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Fire Severity and Size Alter Quaking Aspen (*Populus tremuloides*) Regeneration and Defense Against Ungulate Herbivory

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A thesis submitted to the faculty of
Brigham Young University
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Master of Science

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ABSTRACT

Fire Severity and Size Alter Quaking Aspen (*Populus tremuloides*) Regeneration and Defense Against Ungulate Herbivory

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Master of Science

Human activities and rapid global climate change are altering fire regimes with potential threat to the stability of aspen ecosystems in North America. Aspen is an early successional species that plays an important role in post-fire forest reestablishment, but chronic browsing on juvenile aspen by large ungulate herbivores after fire can be detrimental and lead to regeneration failure. Although larger and more severe fires are expected to become more prominent, whether and how this may influence aspen and ungulate communities remains unclear. The objective of this research was to examine how the relationship between aspen and ungulate communities might be influenced by variation in fire severity and size. In 2012, we examined browse patterns, growth responses and defense chemistry (phenolic glycoside and condensed tannins) concentrations of regenerating aspen that experienced variable burn severity in the 2010 Twitchell Canyon Fire, Utah, USA. We found that greater light availability in higher severity burn environments enhanced aspen tolerance and resistance against herbivory by increasing growth potential and defense chemistry concentrations of aspen. These results suggest that burn severity influences plant-herbivore interactions through bottom-up and top-down forces, and that higher fire severity increases post-disturbance vegetation recruitment potential by increasing resilience to herbivory. In 2013, we characterized aspen and ungulate patterns of 25 fires that spread across five National Forests (Uinta-Wasatch-Cache NF, Ashley NF, Fishlake NF, Dixie NF, and Manti-La Sal NF) in the state of Utah. We identified interaction effects between fire size and severity that strongly influenced aspen and ungulate densities. Fire size and severity are important ecological filters that can interact to affect forest reestablishment and community response. This information is useful in developing decision-making tools for wildfire and ungulate management that can more effectively increase the long-term resilience of forests systems.

Keywords: aspen, browsing, defense chemistry, disturbance, fire, herbivory, ungulates, severity, size

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Chapter 1

Fire Severity Alters Bottom-up and Top-down Interactions between Plant and Herbivore Communities in Mixed Forests

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Fire Severity Alters Bottom-up and Top-down Interactions between Plant and Herbivore Communities in Mixed Forests

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ABSTRACT Fire and herbivory are primary disturbances that often overlap and strongly influence plant community development, but it is unclear how herbivory changes in relation to variability in burn severity. With climate change expected to alter fire regimes globally, creating larger and more variable wildfires (Westerling et al. 2011), there is a critical need to understand how heterogeneity in post-fire habitat conditions modifies plant-herbivore interactions. We examined herbivory patterns, growth responses and defense chemistry expression (phenolic glycoside, condensed tannins) of regenerating aspen (*Populus tremuloides*) that experienced variable burn severity in the 2010 Twitchell Canyon Fire, Utah, USA. Browse damage was approximately 60% lower in moderate and high burn severity plots compared to low severity and unburned plots. Aspen regeneration density was 2.3 and 3.1 fold greater in high and moderate severity burn plots than in low severity and unburned plots. High burn severity stimulated photosynthesis, vertical growth and biomass accumulation. Defense chemistry expression responded dynamically over time depending on burn severity. From June to August, phenolic glycoside concentrations showed no significant change in unburned and low severity fire conditions but increased 79% and 139% in moderate and high severity burn environments. By the end of summer, condensed tannins increased six-fold in high severity burn plots, with increases of 50% or less in the lower burn severity plots. Deer activity was inversely related to fire severity and positively related to browse damage. Elk and cattle activity showed no significant relationship with browse activity. Greater light availability in higher severity burn environments enhanced tolerance and resistance of aspen against herbivory by increasing growth potential and defense chemistry expression of aspen. These results suggest that burn severity influences plant-herbivore interactions through bottom-up and top-down forces, and that higher fire severity increases post-disturbance vegetation recruitment potential by increasing resilience to herbivory.

KEYWORDS aspen, browsing, deer, disturbance, herbivory, phenolics, plant defense, tannins

INTRODUCTION

Disturbances engender lasting effects on the function and composition of plant communities (Hobbs and Huenneke 1992). Fire is among the most widespread and powerful disturbance forces in nature and is influenced by humans at a global scale (Bowman et al. 2009). Understanding the relationship between fire disturbance and plant community development is critical yet challenging. Fire behavior can be erratic; and depending upon the spatial and temporal conditions of fire, it can result in a complex mosaic of burn severity conditions across post-fire landscapes (Reilly et al. 2006). Burn severity has been defined as the magnitude of ecological changes caused by fire (Agee 1996). Varying burn severity results in heterogeneous habitat conditions that can have cascading effects on plant community succession and the abundance and diversity of mammals and insects (Romme 1982, Bailey and Whitham 2002).

Herbivory is also a powerful disturbance force that shapes the evolution of plants and the development of plant communities, and often overlaps and interacts with the effects of fire (Van Langevelde et al. 2003). Chronic or severe herbivory by large populations of ungulate herbivores is one of the most prevalent and destructive stressors in plant communities (Schoenecker et al. 2004, Rackham 2008). Plants employ three general defense strategies against herbivores: they can tolerate herbivore damage through compensatory growth (strategy of tolerance), avoid browsing damage by reducing exposure to herbivores through vertical growth (strategy of escape), or invest resources in producing defense compounds in an effort to deter herbivory (strategy of resistance) (Mauricio et al. 1997, Harding et al. 2009). Post-fire conditions can modify plant resource availability and growth patterns that may influence the efficacy of these defense strategies (Erwin et al. 2001). While it is established that fire and herbivory often overlap and influence plant community development, there is a need for more studies on how heterogeneity in post-fire habitat conditions resulting from variable burn severity may influence susceptibility to and defense against ungulate herbivores.

Plants produce a broad suite of defense compounds to defend themselves from herbivores. Among these are phenolic based compounds including condensed tannins that are produced across a broad group of plant taxa and phenolic glycosides that are expressed in the willow family (*Salicaceae*) (Barbehenn and Constabel 2011, Boeckler et al. 2011, Lindroth and St. Clair 2013). There is evidence that phenolic glycosides can reduce plant tissue consumption by elk (Wooley et al. 2008) and condensed tannins lower the nutritional quality of forage consumed by livestock (Min et al. 2003). Deer have been shown to avoid high level of tannins in their diet, but selected for low level of tannins over a control diet without tannins (Verheyden-Tixier and Duncan 2000). Plants have been shown to invest up to 25% of their resources into the production of phenolic glycosides and condensed tannins, particularly in young saplings that are susceptible to ungulate browsing (Smith et al. 2011a). Alternatively, plants can allocate resources to growth to compensate for tissue loss following herbivory or to escape browsing through vertical growth. According to the growth–differentiation balance theory, there should be a tradeoff between investments in growth and defense (Herms and Mattson 1992). However, the balance in this tradeoff is often modified by environmental conditions, particularly plant resource availability (Osier and Lindroth 2006). Burn severity can affect post-fire soil and plant community properties that influence light environment and soil moisture and nutrient availability (Certini 2005). What remains indefinite, particularly at a mechanistic level, is how resource variation in post-fire environments may influence the efficacy and tradeoffs of plant defense strategies against herbivores.

Fire alters habitat conditions that may create top-down effects on post-fire plant regeneration by altering the behavior of ungulate herbivores. In many systems, browsing and grazing animals are attracted to recently burned patches (Pearson et al. 1995, Klop et al. 2007). Differences in fire severity create heterogeneity in habitat conditions that may influence herbivore movement and foraging patterns (Bailey and Witham 2002, Bates et al. 2006). What is lacking is a better understanding of how different ungulate herbivores utilize post-fire habitats and how their response to variability in burn severity influences patterns of herbivory.

