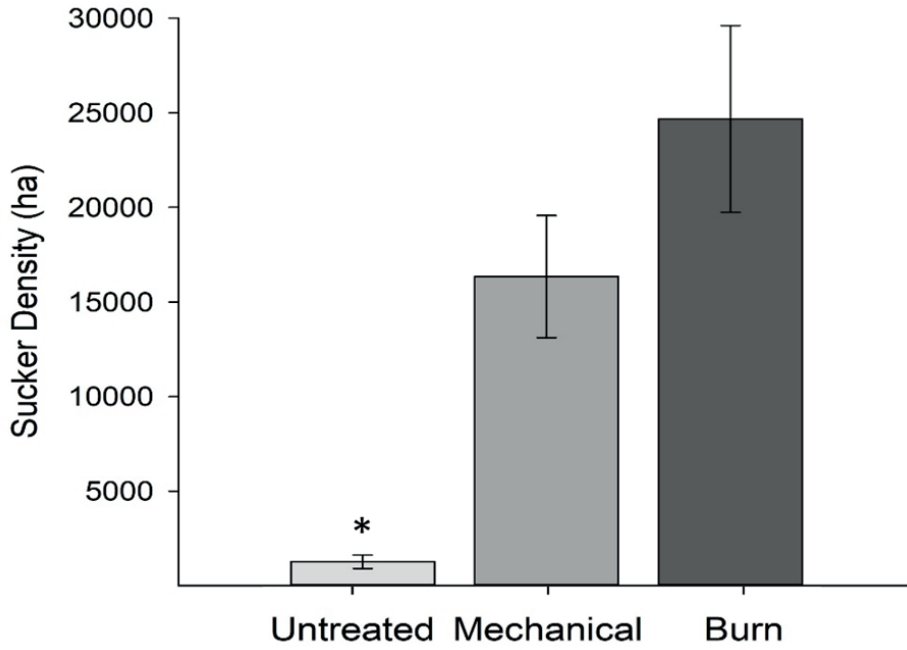
Figure 2-2: Sucker density by treatment (* signifies p <0.05).
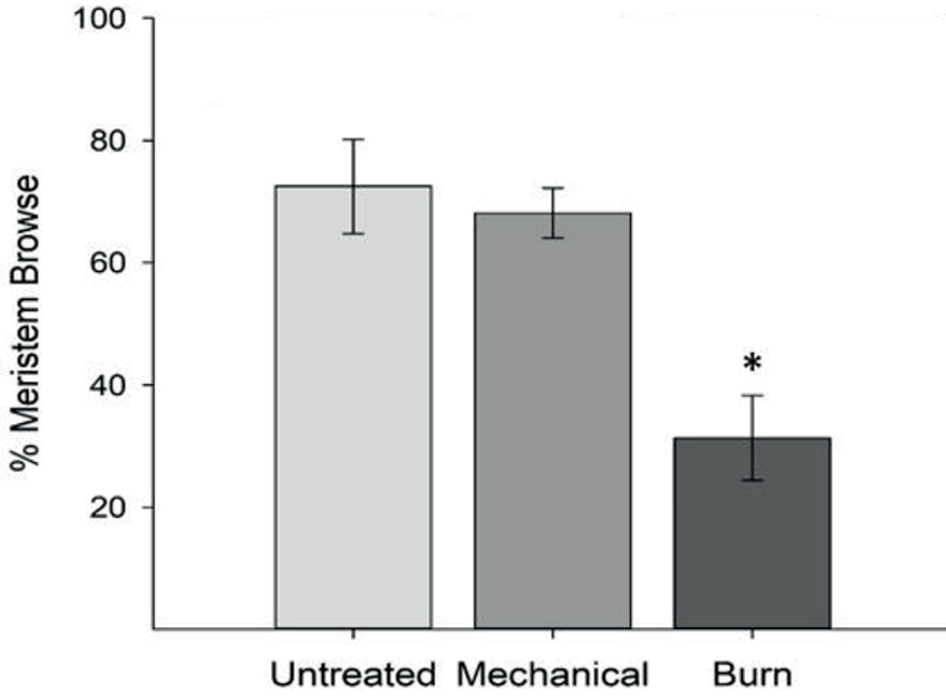
Figure 2-3: Percent (%) meristem browse by treatment (* indicates p <0.05).
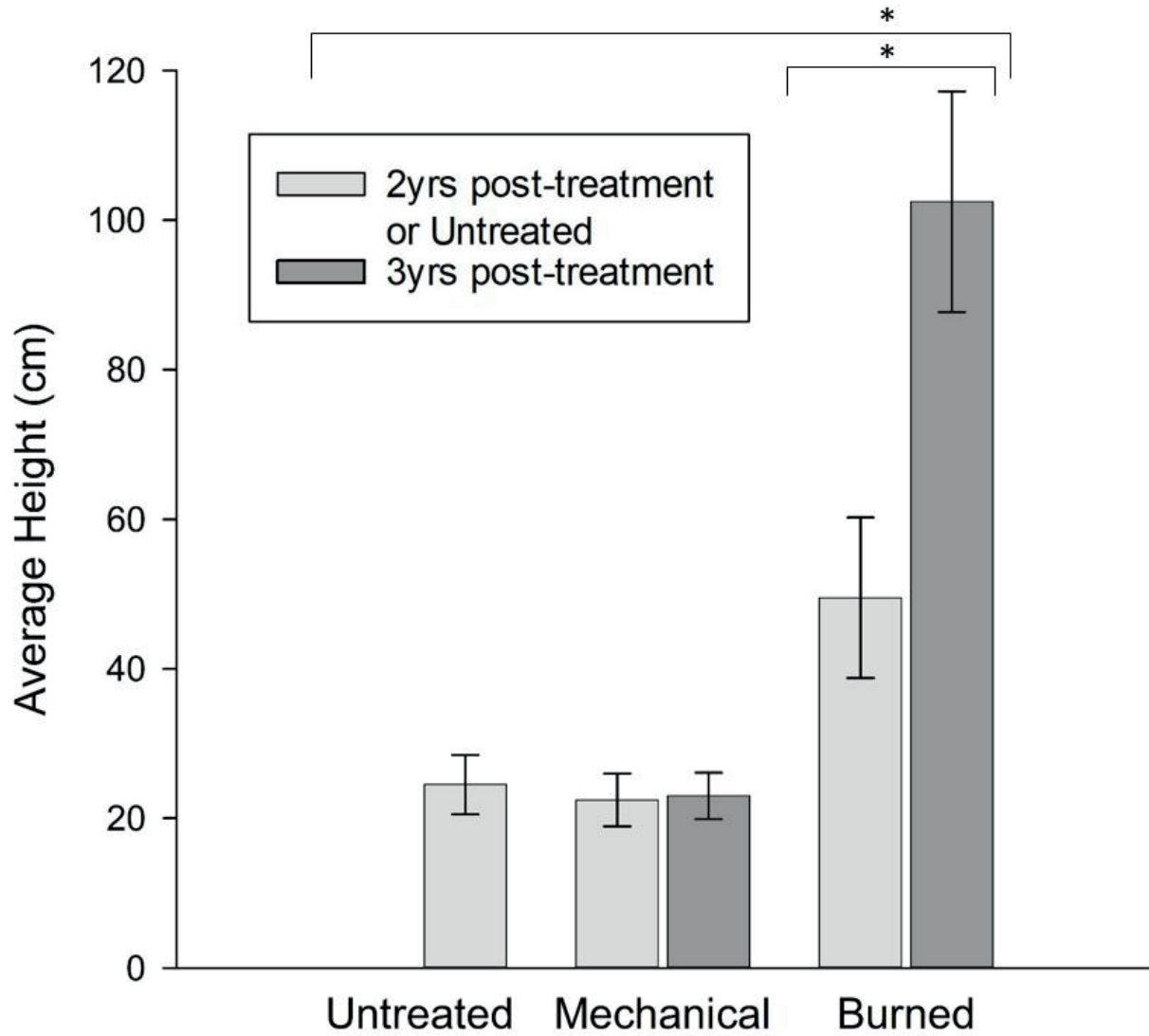
Figure 2-4: Average height of aspen suckers separated by treatment type and time since treatment. Suckers in Untreated and Mechanical treatments were short and did not show progression towards recruitment. Suckers in Burned treatments were taller than mechanical (p= <0.001) and untreated (p = <0.001) and showed significant growth from 2yrs to 3yrs post-treatment (p = <0.001).
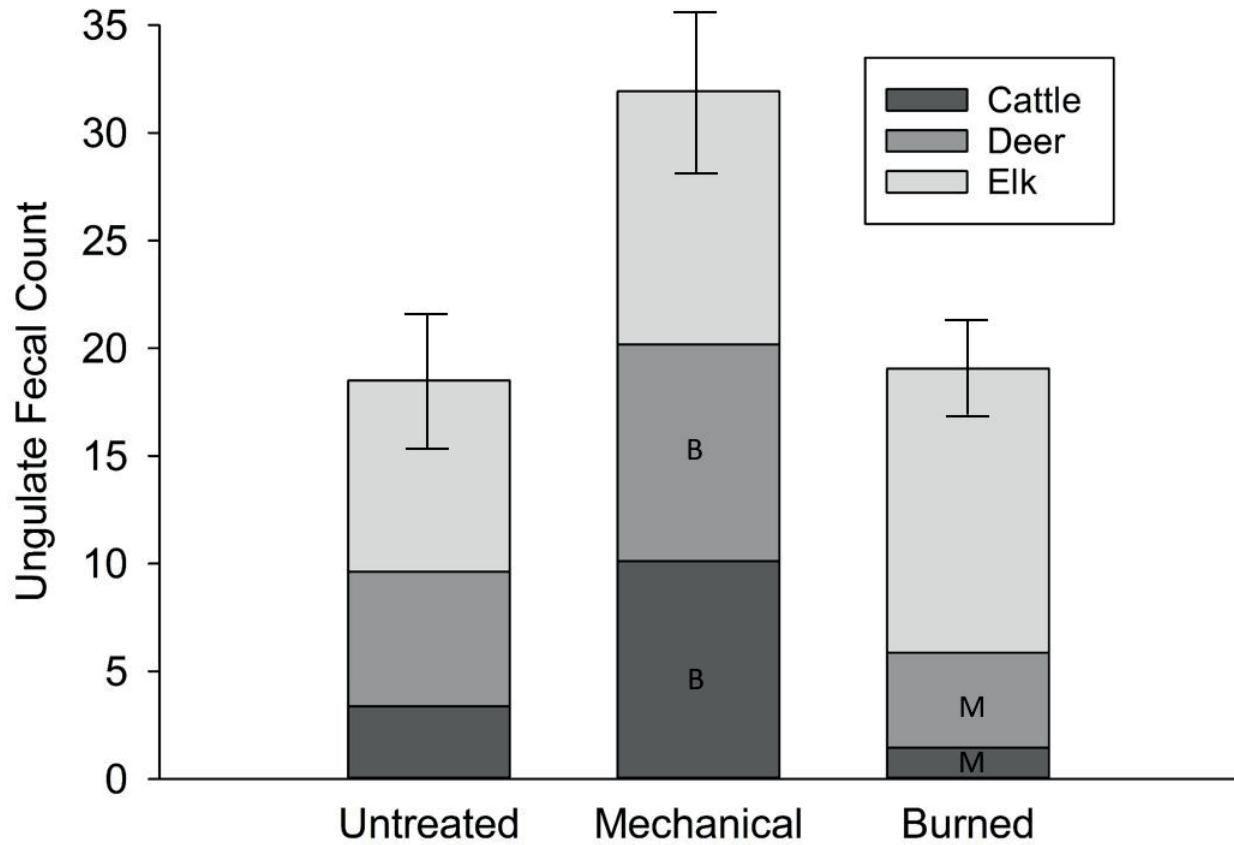
Figure 2-5: Ungulate fecal counts separated by treatment type. Letters indicate treatment in which values differs significantly below α = 0.05 (U = Untreated, M = Mechanical, B = Burned). Error bars reflect standard error. Despite differences in standard error, an ANOVA test revealed no statistical differences between total vegetation in mechanical and burned (p = 0.11) or intact (p = 0.18) treatments.
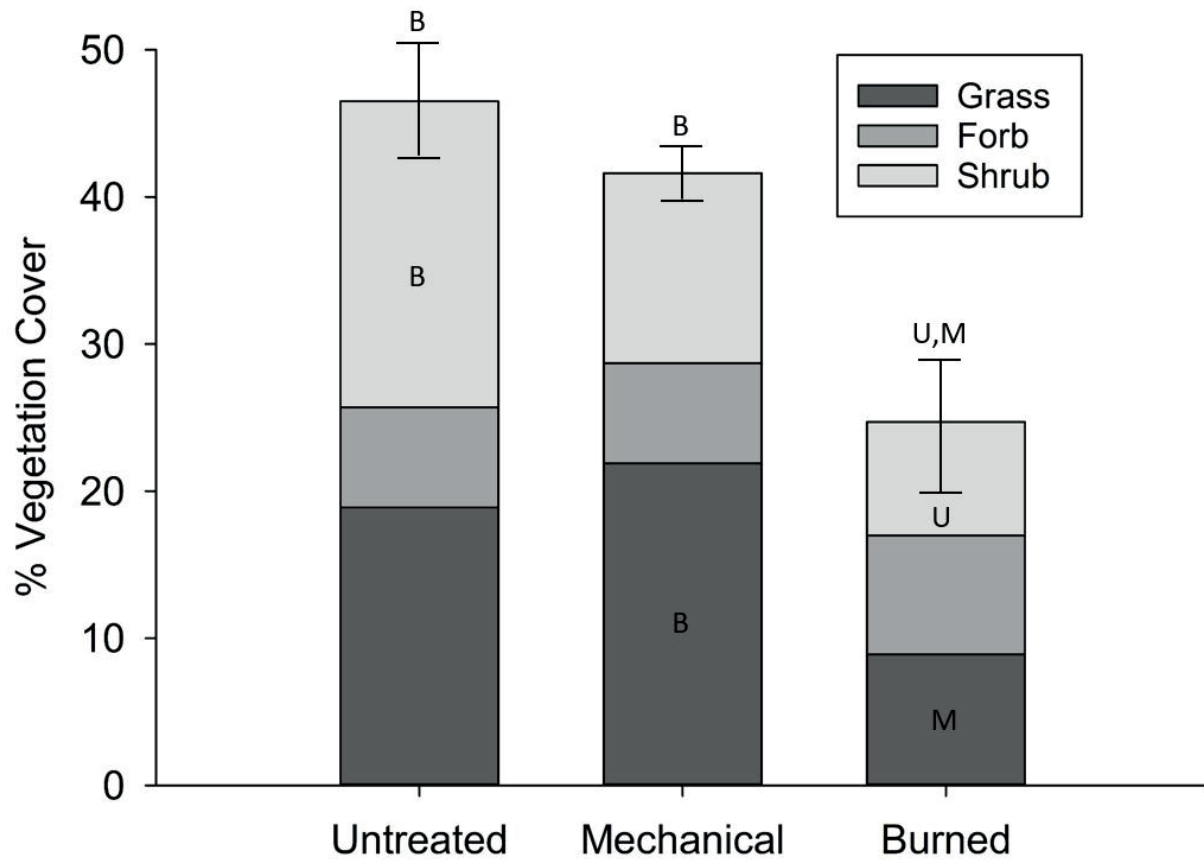
Figure 2-6: Vegetation cover separated by treatment type. Letters indicate treatment in which values differs significantly below α = 0.05 (U = Untreated, M = Mechanical, B = Burned). Other cover types included bare soil, leaf litter, and large woody debris.
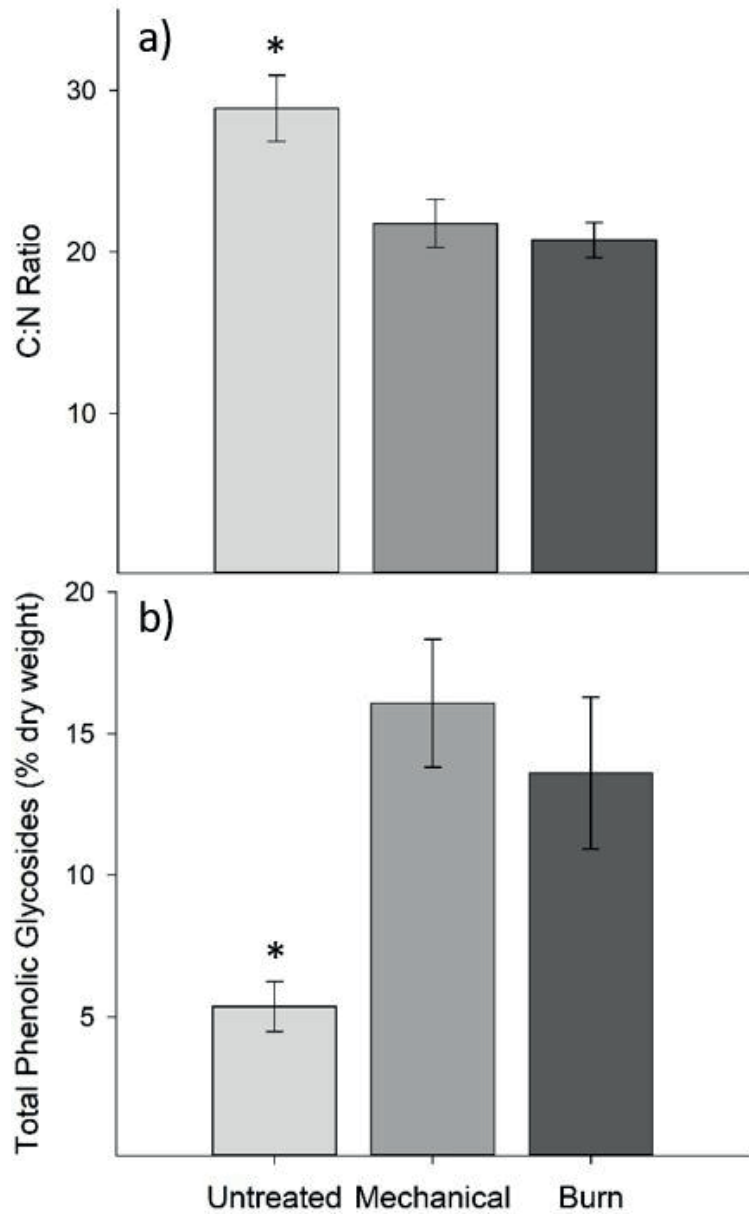
Figure 2-7: C:N ratios (a) and total phenolic glycosides (b) separated by treatment types. Untreated stands had the highest C:N ratios or the lowest nutritional value of leaves (a) as well as the lowest amounts of defense chemistry(b). Mechanical and Burned treatments had similar nutritional value and defense compounds. Error bars show standard error and * indicates significance below α = 0.05.