Aspen forests provide an ideal study system to examine patterns of herbivory and defense strategies and their tradeoffs along gradients of fire severity for three reasons. First, aspen regenerate rapidly from their root system following fire (Smith et al. 2011b), and often experience browsing by ungulate herbivores during that period of time (Seager et al. 2013); second, they produce phenolic based defense compounds, often at very high levels (Lindroth and Hwang 1996); finally, they demonstrate mechanisms of herbivory tolerance and escape through compensatory growth and rapid vertical growth rates (Stevens et al. 2008). The objective of this study was to examine burn severity impacts on herbivore activity, and browse patterns, growth responses and defense chemistry expression of regenerating aspen. The following predictions were tested: (i) post-fire aspen regeneration density increases with fire severity; (ii) high burn severity has positive effects on water relations, nutrient acquisition, carbon metabolism and growth rate of aspen saplings; (iii) high severity burn conditions will alter the production of phytochemical defense compounds that influence browse intensity; (iv) burn severity influences ungulate preference for patch usage; and (v) burn severity modifies tradeoffs between growth and defense of aspen.

METHODS

Study area description

This study was conducted in Shingle Creek and Indian Creek watersheds within the Twitchell Canyon fire complex on the Fishlake National Forest in central Utah (38.425°N

112.499°W). The two watersheds are separated by approximately 10 km. Elevations ranged from approximately 2300 m to 2800 m and stand slopes ranged from 1 to 60 degrees. Average annual precipitation ranges from 40 to 90 cm per year. This area is dominated by mixed stands of aspen and conifer, with ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and subalpine fir (*Abies lasiocarpa*) being the most dominant coniferous species. Douglas-fir (*Pseudotsuga menziesii*), juniper (*Juniperus scopulorum*), and blue spruce (*Picea pungens*) were also commonly seen in our sites. On July 20, 2010, the Twitchell Canyon Wildfire was ignited by a lightning strike in the study area. The fire spanned nearly 90 days and burned over 18,000 hectares of forest, creating a spatially-variable fire-severity mosaic across the landscape (Fig. 1).

Study design

In each of the two watersheds, four groups of adjacent aspen-conifer stand patches (>2 ha) that varied in burn severity were selected for establishment of study plots. Each group had 1 high burned patch, 1 moderate burned patch, 1 low burned patch, and 1 unburned (control) stand patch. Elevation, slope, and aspect of the patches within each group did not differ significantly based on statistical comparisons using an analysis of variance model. Groups of stand patches were initially identified using a burned area reflectance classification (BARC) map derived from multi-spectral satellite imagery developed by United States Department of Agriculture (USDA) Forest Service GIS database (Fig. 1). Fire severity was ground-truthed in the field by verifying overall tree mortality caused by fire, and was assigned to one of the four burn severity classes based on the following criteria: high (>75% overstory mortality), moderate (35-75% overstory mortality), low (<35% overstory mortality), and unburned. The study design was unbalanced as one group did not have patches that met the criteria for low severity and another group was missing an unburned stand patch (see our approach for dealing with this in the statistics section below).

Stand characterization

A single 30 m diameter circular plot (unit of replication) was established at each stand patch. Pre-fire stand composition of each plot was characterized by identifying the species of all overstory and midstory trees (>10 cm DBH) that survived the fire using tree bark and branching patterns. Tree calipers were used for DBH measurements. Slope and aspect were determined using a clinometer and a compass. Stand density was calculated by dividing the total number of trees in each plot by the total plot area. We calculated stand basal area by summing the basal tree area of the same species (basal tree area=π $(DBH/2)^2$) and then dividing by the plot area. Field data for pre-fire tree species composition, stand density, and basal area were collected in August 2012. Aspen to conifer ratios in the unburned, low, moderate, and high severity burned plots were 55:45, 47:53, 52:48, and 43:57 respectively. Basal tree area for unburned, low, moderate, and high severity plots were 38±5, 41±4, 29±3, and 33±3 m^2 ha^{-1}. Average stand densities for unburned, low, moderate, and high severity plots were 639±95, 773±103, 688±89, and 838±84 stems ha^{-1}.

Field measurements

Measurements and sample collections of post-fire aspen saplings, soil and light environment occurred within the same 30 m circular plots outlined above. Based on the rapid growth of post-fire aspen stems and examination of root connections it was evident that the regeneration response was primarily driven by asexual root sprouting. Each plot was divided into four equal-sized quadrants and 2 randomly selected post-fire aspen saplings (>2 m tall) per quadrant (8 per plot) were selected for measurement of gas exchange, water relations and leaf tissue samples. Measurements were pooled and averaged to represent plot-level averages. Since aspen can induce chemistry in response to herbivory, only aspen without browse damage were selected for sampling. Measurements and sample collection occurred June 6-8 and were repeated on August 20-22, 2012. We measured above and below canopy photosynthetically active radiation (PAR) and calculated leaf area index (LAI) using the AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, Washington, USA). Ten light readings were made in each quadrant (40 measurements per plot) and then averaged for the plot. Light measurements were made between 10:00 and 15:00 hours. Plot measurement order was randomized to avoid diurnal biases. Since resource availability can mediate tradeoffs between maximum growth rate and plant defense (Coley et al. 1985), we estimated maximum growth of post-fire aspen at the plot level by collecting the tallest sapling without browse from each quadrant (4 per plot). These saplings were cut at ground level and then transported back to the lab, dried for 48 hours at 70ºC and weighed to determine above ground sapling biomass. For unburned plots, we only sampled saplings <2 m in height and <2.5 cm in DBH to avoid comparing saplings that were established before the fire. Growth rings of all measured saplings were counted to validate if establishment had occurred post-fire. Based on growth rings all but a couple of saplings had established after the 2010 fire. For those that did not, a new sapling was selected that had established post-fire. From each quadrant, a soil core sample was collected to a depth of 10 cm. Each of the four samples was then combined to form a pooled sample from each plot. Ten soil moisture readings were made within each quadrant and the forty values were averaged to obtain a plot level soil moisture value. Soil samples, soil moisture readings and light data were collected in August

2012.

Post-fire aspen regeneration density, height and browse intensity were determined within a 30 x 2 m belt transect centered in the middle of each circular plot in a random direction. Post-fire aspen regeneration density was determined by counting all aspen saplings within the belt transect. We measured the height of all saplings within the belt transect using a measuring stick. Browsing was identified by nipped apical buds and leaves removed below the leaf base-petiole junction (Keigley and Frisina 2008). Browse intensity was calculated as the total number of browsed saplings divided by the total number of aspen stems in each transect. Pellet-groups of mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*), and cattle (*Bos primigenius*) pats within the same belt transect were identified and counted. Deer pellets were discriminated from elk pellets by shape and size (Rost and Bailey 1979). Measurements in belt transects were conducted in August 2012.

Gas exchange and water relations

Photosynthesis measurements were made on the youngest fully expanded leaf of each aspen sapling using a leaf chamber and a portable gas analyzer (LI-COR 6400, LI-COR Environmental Inc., Lincoln, Nebraska, USA). Photosynthesis was measured at a photosynthetic photon flux density (PPFD) of 2000 μmol $m^{-2}s^{-1}$ generated by a blue-red LED light source at ambient temperature and humidity. CO_2 concentrations were controlled at 395 ppm in the chamber using a CO_2 mixer. Rates of photosynthesis were recorded when CO_2 and water vapor concentrations in the chamber were stabilized (minimum of 60 seconds). The aspen stem was then clipped and measured for xylem water potential using a pressure chamber (PMS Instrument Company, Albany, Oregon, USA). Leaf samples were then collected for tissue analysis described below. Measurements were made between 9:00 and 16:00 hours and the plot measurement order was randomized to avoid diurnal biases.

Leaf analysis

Leaf samples were placed in freezer bags and stored between blocks of dry ice for transport back to lab and stored in a freezer at -80°C and freeze dried to preserve tissue defense chemistry. Leaf tissue samples collected from each of the quadrants within each plot were pooled and homogenized in a Wiley Mill using a #10 screen.

Phenolic glycosides (salicortin and tremulacin) were extracted from 50 mg of freeze-dried leaf tissue in 0.66 ml of methanol in 2 ml screw-cap micro-centrifuge tubes. The samples were vortexed at high speed for 3 min. The liquid supernatant was then removed and placed in a separate micro-centrifuge tube. We repeated this procedure two more times until we obtained a 2 ml volume of sample extract. Final concentrations of salicortin and tremulacin were determined using high-performance liquid chromatography (HPLC, Agilent 1100 Series, Santa Clara, California, USA) with a Luna 2, C18 column (150 x 4.6 mm, 5 µs) at a flow rate of 1 ml min^{-1}. Compound peaks were visualized under a UV lamp at a wavelength of 280 nm using purified salicortin and tremulacin standards isolated from aspen leaves according to the methods of Lindroth et al. (1993).

Condensed tannins were extracted from 50 mg of freeze-dried leaf tissue with 1 ml of 70% acetone containing 10 mM ascorbic acid (AA) in 2 ml screw-cap micro-centrifuge tubes. The samples were then vortexted on high at 4°C for 20 min. The liquid supernatant was then removed and placed in a separate micro-centrifuge tube, and the extraction was then repeated. Condensed tannin concentrations were quantified with a spectrophotometer (SpectraMax Plus

384, MDS, Toronto, Canada) using a modified butanol–HCl method (Porter et al. 1986) with a purified condensed tannin standard isolated from aspen leaves according to the methods of Hagerman and Butler (1980).

Total leaf nitrogen concentrations were determined based on the combustion method (Campbell 1992) using a LECO Truspec CN Determinator (LECO Corporation, St Joseph, Michigan, USA). For phosphorus analysis, leaf samples were ashed in a muffle furnace at 495°C for 12 hours, and then dissolved in 2 ml of 100mM HCL and analyzed using a spectrophotometer (Spectra Max plus 384, Molecular Devices, Sunnyvale, California, USA) based on the method of Murphy and Riley (1962).

Foliar chemistry measurements (phenolic glycosides, condensed tannins, N, and P) were summed and averaged to represent a measurement at the plot level instead of an individual sapling level.

Soil analysis

Soil moisture content was measured using a Field Scout 100 time-domain reflectometry (TDR) probe with 12 cm rods (Spectrum Technologies Inc., Plainfield, Illinois, USA). Values were recorded as percent volumetric water content (%VWC). Soil core samples collected from the field were homogenized, dried and analyzed for total N using the combustion method (LECO Truspec CN Determinator). Bioavailable phosphorus was extracted with a sodium bicarbonate solution and analyzed according to the methods of Olsen et al. (1954).

Tradeoffs in growth and defense

We assessed the influence of burn severity on plot-level tradeoffs between maximum growth and plant defense by examining correlations between aboveground biomass and the expression of phenolic glycosides and tannins in aspen saplings at the plot level.

Statistical analysis

Analysis of variance (ANOVA) with linear mixed-effect models were used to examine fire severity effects on stand characteristics, photosynthesis, xylem water potential, foliar nutrients, soil moisture and nutrients, and animal pellet groups. In our mixed-effect models, burn severity was specified as a fixed effect, watershed was specified as a random effect, and the groups nested within each watershed were included as random effects. Mixed-effects models were used because of their flexibility in addressing unbalanced data. Post hoc analyses were conducted using Tukey-Kramer method at alpha=0.05. Adjustments of *P* values for multiple testing were performed according to Benjamini and Hochberg (1995). Photosynthesis and xylem water potential data from June and August was averaged prior to analysis. Repeated measures analysis of variance was used to test for effects of burn severity, time and interaction between the two on phenolic glycosides and condensed tannin expression over time. Normality and equal variance assumptions were examined and met. Since the assumptions of homogeneity of variance were not compromised in our data and differences in sample size among burn severity classes were small, then it is considered appropriate to fit the linear ANOVA model without adjustments (Quinn and Keough 2002).

Pearson correlation analysis was used to examine relationships between elevation, aspect, and slope on aspen and browse intensity; and aspen defense chemistry and aboveground biomass to examine tradeoff relationship between traits of resistance and tolerance. Simple linear regression models were used to examine the relationships of aspen regeneration density, growth, and defense chemistry against burn severity (expressed as tree mortality rate), light environment (expressed as leaf area index), and herbivore browse damage. Relationships of deer and elk pellets and cattle pats densities against aspen density, growth and browse damage were also determined using linear regression models. An analysis of covariance (ANCOVA) model was used to identify potential differences in growth and defense tradeoffs as a function of fire severity class. All statistical analyses were performed using SAS/STAT® software. (SAS Institute 2011).

RESULTS

Environmental factors

Increasing burn severity drastically increased stand understory light penetration but had nominal effects on soil properties. Leaf area index in unburned plots was 31%, 138%, and 182% greater than in low, moderate, and high burn severity plots (Table 1). Fire severity did not significantly affect soil moisture, N or P levels (Table 1). Stand composition, stand density, tree basal area, elevation, aspect, and slope were not significantly correlated with aspen regeneration density, sapling height and aboveground biomass or browsing damage ($P>0.05$).

Water potential and gas exchange

Burn severity had nominal effects on xylem water potential but increased photosynthetic rates (Table 1). The strongest contrast in photosynthetic rates was observed between high severity burn plot and unburned plot, which differed by nearly 45% (Table 1).

Foliar nutrients

Phosphorus concentrations in aspen leaves decreased with greater burn severity. Foliar P concentrations were 28% and 36% lower in moderate and high severity burn compared to low burn severity plots. Foliar N concentrations did not vary significantly among burn severity classes (Table 1).

Sapling density and growth

Aspen sapling density and height showed neutral to positive responses to greater fire severity. Sapling density showed weak positive relationships with fire severity and leaf area index (Table 2). Mean sapling density in moderate and high severity burns was more than double those of low severity and unburned plots (Table 1). Sapling height was not strongly related to burn severity or leaf area index (Table 2). On average, aspen saplings were 25% taller in high severity burn plots compared with unburned and moderate burn plots ($P<0.05$). Aboveground biomass was strongly related to fire severity and more weakly with leaf area index (Table 2). Mean aboveground biomass in high severity plots was 200%, 61% and 85% greater than unburned, low and moderate severity plots respectively ($P<0.01$, except $P=0.075$ for low severity).

Browse intensity

Saplings browsed in moderate and high severity burn plots averaged 14% and 17% respectively, which was significantly lower than 35% in low severity and unburned plots ($P<0.01$; Table 1).

Ungulate activity

Elk and cattle activity were 3-6 times lower than deer activity in our study plots (Table 1). Deer pellet-group density in unburned plots was almost double that of high severity burn plots but was not statistically different than other treatment plots (Table 1). Deer pellet-groups were positively related to browse damage on aspen (r^2=0.33, P<0.001; Fig. 2). Elk and cattle pellets and pats did not differ significantly across burn severity classes (Table 1), and were not strongly related to browse damage (elk, r^2=-0.03, P=0.842; cattle, r^2=0.07, P=0.081). Pellets and pats showed no relationship with aspen regeneration density (deer, r^2=-0.02, P=0.569; elk, r^2=-0.02, P=0.545; cattle, r^2=-0.02, P=0.582), height (deer, r^2=-0.03, P=0.717; elk, r^2=-0.03, P=0.804; cattle, r^2=-0.02, P=0.539), or aboveground biomass (deer, r^2=0.02, P=0.214; elk, r^2=-0.04, P=0.857; cattle, r^2=-0.04, P=0.775).

Foliar defense chemistry

At the beginning of summer, burn severity class had no significant effects on levels of phenolic glycosides or condensed tannins. However, defense chemistry expression changed dramatically over the course of the summer depending on burn severity conditions. In unburned and low severity burn plots, concentration of phenolic glycosides showed no significant change over the summer, but increased 79% and 139% in moderate and high severity burn plots (Fig. 3). No significant relationships were found between early summer defense chemistry levels and other variables in the regression analysis. By the end of summer, condensed tannins increased six fold in high severity burn plots, with increases of 50% or less in the other burn severity classes. Late summer phenolic glycosides and condensed tannins were positively related to burn severity and negatively related to leaf area index (Table 2). Total defense chemistry levels in late summer were negatively related to browse damage (Table 2).

Tradeoffs in growth and defense

Defense chemistry expression and growth of aspen showed strong positive relationships (Fig. 4). The relationship between defense chemistry and growth did not differ across burn severity treatments in the ANCOVA model (P=0.323). However, when we assessed the effect of each burn class independently, we found strongly significant relationships between growth and defense under high burn severity, but not in the other burn classes (Fig. 4). Growth showed a stronger positive relationship with phenolic glycosides (r^2=0.42, P<0.0001), and a positive but weaker relationship with condensed tannins (r^2=0.22, P<0.01).