TABLES

Table 2-1: Statistical table showing results of the optimal linear models for average sucker height, sucker density, and percent meristems browsed. Untreated and mechanical treatment are in reference to burned treatments. Other explanatory variables that were not selected in the optimal models were ungulate fecal counts (total, cow, elk, deer), total phenolic glycosides, vegetation biomass, vegetation cover (total, grass, forb, shrub). (** = p-value < 0.001)

Explanotory Varables	Beta Estimate ± SE	Statistic	p - value	Full model
Average Sucker Height (cm)		*T-value*		R^2
Untreated	-63.3 ± 12.0	-5.3	<0.001**	**0.82**
Mechanical	-31.9 ± 7.7	-4.1	<0.001**	
Time Since Treatment	24.4 ± 4.3	5.7	<0.001**	
Browse	-78.3 ± 12.6	-6.2	<0.001**	
Sucker Density (suckers/ha)				
Untreated	-23,405 ± 6350	-3.7	<0.001**	**0.23**
Mechanical	-8,330 ± 5200	-1.6	0.12	
Percent Meristems Browsed				
Untreated	41.0 ± 6.0	4.2	<0.001**	**0.40**
Mechanical	37.0 ± 8.0	4.6	<0.001**	

CHAPTER 3

Burn Severity in Montane Forests Influences Peak Snow Accumulation

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ABSTRACT

Wildfires are altering landscapes around the world and are steadily increasing in frequency, size, and severity in many areas. As wildfires drastically changes vegetation structure, they also alter moisture inputs and energy fluxes which determine peak snowpack and water available for springtime melt. This melt provides fresh water for over 1 billion people and is critical for forest hydrology. Here we measure peak snow accumulation across ten burn severity gradients in a mid-latitude, subalpine forest. Peak seasonal snowpack across the burn severity gradients increased 15% in snow-water equivalence (SWE) and 17% in depth for every 20% increase in overstory tree mortality due to fire severity. Inter-annual variability played the largest role in determining peak SWE and snow depth, with an estimated 114% more snowpack in 2016 than in 2015. Elevation, canopy height, and the interaction between elevation and percent tree mortality were also included in the top models for peak SWE and depth. We conclude that complex burn severity mosaics across the landscape post-fire play a vital role in the hydrological response of a watershed after fire. As wildfire continues to increase in frequency, severity, and size across many snow-dominated watersheds, it is critical for both scientists and water managers to understand the ramifications of wildfire on snow-water resources under changing fire and climatic conditions.

INTRODUCTION

Fires are one of the most widespread and ecologically impactful disturbances of earth ecosystems (Bowman and others 2009). Human activities are creating novel fire regimes by changing their frequency, size, and severity at a global scale (Adams 2013; Westerling 2016). Fire varies in how it travels across the landscape often creating a "mosaic" of burn severity which can be visualized and monitored from remote sensing applications (Parr and Andersen 2006; Reilly and others 2006). Ecologically, fire severity has large impacts on plant community succession and structure, which can be tied to fundamental changes in watershed hydrology. Patches of burn severity within a fire provide opportunities to understand the legacy effects of variability in post-fire condition on ecosystem hydrology (Turner and others 1999; Wan and others 2014a).

Snow-water resources from mountain watersheds provide fresh water for more than 1 billion people and are critical for the function of montane ecosystems (Barnett and others 2005). Snowpack accumulation and ablation in mountain watersheds has shown to be strongly influenced by forest composition and structure (Veatch and others 2009; Varhola and others 2010; Hubbart and others 2015). Forests can reduce snowpack by intercepting falling snow, making it more vulnerable to loss through sublimation, and increase snowpack by shading it from incoming solar radiation and protecting it from other turbulent fluxes once it has reached the forest floor (Musselman and others 2008; Harpold and others 2014). Other studies have shown these seemingly competing processes are likely mediated by solar insolation, latitude, and topography (Maxwell and others 2019). While several studies have observed the effect of forest fire on snowpack accumulation and ablation in burned and unburned forests, these studies have grouped forests into categories of burned and unburned and have not considered gradients of

burn severity, which are likely to have large effects on peak snowpack or snow available for springtime melt.

Peak seasonal snowpack before springtime melt can be determined by subtracting mid-winter sublimation/evaporation from the total snowfall magnitude (Harpold and others 2014). Mid-winter losses of snowpack through sublimation and evaporation average 15-40% of total snowfall magnitude but may reach more than 60% in thick vegetation and with high solar insolation, high wind speeds, and low humidity (Pomeroy and others 1998a; Varhola and others 2010; Biederman and others 2014). Forest fire has strong and unique effects on snow persistence compared to other forest disturbances such as logging or beetle kill in that: 1) pyrogenic carbon particles (charcoal/soot) which fall from tree snags to the snow's surface have shown to decrease albedo and increase net shortwave radiation thus accelerating mid-winter water losses (Gleason and others 2013); 2) burned forests tend to have higher surface temperatures and wind speeds (Burles and Boon 2011; Winkler 2011) and; 3) severe fires can sterilize soil, killing seed banks as well as standing trees that are normally fire tolerant, lengthening the time of recovery for a watershed after fire (Stephens and others 2009).

Montane forests provide an ideal study system for investigating the effects of burn severity on snowmelt because they exhibit strong patterns of post-fire burn severity and they account for a large part of the annual water budget for forest hydrology and urban water use (LaMalfa and Ryle 2008; Rogers and others 2013). While the general definition of burn severity is defined as "the loss or change in organic matter aboveground and belowground" (Keeley 2009), when measuring snow accumulation and melt, tree mortality and subsequent leaf/needle loss is the primary variable of concern (Pomeroy and others 1998b; Varhola and others 2010) . Thus, the

terms burn severity and percent tree mortality will be used interchangeably throughout the rest of this document.

The objective of this study was to examine factors affecting peak snow-water equivalent (SWE) and snow depth across a gradient of burn severity in a mid-latitude subalpine forest. To our knowledge this is the first study to examine the effects of fire on snow accumulation and density across a burn severity gradient. We hypothesized 1) that more snow will accumulate and be available for springtime melt in severely burned forests due to reduced interception capacity, and; 2) that year, canopy height, basal area, or elevation will have modifying effects on peak SWE and depth by altering snowfall magnitude, mid-winter snowpack energy fluxes, or the interception capacity of the forest canopy.

MATERIALS AND METHODS

Study Site Description

This study took place in the Shingle creek and Indian creek watersheds on the Twitchell Canyon fire complex in south-central Utah, USA (Lat: 38.49 Long: −112.49), which burned in the summer of 2010 (see Figure 3-1). This fire is considered a modern "mega-fire" caused at least partially by years of fire suppression and the effects of a changing climate (Adams 2013). It is also known for its high variability in burn severity (see Figure 3-1). The USDA post fire analysis reported the fire to total 18,160 hectares with 33% high severity, 34% moderate severity, 20% low severity, and 13% unburned (USDA-Forest_Service 2010). Dominant over-story vegetation across the study area includes douglas fir (*Psuedosudot mensezii*), subalpine fir (*Abies lasiocarpa*), ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*), and quaking aspen (*Populus tremuloides*)

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Data from the Kimberly Mine SNOTEL station (Figure 3-1) indicated that the median annual precipitation for the area from 1981-2010 was 83cm with approximately 41cm of that coming as snow. At the same station the average annual temperature was 6.4° C ranging from an average of -3.2° C in January to 16.3° C in August (Anon) (Table 3-1).

Experimental Design

Using NAIP (National Agricultural Imagery Program) satellite imagery as well as fire severity maps from Monitoring Trends in Burn Severity database (MTBS 2010), ten different experimental blocks containing low, moderate, and severe burned treatments were chosen and verified on the ground that had similar elevation, aspect, slope, and vegetation type. All blocks were oriented on a north, northwest, or northeast aspect. The three burn severity classes within each block (low, moderate, and severe) were located within 200 meters of each other. Measurements within each burn severity class were made along two 20m intersecting and perpendicular transects making a 20m circular plot (see Figure 3-2).

Snow-Water Equivalent and Snow Depth

Snow-water equivalent and snow depth were taken the first week of March in both 2015 and 2016 which was estimated based on the 30-year median at the Kimberly Mine SNOTEL Station to be peak snowpack. Snow-water equivalence was taken using a US Federal snow sampler using the protocol from the USDA Snow Sampling Guidebook (USDA 1984). The same 20m transects used for snow depth were used for snow density and snow-water equivalence with the exception that measurements were taken every 10m across each transect totaling five

density/snow-water equivalent measurements per site (see Figure 3-2). These five measurements were averaged and considered representative of the given plot.

Snow depth was measured every 5 meters along each 20 m transect. At each 5 meter increment a depth measurement was taken one meter in front, behind, to each side, and in place of the sampler totaling 45 depth measurements per plot (see Figure 3-2). All depth measurements within a plot are averaged for statistical analysis.

Forest Canopy Characterization

To characterize forest canopies at each plot, the 20m perpendicular transects used for snow depth and density measurements were extended five meters on each side to create two perpendicular 30m transects which outlined a 30m circular plot divided into four quadrats (see Figure 3-2). Starting from the center and working out one quadrat at a time, each tree within each plot was evaluated for height, mortality (dead or alive), DBH (diameter at breast height) and identified to genus. Height was measured using a TruPulse® 360° Rangefinder; trees were considered dead if there was no living tissue such as leaves or needles observable; tree calipers were used to measure DBH and trees were identified to species. While these forests were composed of both aspen (deciduous) and conifer (evergreen) species, all ten gradients were composed of > 90% conifer and had an average canopy height of 9.7 m (SD = ± 1.6).

Burn Severity Mapping

MTBS (Monitoring Trends in Burn Severity) uses Landsat imagery (Anon) and the dNBR (difference in Normalized Burn Ratio) to create burn severity maps that are easy for researchers to access (Eidenshink and others 2007). While care must be taken when evaluating dNBR data

between fires in different ecoregions or vegetation types (Cansler and McKenzie 2012), they can be useful in evaluating single fire events, or fires within a particular region or vegetation type. Using the Normalized Burn Ratio (dNBR) algorithm (Bobbe and others 2001), MTBS provides burn severity maps for any fires over 404 ha (1000 ac) in the western United States (MTBS 2010).

Statistical Analysis

We used a linear mixed-effects model to test how percent overstory tree mortality influenced snow depth and snow-water equivalence (SWE). A mixed-effects model allowed us to test for the influence of percent tree mortality, year, canopy height, basal area, and elevation, while accounting for spatial non-independence in the block design (Harrison and others 2018).

We manually tested all possible combinations of explanatory variables, for both snow depth and SWE (Anderson 2002; Harrison and others 2018). We also tested the interactions between percent overstory mortality and elevation, and basal area and canopy height, as vegetation cover has shown to be less important at higher elevations with intense snowfall events (Robert 2004), and the combination of thick and tall vegetation should exert a stronger force on snowpack accumulation (Lopez-Moreno and others 2007). Before running the models, we calculated pairwise correlations among all independent variables to test for multicollinearity. As elevation and basal area were collinear at 0.9, all models with both elevation and basal area were excluded. Because of the large difference in snow years, the variable Year remained in each model tested. To allow comparison of model coefficients for each parameter, all independent variables were centered by subtracting the mean from each value and scaled by dividing by the standard deviation (Harrison and others 2018). We compared model performance with corrected

Akaike's Information Criterion (AICc), and selected a final model composed of only variables included in at least two of the top three models (Harrison and others 2018; Malone and others 2018). Prior to the analysis, data exploration was performed which included identifying outliers, assessing for homogeneity of variance, normality, zero inflation, multicollinearity, interactions, and independence as outlined by (Zuur and others 2010). We visually inspected residuals of the final models for normality and homogeneity of variance and the data met model assumptions. All analyses were performed in R software (Team 2017), using the packages lme4 (Wood and Scheipl 2014), lmertest (Kuznetsova and others 2015), and mertools (Knowles and Frederick 2016).

RESULTS

Snow-Water Equivalent

The top model for peak SWE included (in order of importance): year, percent tree mortality, elevation, and the interaction between percent tree mortality and elevation (Table 3-2); this model accounted for 85% of variation in SWE. Snow water equivalence increased a total of 75% from unburned forests (0% mortality) to severely burned forests (100% mortality) or in other words SWE increased nearly 15% for every 20% increase in tree mortality (Figure 3-3). Year was the greatest predictor of SWE with SWE on average 10.6 cm greater in 2016 than 2015 (Figure 3-3). Every 100 m increase in elevation increased SWE on average 11.7 cm in SWE ($p = 0.08$) (Table 3-2). While the interaction between percent tree mortality and elevation was included at least two of the top three models, it was not statistically significant. (Table 3-2).

Snow Depth

The top model for snow depth included (in order of importance): year, percent tree mortality, the interaction between percent tree mortality, elevation, canopy height, and slope (Table 3-2); this model accounted for 81% of the variability in snow depth across the study landscape (Table 3-2). Snow depth increased a total of 85% from unburned forests (0% mortality) to severely burned forests (100% mortality) or in other words snow depth increased nearly 17% for every 20% increase in tree mortality (Figure 3-3). Year was the greatest predictor of snow depth with depth on average 27 cm greater in 2016 than 2015 (Figure 3-3). While elevation, canopy height, slope, and the interaction between percent tree mortality and elevation were included in at least two of the top three models, their influence was not statistically significant (Table 3-2).

DISCUSSION

Wildfires regimes are changing in forest ecosystems (Westerling and others 2006), which may have cascading impacts on watershed hydrology (Adams 2013). Our first hypothesis that more snow would accumulate in severely burned forests was strongly supported. We suspect that these increases in peak SWE and depth are strongly influenced by reduced canopy snow interception (Pomeroy and others 1998b; Mahat and Tarboton 2014). Our second hypothesis that other site characteristics such as year, canopy height, basal area, or elevation would have modifying effects by altering mid-winter snowpack energy fluxes was partially supported with SWE and snow depth varying strongly across years (p <0.001) and SWE increasing with elevation (p = 0.08). This data supports previous studies showing increases in peak snow depth and SWE in burned forests (Burles and Boon 2011; Winkler 2011; Gleason and others 2013) but

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for the first time provides novel insights into how snow properties change as a function of burn severity.

Percent Tree Mortality (burn severity) and Peak Snowpack

Peak snowpack levels were correlated with percent tree mortality, with deeper and more dense snowpack forming with greater burn severity (Figure 3-3). These increases are possibly due to tree mortality and needle loss in higher burn severities resulting in lower canopy interception of snow. Previous studies evaluating snowfall interception in forest varying in forest density (Pomeroy and others 1998b; Essery and others 2003; Boon 2009), gradients of insect defoliation (Boon 2007; Mikkelson and others 2013), and burned vs. unburned forests (Burles and Boon 2011; Winkler 2011; Gleason and others 2013) have identified reduced canopy density and foliage loss as contributing significantly to increased snowpack. Our data add further evidence of the impacts of forest disturbance on snow depth and density by identifying a positive linear relationship between burn severity and SWE and snow depth (Fig. 3). As most fires create mosaics of burn severity across forest landscapes (Parr and Andersen 2006; Wan and others 2014b), our data suggest that post-fire burn patterns can strongly influence forest hydrology and water resources.