DISCUSSION

Growth traits and functional responses to burn severity

Aspen growth patterns and leaf functional traits in this system showed similar patterns with previous studies that demonstrated high-severity burn conditions could stimulate aspen regeneration (Bailey and Whitham 2002, Bates et al. 2006). While it has been established that saplings in burned plots typically grow faster than those with no history of recent fire (Hessl and Graumlich 2002), we further documented the specific impacts of variable burn severity on sapling height. Aspen saplings, as expected, were tallest under high severity fire; but interestingly, moderate severity clones did not increase sapling height growth, possibly due to greater investment in sapling density (Table 1). Aboveground biomass of aspen saplings was positively related to fire severity and negatively related to LAI, which indicates that differences in biomass production were likely associated with variable light availability along the burn severity gradient. Faster growth likely improves survivorship through vertical escape from herbivory and compensatory growth following browse damage (Lindroth and St. Clair 2013, Seager et al. 2013).

Environmental modifiers of plant response to fire severity

Post-fire environmental conditions can strongly modify plant function and growth via bottom-up effects. Fire severity can affect plant development by altering soil resource availability (Certini 2005), but fire severity had relatively small effects on soil and plant water and nutrient relations in this study (Table 1). Because aspen is shade intolerant, low light environment can lead to drastic reductions in photosynthesis and growth rates (Calder et al. 2011). Reduced light penetration in unburned areas and low burn severity, due to shading by more intact overstory canopies, likely limit photosynthetic activity and growth of emerging aspen saplings (Table 1) (Pothier and Prévost 2002). The light levels in the unburned and low severity burn plots were near the threshold point at which light limits photosynthesis and growth of aspen, while light in moderate and high severity plots were well above aspen's light saturation point (Kobe and Coates 1997, Wright et al. 1998, Calder et al. 2011).

Herbivory impacts

High browse pressure can reduce tree seedling establishment and recruitment thereby altering patterns of forest development (Baker et al. 1997). Ungulate browsing on aspen saplings can significantly reduce aspen recruitment (Kaye et al. 2005). Browse intensity in high and moderate burn plots sustained only half the damage of low burn or unburned sites (Table 1). This pattern is in contrast with the results reported by Bailey and Whitham (2002) where ungulate herbivory on aspen regeneration was more intense in high severity burn sites (85% browse damage) compared to intermediate-burn sites (36% browse damage). One possibility accounting for these differences was variability in disturbance size. It has been suggested that small burns tend to be more sensitive to browsing because of the extensive damage that large herbivores can cause on small areas (Brown 1985). When the fire is small, the negative impact of overpopulated browsers on aspen stands may overshadow any positive effect of high severity fires. Smith et al. (2011b) also hypothesized that disturbance size may have influenced the ability of aspen to resist browse pressure in their study. However, no study has specifically investigated the effects of fire size on aspen sensitivity to herbivory. The Twitchell Canyon Fire in this study was three times larger than the fire in Bailey and Whitham's study, and produced higher regeneration densities over a larger area. Recent work suggests that burn size and long-term aspen regeneration success are positively correlated (H.Y. Wan et al. unpublished results). We hypothesize that the strong sapling response under high burn severity and large fire size interacted to successfully apportion and disperse browsing intensity by ungulates.

Ungulate species demonstrated variable activity based on habitat burn severity. Our pellet and pat data suggest that deer were several times more abundant on the landscape than elk or cattle and/or spent more time in low severity and unburned habitat conditions. Feeding rates of deer tend to be higher in more covered habitats (Wickstrom et al. 1984). The uniform pattern of elk pellets may be due to the fact that elk are generally less selective than deer and are able to utilize more diverse forage sources (Collins and Urness 1983). Taken together, the data suggests that deer populations had the greatest browsing influence on regenerating aspen in this study system and they tended to be more active in lower fire severity burn environments.

Fire severity effects on defense

In our study system, aspen growing in high burn severity environments was better suited to deal with ungulate browsing in three possible ways. First, greater burn severity resulted in taller saplings and greater aboveground biomass, suggesting more growth potential to compensate for herbivore damage. With greater growth potential coupled with higher stem densities, a population of regenerating saplings may be less susceptible to browse damage. This is referred to as the crowding or “safety in numbers” effect (Karban et al. 1989, Connell 2000). However, such a finding is inconsistent with other studies in which stimulated regeneration response of aspen in high severity burns attracts browsers and sustains greater herbivore damage than low severity sites (Bailey and Whitham 2002, Bates et al. 2006). As outlined above fire size may play an important role in determining browsing outcomes along burn severity gradients. Further research is needed on factors that may interact with burn severity, such as herbivore density, fire size, and competition, to better understand compensatory growth responses.

Second, our data suggest that more severe fires stimulate vertical growth that hastens herbivory escape. Rapid vertical growth is an important herbivory escape strategy for plants at early growth stages (Lindroth and St. Clair 2013). Based on our vertical growth data, saplings in high severity areas would begin to escape browsing (i.e.,>2 m) about 30% faster than saplings in moderate severity burns and unburned environments (Table 1).

Third, aspen saplings appear to have greater resistance against herbivory in high burn severity plots. Our results showed that burn severity and leaf area index are inversely related to phenolic glycosides and tannin production (Table 2), suggesting that greater light availability as a result of higher burn severity can stimulate the production of defense chemicals. This is consistent with studies in controlled environments showing increases in defense chemistry with greater light availability (Lindroth et al. 1993, Osier and Lindroth 2006, Calder et al. 2011). The observed differences in foliar phenolic glycoside concentrations from 20% dry weight in high severity burns to 10% dry weight or less in unburned, and low severity burns in this study (Fig. 3) could increase aspen herbivory risk substantially (Wooley et al. 2008).

Previous studies have shown that phenolic glycosides and condensed tannins often change across a growing season, and can influence performance of insect herbivores (Hwang and Lindroth 1998, Osier et al. 2000, Lindroth et al. 2002). In this study, levels of defense chemistry did not differ in early summer but increased over the summer, with the greatest change recorded in high burn severity plots. Although other studies have reported herbivore induced resistance via phenolic glycoside production and tannins (Stevens and Lindroth 2005), it was unlikely that increases in defense compounds in our high severity plots was driven by herbivore induction because these plots had the lowest levels of browse damage across all burn treatments. Rather differences in light environment seem to be the most likely driver of aspen defense chemistry production between early and late summer as evidence by the strong positive relationship between defense chemistry and light availability (Table 2).

As other forage sources become scarce toward late summer and lose their nutritional quality, browse pressure on aspen may intensify since it maintains its nutritional quality into the fall (Tew 1970, A. Rhodes et al. unpublished data). Large ungulate herbivores often become more selective in their diet during the end of the summer growing period to meet their nutrient and energy needs (Renecker and Hudson 1986). The observed increase in defense chemistry production from early to late summer under higher burn severity appears to match well with potential increases in browse pressure on regenerating aspen as the summer progresses into autumn.

Tradeoffs between tolerance and resistance

Results from controlled studies generally support the hypothesis that there is a tradeoff between growth and defense (Donaldson et al. 2006, Osier and Lindroth 2006), but conflicting examples have also been reported (Stevens et al. 2007). In this study, we found no evidence of tradeoffs between growth and defense under natural experimental conditions. In contrast, a strong positive relationship between growth and defense under high burn severity (r=0.71; P<0.001; Fig. 4) suggests that aspen can simultaneously allocate resources to both growth and defense strategies under favorable environmental conditions. This indicates that plant resource availability is non-limiting in our study system particularly in high severity burn environments (Fig. 4). Much of the previous work on aspen growth and defense tradeoffs has focused on genotypic variation among clones within various resource environments. In this study, we examine relationship between growth and defense in a species that is often clonally integrated at the forest stand level. Our results suggest the absence of a strong tradeoff between growth and defense at the stand level particularly under conditions of high resource availability.