Other factors such as topography, which influences exposure to solar radiation and atmospheric conditions, and wind redistribution of snow are likely to have strong impacts on peak SWE and depth along burn severity gradients. Relatively low solar insolation on north facing aspects (as found in this study) or higher latitudes is likely to lead to low mid-winter losses and higher peak SWE in severely burned forests (Figure 3-3). High solar insolation on south facing aspects or lower latitudes will likely result in high mid-winter losses and lower peak

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SWE in severely burned forests than areas where vegetation offers protection from solar radiation and other turbulent forces (Harpold and others 2014). Maxwell (2019) demonstrated through paired north and south facing and burned and unburned plots, that topographical aspect can have a greater effect on snowpack accumulation than burn condition though this study did not consider burn severity. Wind can also redistribute snow within forest ecosystems (Musselman and others 2015), though high complexity in a fire mosaic may limit the ability of wind to redistribute snow as patch size has shown to limit wind effects on snow (Pomeroy and others 2002). Troendle and Leaf (1980) showed that the greatest snow accumulation occurred in open forest patches which were 3-5 times as wide as the average surrounding canopy height. Low to moderate, and most severely burned patch sizes in this study were near 3-5 times the average height of the surrounding canopy and had no evidence of wind scour or drifting. Some severely burned plots were connected to large swaths of open areas and could have received some redistributed snow as lost vegetation surface with increasing burn severity maintains higher windspeeds into burned stands (Winkler 2011).

While decreased canopy interception of forests over large areas could contribute to increases in snowpack and water resources in watersheds with low solar insolation, Biederman (2014) showed that increases in springtime evaporation in beetle killed forests decreased streamflow despite an increase in peak snowpack. While it is likely that springtime evaporation increases with higher burn severities due to higher net solar radiation (Gleason and Nolin 2016), numerous studies have shown increased streamflow from burned watersheds (Kinoshita and Hogue 2015; Wine and Cadol 2016; Wine and others 2018). These studies attribute increases in streamflow to reduced interception capacity of forests, but also to hydrophobicity of soils or reduced soil infiltration, and accelerated melt rates. No studies we are familiar with to this date have

examined water partitioning of snowpack between sublimation, evaporation, soil infiltration, and streamflow at the catchment level in burned montane forests.

Inter-Annual Variation and Peak Snowpack

Year was the greatest predictor of snowpack in the mixed effects model (Table 3-2) which is not uncommon in multiyear studies of snowpack (Winkler and Moore 2006). Despite significant increases in quantity of snowfall in the 2016 vs 2015 winter season, patterns of snowfall across the burn severity gradient did not change between years as indicated by the parallel lines between years in Figure 3-3. As forest canopies have a limit to how much snow they can hold, higher snowfall magnitude or storm intensities have shown to result in deeper snowpack in dense or undisturbed forests (Robert 2004; Winkler and Moore 2006; Jost and others 2007). This should result in a smaller ratio or flatter line for 2016 in Figure 3-3 but this was not observed. It is likely that neither 2016 or 2015 winter seasons had sufficient snowfall levels to overcome the forest canopy interception capacity resulting in similar rates of canopy penetration by snow and an equal ratio between lightly burned and severely burned forests (Varhola and others 2010). Storm frequency and storm intensity was evaluated between years for storm anomalies that could affect snowpack development under forest canopies, but none were apparent. It is likely that snowpack magnitudes were not sufficient to saturate the interception capacity of the forest canopy at these elevations (2300-2570 m) and that patterns of increased snow accumulation with high burn severity may diminish at higher elevations.

Slope, Elevation, Basal Area, and Canopy Height

Results from the mixed effects model show that neither percent slope, basal area, or canopy height had a significant influence ($\alpha = 0.05$) on peak SWE or snow depth across the burn severity gradients (Table 3-2). There are several possible reasons why these variables were not significant: 1) the main effects of year and burn severity were strong enough to statistically drown out the effects of less important variables (Harrison and others 2018); 2) the ranges or scale of the non-significant variables were too small to capture their effects; 3) the metrics actually have no real predictive power in determining peak SWE or snow depth. We believe a combination of these reasons are likely why they were not important predictors in our models (Table 3-3).

Conclusion and Implications

Burn severity can greatly alter peak seasonal snowpack accumulation by removing forest canopy density and reducing snowfall interception capacity (Figure 3-3). While future studies are needed to calculate springtime evaporation in post-fire areas and predict streamflow output, our data suggest that higher burn severities under future climate and fire regimes, may buffer the effects of rising global temperatures and earlier snow melt by increasing available seasonal peak SWE. Energy balances in burned forests should be calculated to include differences in topographical aspect, which heavily influences solar irradiance on snowpack, and incorporated into landscape scale models to form predictions of the effects of wildfire disturbance on water availability. As fires continue to become more frequent and severe and as demand for water by humanity steadily increases, there is a critical need to better understand how changing fire regimes are altering hydrological resources.

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Figure 3-1: Site locations for burn severity gradients in the Twitchell Canyon Fire Complex. Burn severity maps were obtained from Monitoring Trends in Burn Severity (MTBS) website. Pixels are 30m x 30m.
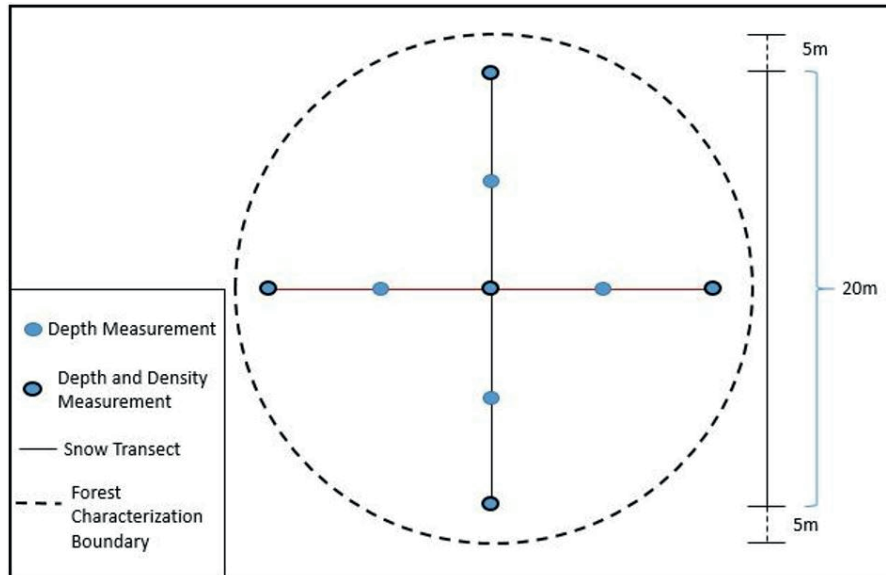
Figure 3-2: Plot diagram for both snow sampling and forest characterization of burn severity gradients. Depth measurements include a measurement one meter in front, behind, and to each side of the point indicated on the figure above.
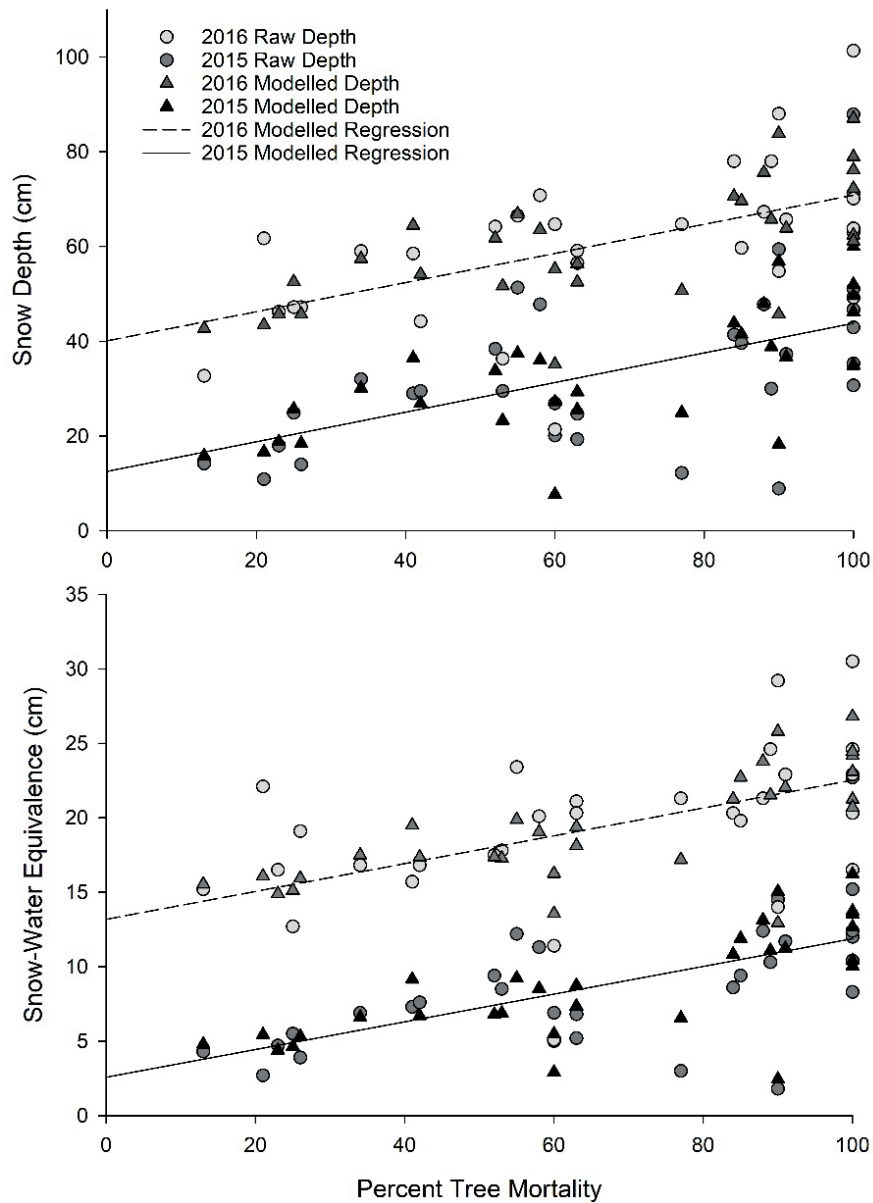
Figure 3-3: Snow depth and snow-water equivalent across a gradient of burn severity or tree mortality. Modelled data are predicted values from the top mixed effects model outlined in Table 1. A 15% and 17% increase in SWE and snow depth respectively are observed with every 20% increase in percent tree mortality. Models closely resembled raw data, with an R^2 of 0.85 for SWE and 0.81 for snow depth.

Table 3-1: Meteorological variables collected from Kimberly Mine SNOTEL station during the 2014-15 and 2015-16 winter season.

	2014-15 Dec-Feb	2015-16 Dec-Feb
	Mean	Mean
Temperature (C°)	-2.0	-4.6
Precip Accumulation (cm)	20	41
Max SWE (cm)	19	36
Day of Max SWE	March 4th	March 30th
Max Snow Depth (cm)	71	152

Table 3-2: Results of the top mixed effects model for both snow depth and snow-water equivalence. Percent tree mortality and year are the most important variables in determining both SWE and snow depth.

Fixed Effects	Beta Estimate ± SE	Statistic	p - value	Full Model
Snow-water Equivalence (SWE)		t-value		R^2
Percent Tree Mortality	3.1 ± 0.7	7.2	< 0.0001**	**0.85**
Elevation	1.2 ± 0.6	2.0	0.08*	
Year	10.6 ± 0.8	13.7	< 0.0001**	
Percent Tree Mortality*Elevation	0.7 ± 0.4	1.6	0.12	
Snow Depth				
Percent Tree Mortality	9.5 ± 1.5	6.5	< 0.0001**	**0.81**
Elevation	3.9 ± 2.5	1.6	0.16	
Canopy Height	-1.8 ± 1.5	-1.2	0.22	
Slope	2.7 ± 2.3	1.2	0.26	
Year	27.0 ± 2.6	10.3	<0.0001**	
Percent Tree Mortality*Elevation	2.3 ± 1.5	1.6	0.12	

Table 3-3: Raw data and covariates used in analysis organized by block.

Block	Burn Severity	Modelled Depth 2015 (cm)	Raw Depth 2015 (cm)	Modelled Depth 2016 (cm)	Raw Depth 2016 (cm)	Modelled SWE 2015 (cm)	Raw SWE 2015 (cm)	Modelled SWE 2016 (cm)	Raw SWE 2016 (cm)	Percent Mortality	Canopy Height (m)	Basal Area (m/ha)	Elevation (m)	Slope (%)
1	Low	18.5	14.0	45.7	47.2	5.3	3.9	15.9	19.1	26%	11.1	7.2	2427	15.0
1	Moderate	29.3	24.7	56.4	56.5	8.7	6.8	19.4	21.1	63%	10.0	7.8	2427	18.5
1	Severe	36.7	37.3	63.9	65.7	11.2	11.7	22.0	22.9	91%	10.1	7.4	2427	17.2
2	Low	15.9	14.2	42.7	32.7	4.8	4.3	15.5	15.2	13%	11.0	12.1	2388	1.6
2	Moderate	16.6	10.9	43.5	61.7	5.4	2.7	16.1	22.1	21%	12.0	4.1	2388	7.3
2	Severe	38.8	30.0	65.8	78	11.1	10.3	21.5	24.6	89%	7.3	2.7	2388	2.6
4	Low	7.7	26.9	35.2	21.4	2.9	6.9	13.6	5.1	6%	13.5	7.5	2374	6.5
4	Moderate	23.3	29.5	51.7	36.3	6.9	8.5	17.3	17.8	53%	10.1	6.5	2374	3.5
4	Severe	35.0	42.9	62.4	49.2	10.4	12	21.2	20.3	100%	9.3	5.6	2374	7.0
6	Low	18.8	18.0	45.8	46.2	4.4	4.7	14.9	16.5	23%	10.2	4.4	2356	22.1
6	Moderate	25.6	19.3	52.5	59.1	7.3	5.2	18.1	20.3	63%	11.7	6.4	2356	17.6
6	Severe	34.9	30.7	61.2	71.2	10.0	8.3	20.7	20.3	100%	11.2	2.9	2356	22.2
7	Low	18.3	8.9	45.7	54.8	2.4	1.8	12.9	14	9%	6.6	9.3	2300	16.4
7	Moderate	27.3	20.1	55.2	64.7	5.5	5	16.3	11.4	60%	7.0	6.3	2300	12.2
7	Severe	24.9	12.2	50.7	64.7	6.5	3	17.2	21.3	77%	12.3	6.7	2300	14.3
8	Low	30.1	32.0	57.4	59	6.6	6.9	17.5	16.8	34%	8.8	14.8	2555	22.5
8	Moderate	37.5	51.3	66.9	66.5	9.2	12.2	19.9	23.4	55%	7.7	12.6	2555	25.7
8	Severe	47.9	47.8	75.6	67.3	13.1	12.4	23.8	21.3	88%	9.5	6.7	2555	17.3
9	Low	25.7	24.9	52.6	47.2	4.6	5.5	15.1	12.7	25%	8.1	10.8	2551	24.6
9	Moderate	36.0	47.8	63.6	70.8	8.5	11.3	19.0	20.1	58%	9.2	9.7	2551	23.9
9	Severe	49.6	35.3	76.2	70.1	13.5	10.4	24.2	22.9	100%	9.6	11.1	2551	16.2
10	Low	33.8	38.4	61.8	64.2	6.8	9.4	17.4	17.5	52%	9.0	11.1	2559	32.0
10	Moderate	43.8	41.4	70.6	78	10.8	8.6	21.3	20.3	84%	9.8	8.6	2559	24.7
10	Severe	52.0	46.7	78.9	63	12.7	12.4	23.1	16.5	100%	8.1	7.9	2559	25.8
11	Low	36.5	29.0	64.5	58.5	9.2	7.3	19.5	15.7	41%	11.0	17.3	2566	21.2
11	Moderate	56.9	59.4	83.8	88	15.0	14.5	25.8	29.2	90%	9.2	10.0	2566	24.7
11	Severe	60.0	87.9	87.0	101.3	16.2	22.7	26.8	30.5	100%	9.2	10.4	2566	17.4
12	Low	26.9	29.5	54.2	44.2	6.7	7.6	17.4	16.8	42%	9.3	9.6	2569	15.7
12	Moderate	41.5	39.6	69.7	59.7	11.9	9.4	22.7	19.8	85%	9.4	10.3	2569	15.7
12	Severe	46.2	51.1	72.3	63.8	13.7	15.2	24.4	24.6	100%	10.7	8.1	2569	17.2

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CHAPTER 4

Wildfire and Topography Impacts on Snow Accumulation and Retention in Montane Forests

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ABSTRACT

Wildfires are among the most widespread disturbances of ecosystems and have been increasing in frequency, severity, and size in many parts of the world. Forest fires can fundamentally affect snowpack and watershed hydrology by restructuring forest composition and structure. Topography is an important factor in snowpack accumulation and ablation as it influences exposure to solar radiation and atmospheric conditions. Few direct measurements of post-fire snowpack have been taken and none to this date that evaluate how topographical aspect influences the effect of forest fire on snowpack accumulation and ablation. We set up a two-year experiment on the Twitchell Canyon fire in south-central Utah on both north and south facing aspects and burned and unburned forest conditions across three replicated blocks. There was a significant interaction between wildfire and aspect for snow depth in which burn conditions decreased snow depth on south facing aspects but not on northern facing aspects when compared with unburned forest on the same aspects. Snowpack disappeared earlier in burned areas than unburned areas, particularly on south facing slopes. Snow water equivalence (SWE) did not vary between burned and unburned forest. Year and topographical aspect were the main drivers of both snow depth and SWE. A review of five similar studies suggests that sites at southern latitudes and lower elevations could be more susceptible to reduction in snowpack after wildfire.

INTRODUCTION

Increasing temperatures (Brown and Mote 2009) and disturbance such as wildfire affect snowpack characteristics, altering the timing and amount of snowmelt available for downstream communities and ecosystems (Kinoshita and Hogue 2015; Wine and Cadol 2016; Winkler 2011). Because human activities are altering the frequency, severity, and size of wildfires globally (Bowman et al. 2009), there is a critical need to understand how changing fire regimes might alter snowpack characteristics that are vital to water security and ecosystem function (Adams 2013; Miller et al. 2009; Westerling 2016). Fire fundamentally affects watershed hydrology by restructuring the vegetation community, affecting the accumulation and loss of snow through interception, sublimation, and shading (Broxton et al. 2015; Musselman et al. 2008). In montane regions, where the majority of snowpack occurs, topographic position (i.e. slope, elevation, and aspect) strongly influences snowpack dynamics (Geddes et al. 2005; Jost et al. 2007; Pomeroy et al. 1998) but little is known about how variation in topography in burned forest landscapes influences snowpack characteristics (Harpold et al. 2014).

Losses to snowpack from mid-winter fluxes such as sublimation and evaporation are mediated by surrounding vegetation (Biederman et al. 2014a; Molotch et al. 2007). Dense forest canopies intercept falling snow, facilitating losses that can exceed 60% of a total annual snowpack (Hedstrom and Pomeroy 1998). Conversely, vegetation can protect snowpack from solar radiation both increasing snowpack quantity and decreasing the rate of melt (Musselman et al. 2008). Varhola et al. (2010) found in a review of 33 peer reviewed articles spanning 65 sites across North America and Europe that forest cover could explain 57% of changes in snow accumulation and 72% in snow ablation. Topography also changes the intensity of solar radiation, temperature, and atmospheric conditions affecting peak snowpack or snow available for springtime melt; the deepest snowpack normally occur on north-east facing aspects and

shallowest snowpack on south-western facing aspects (Robert 2004). Given the strong controls of both vegetation and topography on snowpack, it is critical for water management to better understand how wildfire impacts on forest structure interact with topography to affect snow-water resources.

The timing of spring snowmelt affects the amount of water available for both societal and ecological uses. Earlier snowmelt brought on by warming temperatures is a great concern for areas dependent on snowpack for water supply (Stewart et al. 2004). Faster snowmelt can create destructive pulses of abnormally high streamflow causing erosion, reservoir overfilling and flooding (Lyon et al. 2008; Stewart et al. 2004). Several studies have shown most water storage facilities in the Northern Hemisphere to be insufficient to hold faster streamflow inputs due to global climate change (Barnett et al. 2005; Nijssen et al. 2001; Vorosmarty 1997). Large disturbances such as wildfire in upstream watersheds could exacerbate these conditions causing essential water resources to be lost downstream to oceans, ecological degradation and dangerous flooding conditions in the springtime, and significant shortages of water supply in late summer.

While differences in snowpack characteristics are well understood in forested vs open meadows (Varhola et al. 2010) and disturbances such as logging clear-cuts (Woods et al. 2006) or insect infestations (Mikkelson et al. 2013), direct measurements of snowpack in post-fire landscapes have only been evaluated in a few studies which vary in results and do not consider interactions between burned forest and topography (Burles and Boon 2011; Farnes 1996; Gleason et al. 2013; Harpold et al. 2014; Skidmore 1994; Winkler 2011). Gleason et al. (2013) demonstrated that pyrogenic carbon particles and larger burned woody debris found in burned forest stands can drastically decrease snow spectral albedo and increase net shortwave radiation. These changes in albedo and shortwave radiation foster increased energy inputs into snowpack in

burned forests more than in clear-cut or insect infested forests and will likely lead to different outcomes in the accumulation and ablation of snow-water resources (Gleason and Nolin 2016; Harpold et al. 2014). Increased surface temperatures and wind speeds have also been documented in burned forests when compared with unburned forests (Burles and Boon 2011; Winkler 2011). While forest fires have shown to reduce soil infiltration rates (Granged et al. 2011; Versini et al. 2013), transpiration rates (Cardenas and Kanarek 2014; Zhou et al. 2013), and alter other factors which may affect the hydrologic response of a watershed to fire, this study focuses on the peak accumulation and melt of snowpack or water made available for springtime melt.

We investigated the effects of wildfire and topographic position on snowpack across three replicated blocks, in a two-year study in south-central Utah. Specifically, we asked: what is the role of wildfire, aspect, and their combination on peak snow depth, snow density, and snow-water equivalence (SWE) as well as snow ablation rates, and snow-free dates? We hypothesized that in post-fire landscapes we would find the greatest snow accumulation on burned north facing aspects due to reduced forest canopy and the least snow accumulation on burned south facing aspects due to more solar radiation reaching the forest floor (Harpold et al. 2014). We also hypothesized that increased available energy for melt in post fire landscapes (Burles and Boon 2011; Gleason and Nolin 2016) will result in earlier snow free dates and faster ablation rates in both north and south facing burned forests.