CONCLUSION

Fire activity in the Western United States has increased in recent decades (Westerling et al. 2006), and wildfire suppression costs by federal land management agencies averaged US$1.5 billion annually for the past five years, which was triple the inflation-adjusted costs in 1985 (National Interagency Fire Center 2013). This trend is expected to continue as influences of human activity and climate change on fire regimes persist (Westerling et al. 2011). Effective fire management strategies require an understanding of how changing fire behavior is likely to affect ecological relationships. Fire suppression in many forests systems during the 20th century has increased stand densities and fuel loads which raises the likelihood of high intensity and widespread wildfires (Sampson et al. 1994). Rising temperatures are expected to shorten the duration of mountain snow cover (Brown et al. 1995), which may cause fire seasons to lengthen (Flannigan et al. 2009) and more browse potential by ungulates earlier and later in the growing season (Martin and Maron 2012). These changes are believed to have significant impacts on species abundances and distribution in many forest ecosystems (Shinneman et al. 2013). In this study, we have identified cascading effects of burn severity that strongly influence bottom-up and top-down interactions between plant and herbivore communities. Given the dramatic increase in fire occurrences, size, and severity in recent years, we suggest that forest management should incorporate detailed examination of fire characteristics to increase forest resilience in the long run. Careful application of this knowledge should reduce costs and improve efficacy in forest restoration and fire management.

Aspen and other post-disturbance pioneering species play a fundamentally important role in facilitating the post-disturbance re-establishment of forest communities (St. Clair et al. 2013), but intense browsing by ungulates can be detrimental to their establishment and recruitment (Baker et al. 1997). Therefore, maintenance and protection of pioneering species in burned areas with abundant ungulate browsing activity is of particular importance. Based on the results in this study, when recruitment of aspen is desired we recommend avoiding scenarios that result in small fires and low-severity burn conditions.

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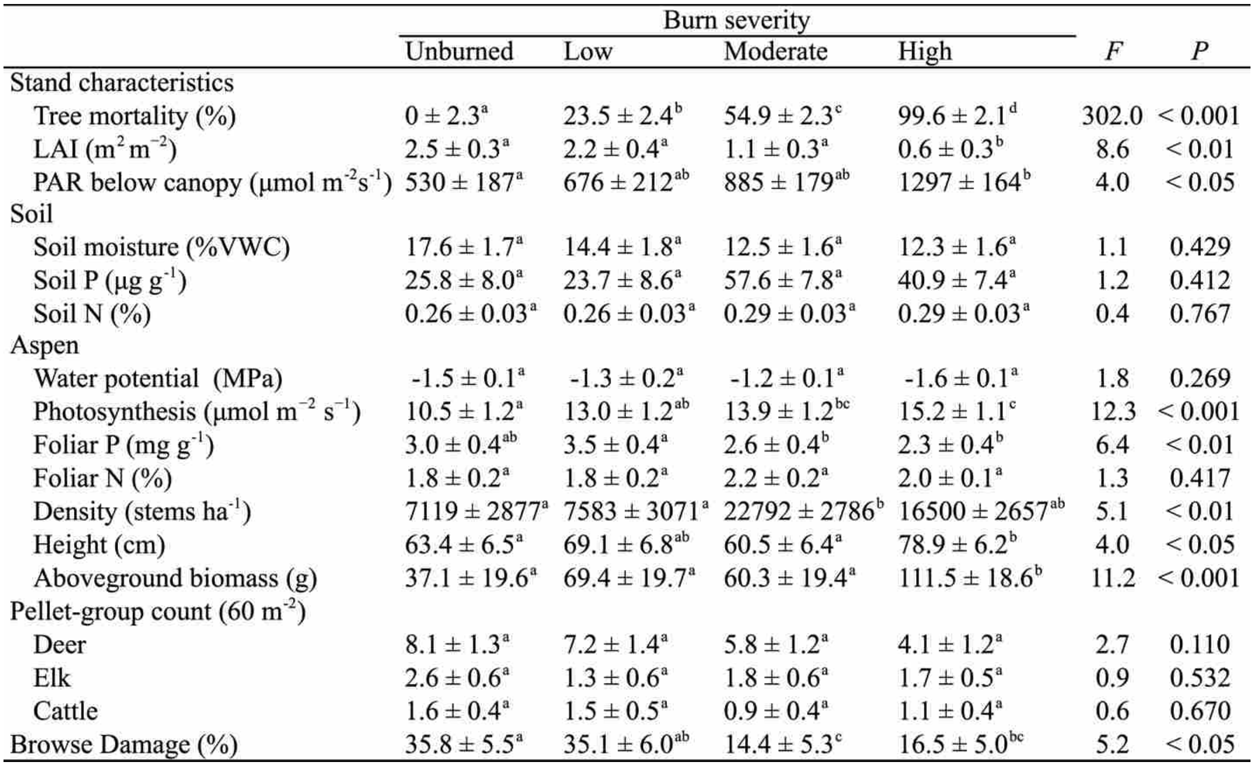
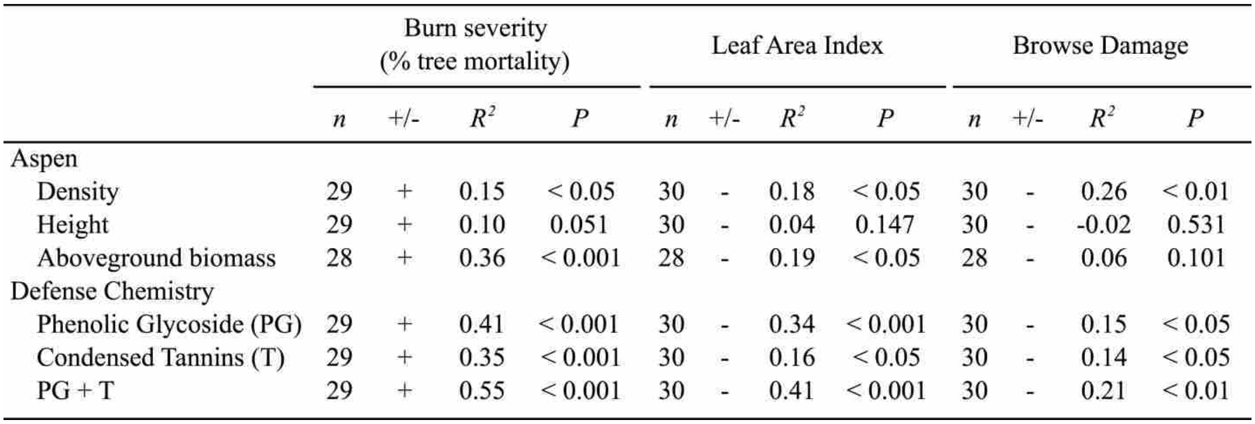
Table 1. Effects of burn severity on stand characteristics, soil properties, aspen functional traits, and ungulate pellet-group counts. Means±SE are presented. Degrees of freedom were identical across all variables (df1=3, df2=26), with the exception of tree mortality rate (df1=3, df2=25) and aboveground biomass (df1=3, df2=24). Pairwise differences were determined using Tukey-Kramer method at α=0.05, with superscript letters denoting significant pairwise differences.



	Burn severity					
	Unburned	Low	Moderate	High	*F*	*P*
Stand characteristics						
Tree mortality (%)	0 ± 2.3^{a}	23.5 ± 2.4^{b}	54.9 ± 2.3^{c}	99.6 ± 2.1^{d}	302.0	< 0.001
LAI (m^{2} m^{-2})	2.5 ± 0.3^{a}	2.2 ± 0.4^{a}	1.1 ± 0.3^{a}	0.6 ± 0.3^{b}	8.6	< 0.01
PAR below canopy (μmol m^{-2}s^{-1})	530 ± 187^{a}	676 ± 212^{ab}	885 ± 179^{ab}	1297 ± 164^{b}	4.0	< 0.05
Soil						
Soil moisture (%VWC)	17.6 ± 1.7^{a}	14.4 ± 1.8^{a}	12.5 ± 1.6^{a}	12.3 ± 1.6^{a}	1.1	0.429
Soil P (μg g^{-1})	25.8 ± 8.0^{a}	23.7 ± 8.6^{a}	57.6 ± 7.8^{a}	40.9 ± 7.4^{a}	1.2	0.412
Soil N (%)	0.26 ± 0.03^{a}	0.26 ± 0.03^{a}	0.29 ± 0.03^{a}	0.29 ± 0.03^{a}	0.4	0.767
Aspen						
Water potential (MPa)	-1.5 ± 0.1^{a}	-1.3 ± 0.2^{a}	-1.2 ± 0.1^{a}	-1.6 ± 0.1^{a}	1.8	0.269
Photosynthesis (μmol m^{-2} s^{-1})	10.5 ± 1.2^{a}	13.0 ± 1.2^{ab}	13.9 ± 1.2^{bc}	15.2 ± 1.1^{c}	12.3	< 0.001
Foliar P (mg g^{-1})	3.0 ± 0.4^{ab}	3.5 ± 0.4^{a}	2.6 ± 0.4^{b}	2.3 ± 0.4^{b}	6.4	< 0.01
Foliar N (%)	1.8 ± 0.2^{a}	1.8 ± 0.2^{a}	2.2 ± 0.2^{a}	2.0 ± 0.1^{a}	1.3	0.417
Density (stems ha^{-1})	7119 ± 2877^{a}	7583 ± 3071^{a}	22792 ± 2786^{b}	16500 ± 2657^{ab}	5.1	< 0.01
Height (cm)	63.4 ± 6.5^{a}	69.1 ± 6.8^{ab}	60.5 ± 6.4^{a}	78.9 ± 6.2^{b}	4.0	< 0.05
Aboveground biomass (g)	37.1 ± 19.6^{a}	69.4 ± 19.7^{a}	60.3 ± 19.4^{a}	111.5 ± 18.6^{b}	11.2	< 0.001
Pellet-group count (60 m^{-2})						
Deer	8.1 ± 1.3^{a}	7.2 ± 1.4^{a}	5.8 ± 1.2^{a}	4.1 ± 1.2^{a}	2.7	0.110
Elk	2.6 ± 0.6^{a}	1.3 ± 0.6^{a}	1.8 ± 0.6^{a}	1.7 ± 0.5^{a}	0.9	0.532
Cattle	1.6 ± 0.4^{a}	1.5 ± 0.5^{a}	0.9 ± 0.4^{a}	1.1 ± 0.4^{a}	0.6	0.670
Browse Damage (%)	35.8 ± 5.5^{a}	35.1 ± 6.0^{ab}	14.4 ± 5.3^{c}	16.5 ± 5.0^{bc}	5.2	< 0.05

Table 2. Coefficients of determination indicating relationships between fire severity, leaf area index and browse damage on growth and late summer defense chemistry traits of aspen. Positive/negative relationship between variables is specified by + or – sign.



	Burn severity (% tree mortality)				Leaf Area Index				Browse Damage			
	n	+/-	R^2	*P*	*n*	+/-	R^2	*P*	*n*	+/-	R^2	*P*
Aspen												
Density	29	+	0.15	< 0.05	30	-	0.18	< 0.05	30	-	0.26	< 0.01
Height	29	+	0.10	0.051	30	-	0.04	0.147	30	-	-0.02	0.531
Aboveground biomass	28	+	0.36	< 0.001	28	-	0.19	< 0.05	28	-	0.06	0.101
Defense Chemistry												
Phenolic Glycoside (PG)	29	+	0.41	< 0.001	30	-	0.34	< 0.001	30	-	0.15	< 0.05
Condensed Tannins (T)	29	+	0.35	< 0.001	30	-	0.16	< 0.05	30	-	0.14	< 0.05
PG + T	29	+	0.55	< 0.001	30	-	0.41	< 0.001	30	-	0.21	< 0.01

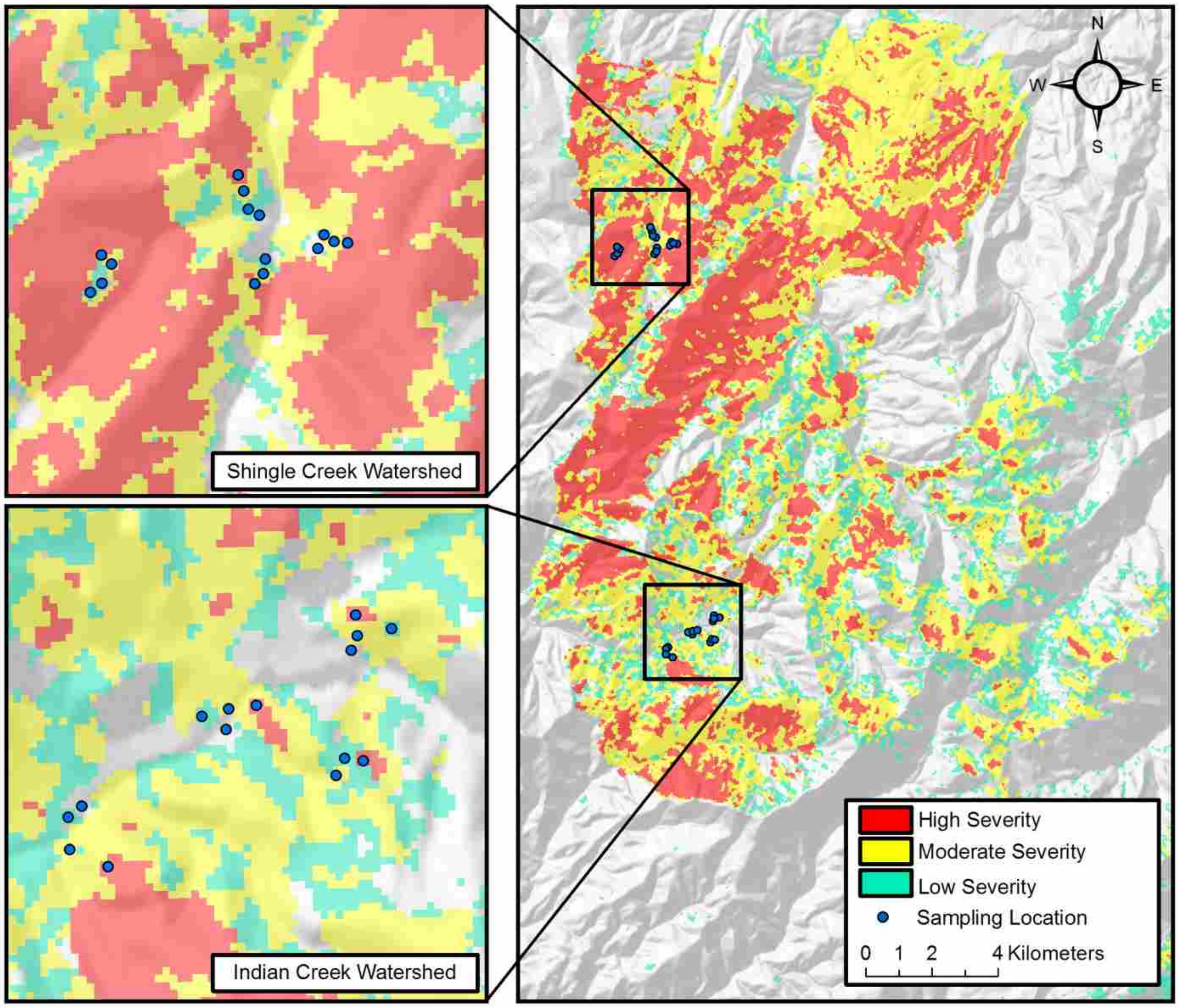


Fig. 1. Burn severity map of the Twitchell Canyon fire based on Burn Area Reflectance Classification (BARC). The map was derived from multi-spectral satellite imagery developed by United States Department of Agriculture (USDA) Forest Service GIS database. Precise locations of sampling plots in the two watersheds are shown.