MATERIALS AND METHODS

Study Site Description

Study sites were located in the Shingle Creek watershed within the Twitchell Canyon fire complex east of Beaver, Utah (Lat: 38.49 Long: -112.49). The Twitchell Canyon fire burned over 18,500 hectares in the summer of 2010, 67% of which was considered moderate-high burn severity (USDA-Forest Service 2010). The study area occurred in a subalpine zone between 2900-3100m composed of douglas fir (*Psuedotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*), and quaking aspen (*Populus tremuloides*). The median annual precipitation for the area from 1981-2010 was 83cm, 47cm coming as snow within the months of November through April (Table 4-1). Average annual temperature was 6.4 C, ranging from an average of -3.2 C in January to 16.3 C in August (NRCS-Kimberly_Mine_Snotel 2017).

Experimental Design

Using NAIP (National Agriculture Imagery Program) (USDA 2010) satellite imagery and burn severity maps provided by Monitoring Trends in Burn Severity (MTBS) (MTBS 2010) we identified three blocks containing paired burned and unburned sites on both north and south facing aspects (Figure 4-1 and Figure 4-2). Each of the four treatments in every block were separated by a maximum of 0.5 km, varied in elevation by less than 200 meters (2900–3100m), and were within 50-150 meters from the forest edge. The average slope of transects on northern aspects was 18.5° and 13° on southern facing aspects. Dominant overstory vegetation, canopy height, and density were uniform between north and south facing aspects within blocks (Figure 4-2).

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Snowpack Sampling

Snow depth, density, and snow-water equivalence (SWE) were collected the first week of March (estimated peak snowpack) in both the 2015-16 and 2016-17 winter seasons (5-6 years after fire). Actual peak snowpack occurred Feb 24th in 2016 and March 6th in 2017 according to the Kimberly Mine SNOTEL station approximately 8 km away (Figure 4-1).

Snow depth was taken along two parallel one-hundred meter transects which were thirty meters apart within each treatment plot (Figure 4-1 and Figure 4-2). Every five meters along each transect, depth measurements were taken in front, behind, to each side, and in place of the observer using a 2.5 meter graduated depth pole (Veatch et al. 2009). Vegetation tree regeneration across the burned transects was limited to aspen and did not interfere with snow depth measurements; any portion of transect that fell within a tree well in either burned or unburned plots was measured and counted.

Density and SWE were measured using a standard US Federal snow sampler every 25m on one of the two transects in each treatment totaling five measurements per plot. Standard protocol for measuring snow density and SWE found in the USDA snow survey sampling guide was used (USDA 1984). When a density sampling point landed in a tree well or if regenerating vegetation was present beneath the snow surface, the sampling point was moved one meter to the side until the sample point was no longer touching regenerating vegetation or within one meter of a tree well. All samples were collected on clear days between 9:00 and 16:00 hours and within 48 hours of one another in each year.

Snow Ablation

To capture continuous snow accumulation and ablation throughout the 2016-2017 winter season, time triggered cameras were placed in each of the four treatment plots within each of the three blocks for a total of 12 camera locations. While cameras were able to capture daily snow accumulation and ablation rates, they were unable to quantify sublimation or evaporation. Snow that is sublimated or evaporated differs from snowmelt in that it does not contribute to the local water budget. Both sublimation and evaporation rates likely varied between treatments and would have different implications for water supply. Cameras were placed facing uphill from the bottom of each treatment (Figure 4-2). A snow depth pole marked in 15cm increments was placed approximately 3 meters away and in view of the camera. Depth poles were placed in a canopy gap with no overstory canopy directly above. Cameras were programmed to take one photo each day at noon from October 28th, 2016 until June 16th, 2017. Snow ablation rates were calculated by taking snow depth on March 6th (peak snowpack) and dividing it by the number of days it took for snow to no longer be recorded on the snow depth poles.

Statistical Analysis

We tested for differences in snow depth, density, and SWE using the interaction between aspect and burn condition as well as year as fixed effects in a linear mixed effects model. Block was used as a random effect to account for spatial autocorrelation or differences between blocks. To avoid pseudo-replication, we averaged all measurements within a treatment. As elevation differed between blocks by less than 100 meters and slope varied less than 10% from the average, they were considered accounted for in the experimental design and were excluded from the model. A mixed effects model was used because of its unique ability to handle the multilevel

structure of treatments and blocks present in the experimental design (Harrison et al. 2018).

Assumptions of normality were assessed with a normal probability plot and homogeneity of variance evaluated graphically using boxplots. The data did not violate assumptions of normality or homogeneity of variance. There was no evidence of collinearity above 0.6 (Zuur et al. 2010). Post-hoc pairwise comparisons of the burn and aspect interaction was done using Tukey multiple comparisons in the emmeans (Lenth 2017) R package.

Differences in snow-free dates and ablation rates between treatment types were analyzed using a linear model including snow-free date or snow ablation rate between treatment types followed by a one-way analysis of variance (ANOVA). Assumptions of normality were verified using a normal probability plot and found to be normally distributed. Bartlett tests were used to test for homogeneity of variance and none was found (Bartlett 1937; Winer et al. 1971). A post hoc analysis using Tukey-Kramer multi comparison methods at alpha = 0.05 was later used to detect differences between individual treatments. All statistical analysis were performed using program R software (Team 2017) and packages: lme4 (Wood and Scheipl 2014), lmertest (Kuznetsova et al. 2015), mertools (Knowles and Frederick 2016), and emmeans (Lenth 2017).

<div align="center">RESULTS</div>

Snow Depth

There was a significant interaction between wildfire and aspect for snow depth in the mixed effects model (p = 0.001) in which burn conditions decreased snow depth on south facing aspects (23% decrease; p = 0.01) but not on northern facing aspects (p = 0.24) when compared with unburned forest on the same aspects (Figure 4-3). When north and south aspects were combined, snowpack in burned forest was on average 5% more shallow than in unburned forest (p = 0.066).

Year was the greatest predictor of snow depth with 29% deeper snow in the 2016-17 season than in the 2015-16 winter season (p = < 0.001). Despite differences in snowfall between years, trends in snow depth between treatments remained consistent (Figure 4-3). Aspect was the second greatest predictor of snow depth with 44% deeper snowpack in northern facing forests than southern facing forests. Greater variation in snow depth was observed between north and south facing aspects in the presence of wildfire than in unburned forests with an average of 55cm difference between north and south burned aspects and 21cm between unburned aspects.

Snow Density

The interaction between burn condition and aspect was significant for snow density in the mixed effects model (p = 0.016). Trends showed a pattern opposite to snow depth, with snow 12% more dense on southern facing burned aspects (p = 0.25) and 10% more dense on northern facing unburned aspects (p = 0.69; Figure 4-3) when compared with treatments on the same aspect. Post-hoc pairwise comparisons reveal that snow density only differed significantly between unburned north facing aspects and burned south facing aspects (p = 0.04). Snow was on average 6% more dense on southern facing aspects than on northern facing aspects (p = 0.009), was equally dense between burned and unburned forests when north and southern aspects were combined (p = 0.08) and was approximately 45% more dense in the 2015-16 season than in the 2016-17 season.

SWE

The only significant predictors for snow water-equivalence in the mixed effects model were Aspect, with approximately 38% more SWE at peak snowpack on northern facing aspects (p = 0.01), and Year, with 70% more SWE at peak snowpack in the 2016-17 season than in 2015-16

winter season (p = <0.001). Pairwise comparisons of treatments revealed differences in SWE between burned north and south forests (p = 0.059), unburned north and burned south forests (p = 0.006), and unburned north and south forests (p = 0.04) Burned forests with north and south facing aspects combined had 11% less SWE than unburned forests (p = 0.28).

Snow-Free Date

Burned forests were completely free of snow an average of 4 days (northern aspects; p = 0.79) and 14.5 days (southern aspect; p = 0.05) earlier than unburned forests on the same aspect (Table 4-2). Snow accumulation stayed relatively similar between treatments until peak snowpack (March 6th) but large differences in ablation rates between treatment types after peak snowpack were observed (Figure 4-4). In unburned forest conditions, snow-free dates occurred an average of two weeks earlier on southern facing aspects than on northern facing aspects making aspect and burn condition equally impactful on snow persistence (Table 4-2).

Snow Ablation Rate

Both south (p = 0.024) and north (p = 0.37) facing burned sites had faster ablation rates than unburned sites on the same aspect (Table 4-2). The fastest melt rate occurred on southern facing burned aspects with an average of 3 cm/day and the slowest melt rate occurred on southern facing unburned aspects with 1.6 cm/day. Because of greater snow depths, northern facing burned aspects had an ablation rate of 1.7 cm/day despite a later snow-free date.

DISCUSSION

Although fires are a natural disturbance, their recent increases in frequency, size and severity as well as changes in global climate may create novel patterns in annual water availability for growing human populations (Barnett et al. 2005). This study documents the response of snow accumulation and snow ablation on both north and south facing aspects after a large wildfire in a subalpine forest. Our first hypothesis that snow accumulation would increase on burned north facing aspects and decrease on burned south facing aspects was partially supported; burn conditions did significantly decrease snow levels on south facing aspects but unburned and burned transects on northern facing aspects were not statistically different (Figure 4-3). Our second hypothesis that earlier snow free dates and faster ablation rates would occur was supported, with snow disappearing on average 4 days (northern aspects) and 14.5 days (southern aspects) earlier than unburned forests (Figure 4-4; Table 4-2).

Using daily snow depth measurements as well as extensive peak snowpack surveys over two separate water years, our data provide new insights into the accumulation and ablation of snowpack in topographically complex burned forests. Specifically: (1) despite changes in snow depth, no changes in SWE were detected between burned or unburned forests on north or south aspects (2) inter-annual variability and aspect were the primary drivers of snow accumulation; (3) topographical aspect and burned forest condition had an equal effect on snow free dates on southern facing aspects; (4) snow ablation occurred more quickly in all burned treatments (5) a review of other studies measuring snowpack in burned and unburned forests reveals possible trends in snowpack response to burned forest conditions based on elevation and/or latitude. These trends in accumulation and ablation of snowpack following disturbance could contribute to uncertainties in water supply and management decisions (Barnett et al. 2005; Lyon et al. 2008)

Fire Effects on Snowpack Characteristics

Previous studies have shown a wide range of responses of peak SWE to burned forest conditions (Burles and Boon 2011; Harpold et al. 2014). Table 4-3, summarizes the major peer reviewed studies in which peak SWE was directly measured in paired burned and unburned forested plots. To limit the effect of solar radiation on results, or because of lack of topographical variation, all of these studies were performed on north facing or relatively flat study sites and did not consider topography. In these studies, the responses of peak SWE to burned forests ranged from a 10% decrease, to 50% increase (Table 4-3). In our study we observed an average decrease in peak SWE in burned forests (10% north, 11% south) though neither of these were statistically significant (Figure 4-3).

The wide range of responses of snowpack to burned vs. unburned forest conditions suggest that other variables could be having a larger effect on peak SWE than burn condition alone. Some variables of interest include elevation, latitude, and slope angles (Table 4-3). Elevation has been shown to diminish the effects of vegetation on snow accumulation between intact forests stands and forest clearings (Jost et al. 2007; Musselman et al. 2015); as greater snowfall occurs with higher elevation, the ability of snow to overcome the interception capacity of a forest canopy and reach the ground where it can be shaded from solar radiation is increased (Robert 2004; Varhola et al. 2010). Both latitude and slope angles change the angle of the sun and as a result the amount of energy available for melting and evaporative processes (Golding and Swanson 1986; Musselman et al. 2008; Rowland and Moore 1992). The latitudinal gradient of snowpack response to wildfire is particularly interesting indicating that the effect of wildfire on snow ablation may be intensified in southern latitudes, which experience higher solar insolation (Table 4-3). Though more replication across both latitude and elevation would be required to

determine the magnitude of this effect, this small meta-analysis gives evidence that latitude and solar insolation may be the primary drivers of snow ablation in post-fire landscapes.

While snow accumulation in burned forest stands varied greatly between studies, snow ablation rates, or the timing of release of snow water resources, remained constant with snow melting earlier and faster in burned forest plots in all studies (Table 4-3). This occurred despite increased snow accumulation in burned forests in some studies (Burles and Boon 2011). Our results were moderate with snow disappearing 4 days (North) and 14.5 days (South) earlier in burned forest than in unburned forests (Figure 4-4). While few studies quantified solar radiation or wind speed in burned and unburned forests, solar radiation and wind speed would be expected to increase in burned forests as has been documented in clear-cut or insect infested forests (Biederman et al. 2014a; Golding and Swanson 1986). Calculations determining partitioning of snow ablation into snowmelt, which contributes to the local water budget, and sublimation and evaporation which does not, were lacking in all the studies in summarized in Table 4-3. Still, sublimation and evaporation may account for a large part of the water budget (Biederman et al. 2014b; Strasser et al. 2008) and likely varies between burned and unburned forests, north and south facing aspects, and elevation and latitude. Partitioning between vapor loss, infiltration, and streamflow in burned forest stands is yet to be explored in peer-reviewed literature.

Several studies observing stream discharge from burned watersheds have found dramatic increases in springtime runoff ranging from 100-1100% (Kinoshita and Hogue 2015; Wine and Cadol 2016). While we did not observe large increases in snow accumulation in burned forests that might lead to such an increase (Figure 4-3), we did observe faster ablation rates and a shortened melting period which could increase the amount of streamflow at one time (Figure 4-4). The observed increase in streamflow discharge after large wildfires could be a result of

decreased soil infiltration and increased surface flow on post-fire hydrophobic soils (Granged et al. 2011; Versini et al. 2013); 2) as well as decreased evapotranspiration from lack of live plant tissue in burned forest stands (Lane et al. 2006)

Aspect Effects on Snow Characteristics

Topographical aspect has long been observed to affect both accumulation and ablation of snowpack in subalpine forests (Jost et al. 2007). Thus, it is important to consider how the effects of disturbances change on various topographical aspects. As expected, aspect was the greatest predictor of snowpack accumulation and ablation after the year in which snowpack was observed (Figure 4-3). Studies done in other disturbance types such as logging or beetle killed forests have discovered that aspect typically has a stronger effect than vegetation on snowpack accumulation and ablation (Geddes et al. 2005; Jost et al. 2007; Robert 2004) especially in open or deciduous forest types (Murray and Buttle 2003).

Fire Effects on Snowpack Characteristics Modified by Aspect

The amount of peak snowpack, or snowpack available for springtime melt, should be governed by two competing processes: 1) more snowpack accumulates in burned forests due to a reduced capacity of the forest canopy to intercept falling snow; and 2) less snowpack accumulates in burned forests due to a reduced capacity of the forest canopy to shade snowpack from incoming solar radiation and protect it from other turbulent fluxes (Harpold et al. 2014; Musselman et al. 2015). Our study provides evidence that these two processes are both present at the landscape scale and are mediated by topographical aspect in the presence of fire (Figure 4-3).

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While the effects of wildfire on snowpack were present, they were only statistically significant with snow depth on south facing aspects (Figure 4-3). Snow depth may have achieved statistical significance because of the higher sampling density than snow density or SWE in the experimental design. Depth samples were taken every five meters along two one-hundred meter transects, while snow density and SWE samples were only taken every twenty-five meters along a one-hundred meter transect (Figure 4-3). Another possible reason why snow depth showed clear patterns while density and SWE were less clear is because of the inverse relationship of snow depth and snow density. As snow depth increased within a treatment, snow density showed a decreasing trend. Conversely, as snow depth decreased, snow density increased having a neutralizing effect on SWE (Figure 4-3).

Wind speeds can play a large role in snowpack accumulation and ablation by transporting snow and increasing sublimation and evaporative processes (Musselman et al. 2015; Woods et al. 2006). Increases in snow depth in burned north forests compared to unburned north forests and decreases in depth in burned south forest compared to unburned south forests suggest that wind transport of snow was not a large driver of snowpack accumulation in this study (Figure 4-3).

Snow ablation patterns followed predictable sequences of melting faster and earlier on southern facing aspects and on both north and south facing burned aspects (Figure 4-4; Table 4-2). Previous studies done in intact forests have shown similar results of increased influence of topographical variables on snow ablation with decreased forest canopy density (Hubbart et al. 2015; Musselman et al. 2015). Based on evidence from our results as well as the studies performed in Table 4-3, we propose that forest fire more heavily impacts snow ablation than snow accumulation and that rapid snow ablation events hold greater potential for ecological and

societal concern. While site specific characteristics such as elevation, vegetation type, latitude, snow quantity, wind patterns, and forest canopy densities should be considered (Varhola et al. 2010) we would expect faster ablation rates and earlier snow-free dates on both north and south facing burned aspects in subalpine forest systems.

Conclusion

This study emphasizes the importance of considering topographical variables when discussing forest cover and/or disturbance on snowpack. We found that post-fire conditions had an opposite effect on snow properties with increased snow depth on burned north aspects and decreased depth on burned south facing aspects. We also find that snow ablation occurs more rapidly in both north and south facing burned forests that in unburned forest. This is consistent with other studies showing faster snow ablation in north facing burned forest vs. unburned forests despite increased depth in burned forest stands (Table 4-3). Possible latitudinal and elevational gradients amongst these studies is also highlighted, suggesting a potential reduction of snowpack in burned forest stands at southern latitudes. With increasing global water demands, uncertain consequences of global climate change, and forest fires increasing in frequency, size, and severity, it is important for us to improve our understanding of how wildfires affect snow-water resources and be able to predict the consequences for both ecosystems and society. Future studies should include calculating energy balances on various topographical aspects within burned forests and incorporating those into landscape-wide models, as well as observing discharge rates and water quality metrics from burned watershed effluent and their effect on downstream ecology and infrastructure.