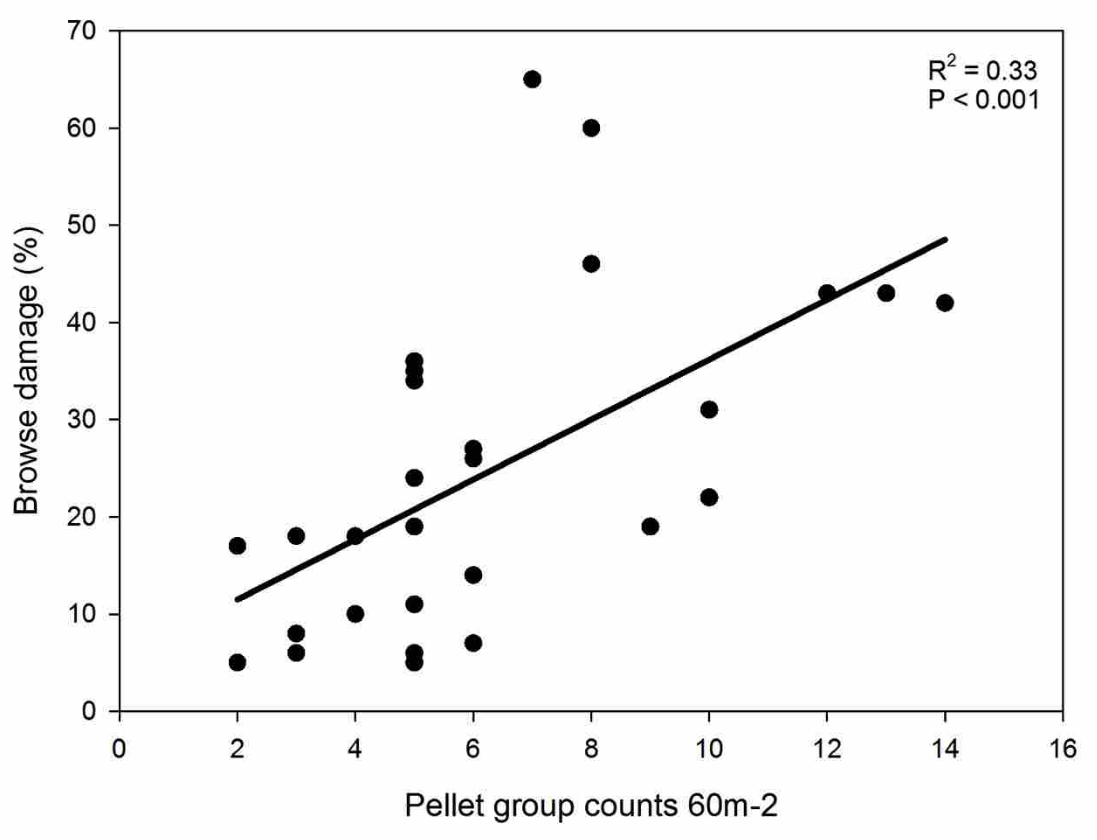


Fig. 2. Regression analysis indicating a positive relationship between percentage browse damage and deer pellet groups (*n*=30). Each point represents the number of deer pellet counts within each plot.

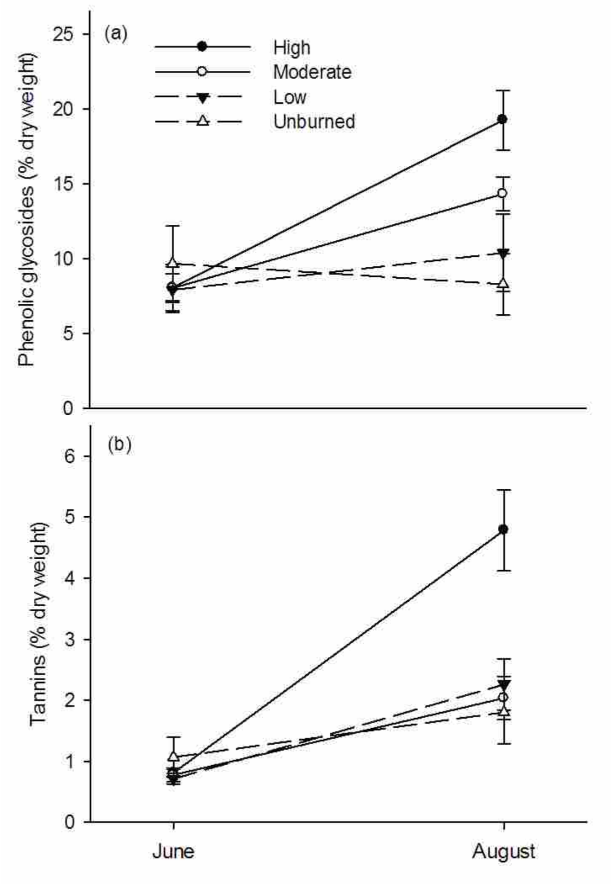


Fig. 3. Burn severity effects on the expression of (a) phenolic glycosides and (b) condensed tannins across time. Means±SE are presented. Main effects and interactions of burn severity and time were assessed using repeated measure ANOVA model (*n*=30). The main effect of burn severity was not statistically significant for phenolic glycosides (*F*=1.9, *P*>0.05), but was significant for condensed tannins (*F*=5.7, *P*<0.01). There was a strongly significant time effect for phenolic glycosides (*F*=34, *P*<0.001) and condensed tannins (*F*=51, *P*<0.001). Burn severity effects on defense chemistry were lacking early in the summer, but higher burn severity classes differentially affected defense chemistry expression in the late summer. Burn severity and time displayed strong interaction effect on phenolic glycosides (*F*=12, *P*<0.001) and condensed tannins (*F*=7.6, *P*<0.001).

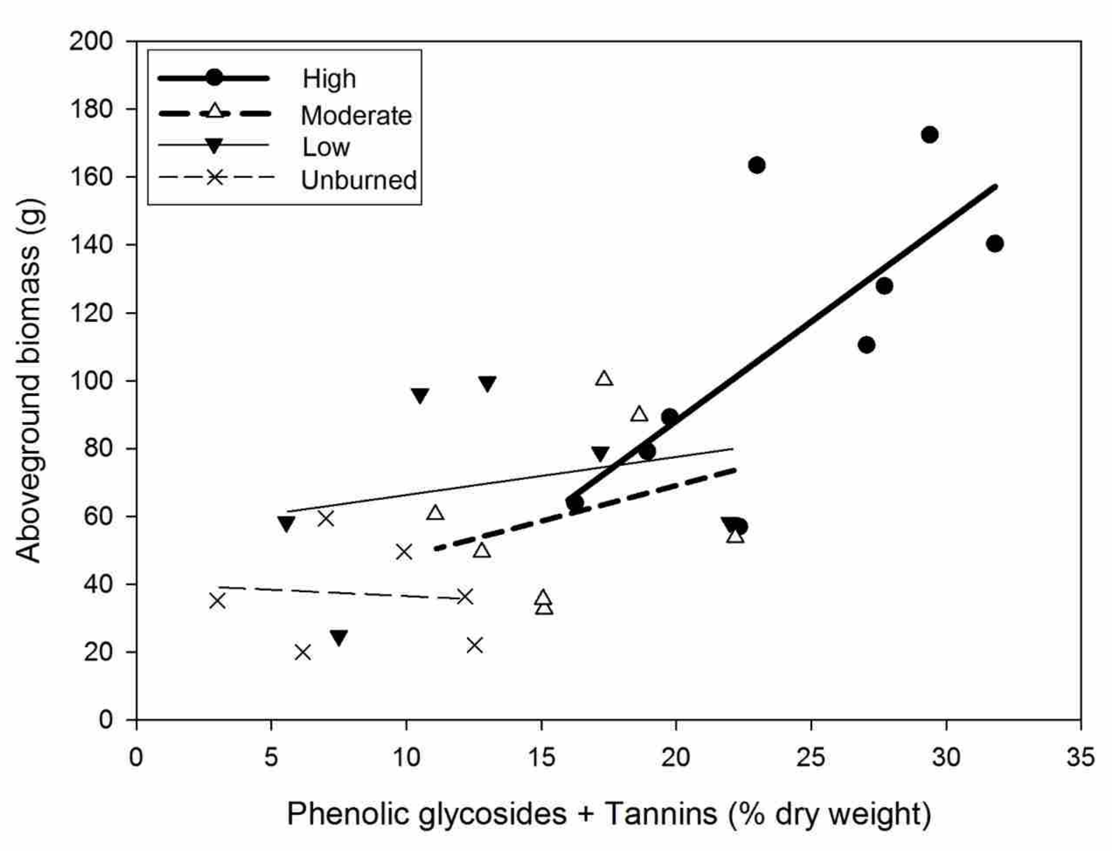


Fig. 4. Correlation analysis examining potential tradeoffs between defense chemistry expression and growth of aspen under each of the four burn severity categories. Each point represents the mean aspen saplings response within each plot (*n*=28). There was a positive relationship between defense chemistry and growth across all burn severity classes (*r*=0.71; *P*<0.001; line not shown) and for the high severity burn condition (*r*=0.72; *P*=0.029), but not among other burn classes (unburned, *r*=0.14, *P*=0.854; low severity, *r*=0.23, *P*=0.659; moderate severity, *r*=0.30, *P*=0.516).