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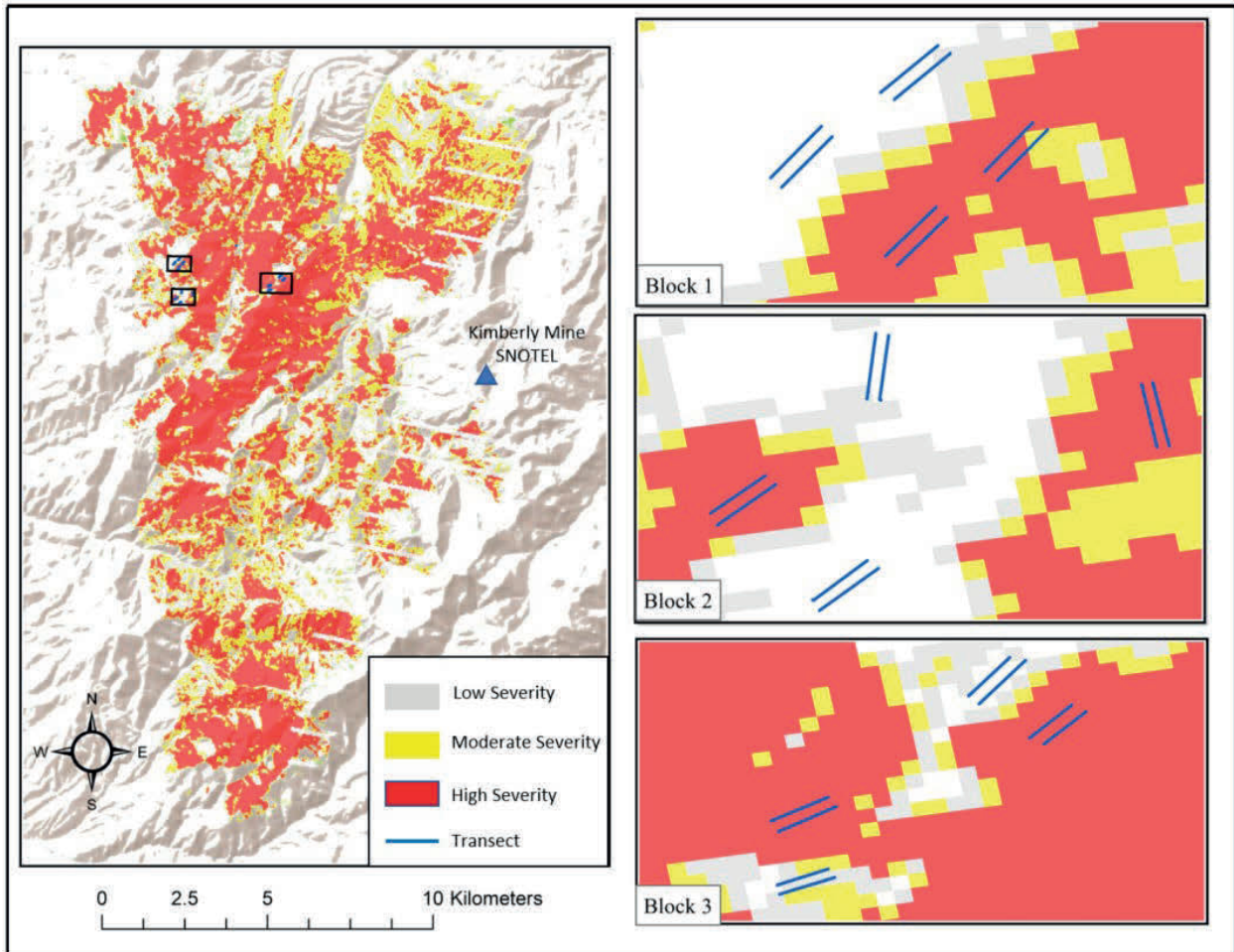
Figure 4-1: Burn severity map of Twitchell Canyon fire showing one-hundred meter transects across three blocks including treatments of burned and unburned, north and south facing aspects. Pixels are 30x30 meters and all treatments within blocks were at the same elevation ranging from 2900 to 3100 meters.
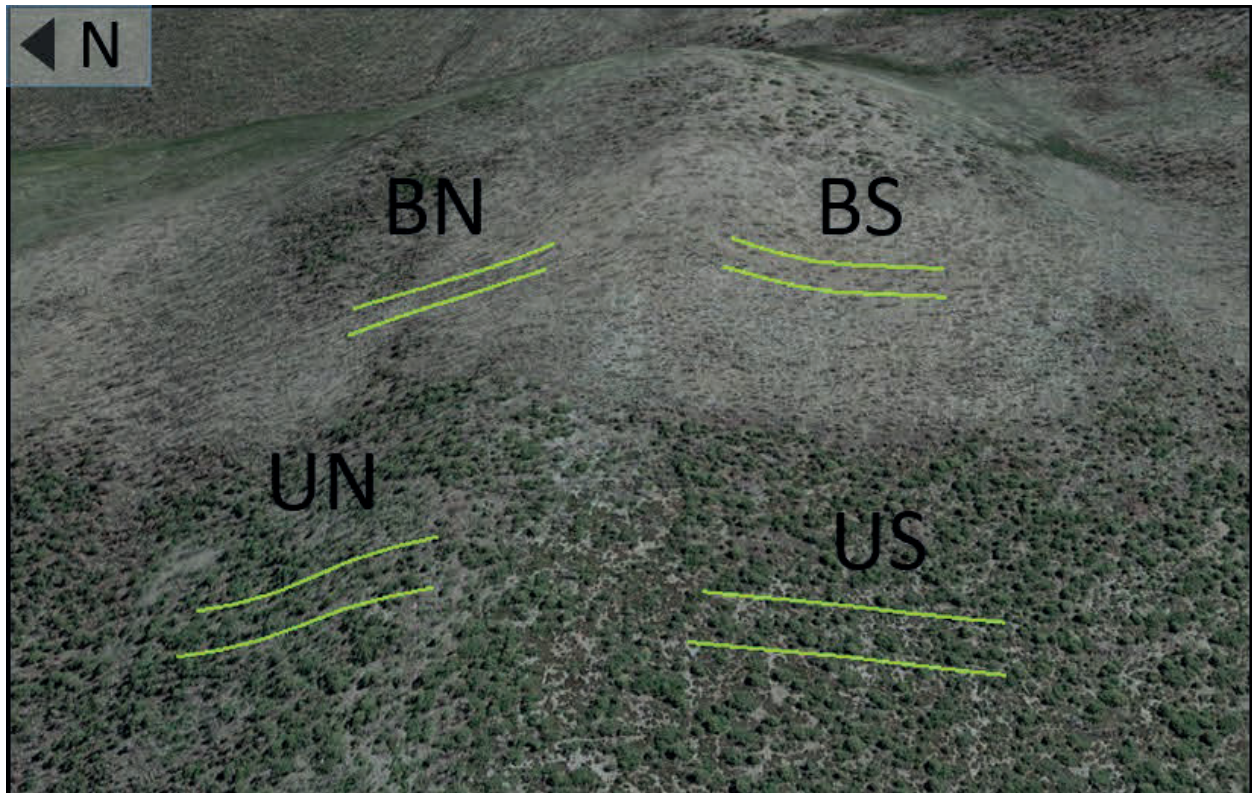
Figure 4-2: Google Earth Imagery of Block 1 showing 100 meter transects where snow sampling took place. BN =Burned North, BS = Burned South, UN = Unburned North, and US = Unburned South.
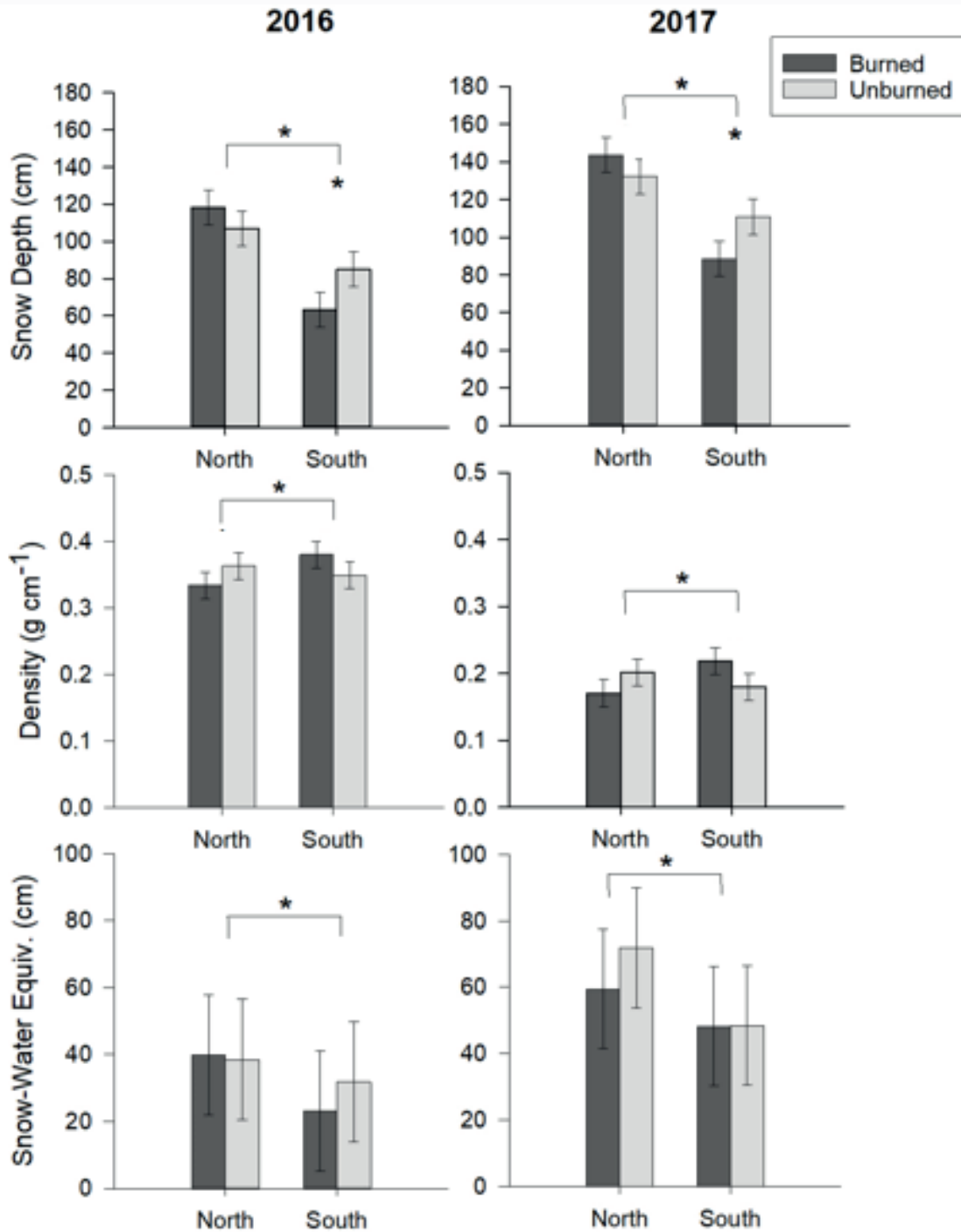
Figure 4-3: Results of linear mixed effects model including depth, density, and SWE data from 2016 and 2017. Data is averaged between the three blocks. While not shown above, all interactions between years were significant with more snow in 2017 (p = <0.001). Standard error bars show the standard error of the linear mixed effects model which included the interaction between aspect and burn condition.
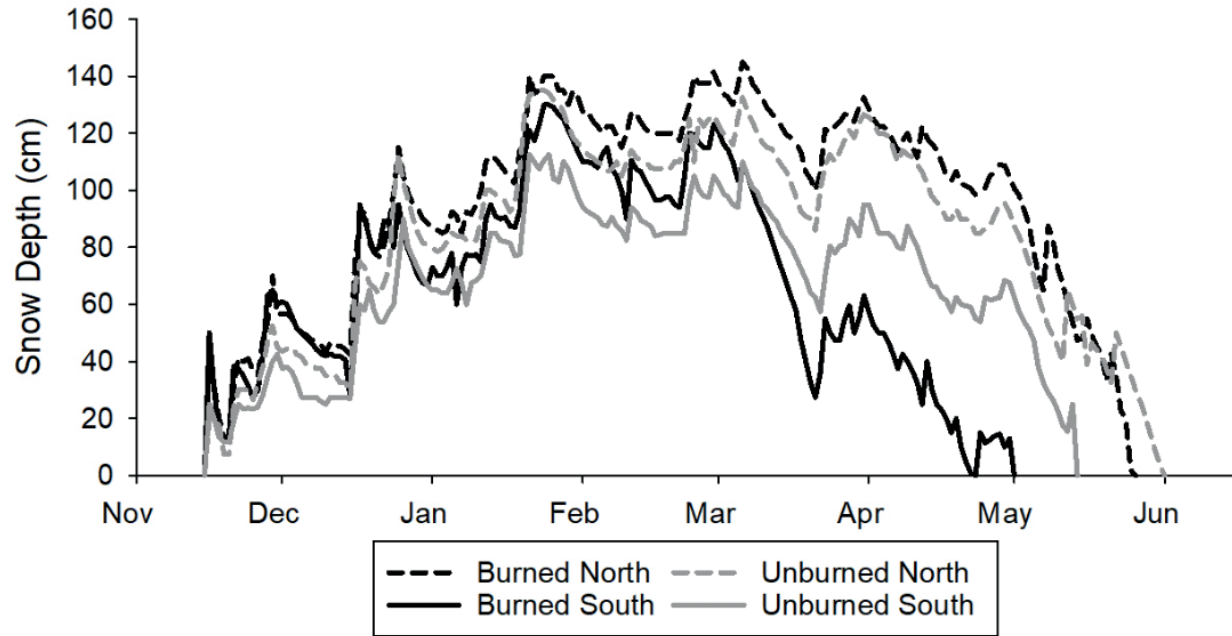
Figure 4-4: Averaged snow depth data between three blocks consisting of burned and unburned, north and south facing aspects. Data reveals accelerated ablation in burned forests on both north and south facing aspects.

TABLES

Table 4-1: Meteorological data taken from Kimberly Mine SNOWTEL site and separated into winter and spring months. Mean dew point was retrieved from Oregon State PRISM data.

| | 2015-16 | | 2016-17 | |
| | Dec-Feb | March-May | Dec-Feb | March-May |
	Mean	Mean	Mean	Mean
Temperature (C°)	-3.7	2.9	-3.2	3.7
Mean Dewpoint (C°)	-12.22	-6.89	-10.8	-7.57
Precip Accumulation (mm)	429.1	-	452	-
Max SWE (mm)	361.2	-	398.8	-
Day of Max SWE	Feb 24th	-	March 6th	-
Snow-Free Date	May 19th	-	May 21st	-

Table 4-2: Results of One-Way ANOVA and Tukey HSD correction for Snow-free dates (days) and snow ablation rates (cm/day) within each treatment type. ** Represents p-value <0.05 * Represents notable findings of p-value 0.05 - 0.10.

Snow_Free Date					Snow Ablation Rate				
Treatment	Diff	lwr	upr	p-value	Treatment	Diff	lwr	upr	p-value
BS-BN	-25.0	-38.18	-11.82	**0.002	BS-BN	0.45	-0.28	1.17	0.2
UN-BN	4.0	-10.74	18.74	0.786	UN-BN	-0.33	-1.06	0.4	0.37
US-BN	-10.5	-25.24	4.24	0.163	US-BN	-0.46	-1.18	0.27	0.19
UN-BS	29.0	14.26	43.74	**0.002	UN-BS	-0.78	-1.51	-0.05	**0.04
US-BS	14.5	-0.24	29.24	*0.053	US-BS	-0.9	-1.63	-0.17	**0.024
US-UN	-14.5	-30.64	1.64	*0.075	US-UN	-0.12	-0.85	0.61	0.9

Table 4-3: A list of studies which include direct measurements of snowpack in both burned and unburned forested plots. All studies took place on northern facing aspects or on relatively flat ground. Studies are organized by latitude. Possible patterns exist in latitudinal and/or elevational gradients as well as slope angles.

	Latitude	Elevation	Slope Angle	Change in SWE
Harpold 2014	35.8°	2700-2800m	15-18°	10% Decrease in Burned Forest
Our Results	38.5°	2900-3100m	15°	No Change in SWE
Gleason 2013	44.3°	1750m	0°	11% Increase in Burned Forest
Skidmore 1994	44.7°	2000m	0°	7% Increase in Burned forest
Burles 2011	49.4°	1680-1775m	4-8°	50% and 58% Increase in Burned Forest
Winkler 2011	51.2°	1250-1300m	0°	25% Increase in Burned Forest