Chapter 2

Legacy Effects of Fire Severity on Aspen Regeneration along a Fire Size Gradient

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Legacy Effects of Fire Severity on Aspen Regeneration along a Fire Size Gradient

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ABSTRACT Human activities and climate change are increasing the size and severity of wildfires in many ecosystems (Westerling et al. 2011). Herbivory interacts with fire disturbance, but little is known about how plant-herbivore relationships are influenced by variability in fire size and severity at large temporal and spatial scales. To characterize the effects of fire size and severity on plant and herbivore communities in forest ecosystems, we examined aspen regeneration and ungulate use patterns across 25 fires that varied in size in five National Forests (Uinta-Wasatch-Cache NF, Ashley NF, Fishlake NF, Dixie NF, and Manti-La Sal NF) in the state of Utah. These fires dated from 1992 to 2002 and were at least 10 years old when this study was conducted. Fire size and severity were positively related to aspen regeneration and recruitment densities. There was a significant fire size and severity interaction effect on aspen regeneration, such that the positive influence of fire size increased with greater fire severity. Change in the extent of aspen cover was indifferent to fire size. Deer and cattle densities decreased slightly with increasing fire size and severity, but elk density showed no difference. Deer preferred low severity patches in smaller fires, but appeared to avoid low severity patches as fire became larger. Our results suggest that fire size and severity are important ecological filters that can interact to affect forest reestablishment and community response. Effective management of forest systems in changing fire regimes will require an understanding of the legacy effects of fire size and severity at the landscape level.

KEYWORDS aspen, cattle, deer, elk, fire, herbivore, recruitment, regeneration, severity, size, ungulate

INTRODUCTION

Disturbance plays a principal role in shaping the development of plant communities. However, increased human activities have altered natural disturbance dynamics (Abugov 1982, Franklin et al. 2002, Laska 2001, Oliver 1996, Sousa, 1984). Human activities including exotic species introductions, logging, grazing, fire suppression, and human-induced climate change can modify the size, severity, frequency, and duration of disturbance (Baker 1995, Mack and D'Antonio 1998, Turner et al. 1998, Liu et al. 2010). Altered disturbance regimes have the potential to reduce productivity, species abundance and diversity (Reich et al. 2001), and disrupt successional processes (Folke et al. 2004), all of which can decrease plant community resilience to biotic stresses (Wallin et al.1994). Human activity and climate change are expected to modify fire regimes at a global scale (Westerling et al. 2011). For that reason, there is an urgent need to enhance our understanding of the ecological impacts of changing fire behavior.

Fire influences terrestrial ecosystem patterns and processes, including vegetation distribution and structure (Bowman et al. 2009). It strongly impacts successional patterns in many forest systems by replacing less fire tolerant species with fire tolerant species (Heinselman 1981, Romme 1982, Abrams 1992). The extent of such impact is bounded by the size of the area burned. Fire size alters ecological succession by influencing diversity and abundance of seedling recruitment (Miller 1982, Turner et al. 1997). Over the past few decades, there has been a rising trend in occurrence of larger fires worldwide (Arno and Allison-Bunnell 2002, Stephens 2005, Westerling et al. 2006, Miller et al. 2009). However, we lack understanding of the consequences of variable fire regimes on forests forest regeneration, as well as the abundance and distribution of communities that are supported in these forests.

The impact of fire is often heterogeneous across landscapes due to variation in distribution and quality of fuel loads, topography and weather conditions. Consequently, a complex mosaic of burned conditions, or fire severity, is often established across post-fire forest landscapes. Evidence shows that plant functional processes such as growth (Chappell and Agee 1996), nutrient uptake (Shenoy et al. 2013), and seedling establishment (Chappell and Agee 1996, Turner et al. 2003) vary depending on fire severity. It has been recognized that the percentage of high-severity burned patches generally increases with annual burn size (Lutz et al. 2009, Miller et al. 2009). Fire severity can interact with disturbance size to affect biotic cover and richness of plant community (Turner et al 1997). Most studies examining post-fire effects in forest systems have not considered the single and combined effects of fire size and severity.

Herbivory is an important disturbance effect that affects post-disturbance plant community regeneration and assembly (Hobbs 1996). In many ecosystems, ungulate herbivores are attracted to recently burned patches (Pearson et al. 1995, Archibald et al. 2005, Klop, van Goethem and de Iongh 2007). The negative impact of chronic herbivory in burned areas can overshadow the initial advantage that fires provide for fire dependent plant species recruitment (Endress et al., 2012) and lead to regeneration failure (Cates and Gordon 1975, Tripler et al. 2002, Spiller and Agrawal 2003). While ungulate herbivory can directly influence the abundance and species composition of vegetation (Côté et al. 2004), their impact on forests can also be indirect. For example, ungulates can modify the extent, frequency, and intensity of fire disturbance by altering the quality and quantity of fuel load (Hobbs 1996, Tremblay et al. 2006). Lengthened fire return intervals as a product of decreased fuel load from browsing can indirectly affect successional trajectory of forests (Johnstone and Chapin, 2006). Moreover, fire size and severity also modify ungulate community. Under specific conditions, variability in fire size and spatial pattern has potential impact on the survival of ungulate species (Turner et al. 1994). In addition, fire severity displays strong influence on bottom-up and top-down interactions between plant and ungulate herbivore communities (H.Y. Wan et al. unpub. results). It has been postulated that the impact of ungulates is likely to be greater on smaller burned patches than in larger burned areas (Pastor et al. 1988, Smith et al. 2011, Endress et al. 2012, H.Y. Wan et al. unpub. results), but research that directly addresses the effect of fire severity on ungulate activity and forest regeneration pattern as a function of fire size is lacking.

We used quaking aspen (*Populus tremuloides*) forests as study system to examine the roles of fire size and severity on vegetative regeneration and herbivore community responses in forest systems. Aspen is an early successional species that thrives under frequent disturbance regimes by rapidly regenerating new saplings from rootstocks following fire (Romme et al. 1995, Fraser et al. 2004, Paragi and Haggstrom 2007). In the presence of intensive ungulate herbivory, however, aspen regeneration response can be adversely affected due in part to the high susceptibility of young aspen saplings to mammalian herbivores (Baker et al. 1997, Kaye et al. 2005). Diminishing aspen regeneration caused by ungulate herbivory may favor conifer expansion to the exclusion of aspen, that can lead to loss of aspen from forest landscapes (Kaye et al. 2005, Strand et al. 2009). Despite the adverse effects that herbivory can have on aspen regeneration, patterns of successful aspen regeneration has been documented in burned areas with high ungulate herbivore densities (Smith et al. 2011). While aspen may be able to persist within the range of historical variability in past fire regimes, the future of aspen forests is uncertain due to foreseeable climate change-induced fluctuations in fire severity and size.

In this study, we are interested in the responses of aspen and herbivore community to fire severity along a fire size gradient. We integrated field data and remotely sensed data to test the following hypotheses: (i) large and high severity fire promotes aspen resilience by increasing aspen regeneration and recruitment; (ii) large fire favors the expansion of aspen cover within the burned area; and (iii) the influence of fire severity on ungulate community activities within aspen stands persists in burned environments (i.e., 10+ years after occurrence of fire) and varies with fire size.

METHODS

Study locations

This study included an analysis of 25 fires that occurred in aspen forests throughout the state of Utah (Fig. 1). A map layer including polygons for all fires that have occurred since 1981 was obtained from the Utah Division of Natural Resources. All were at least 10 years old at the time of data collection. We selected fires that ranged from 1993 and 2002 to observe the long-term pattern of post-fire aspen regeneration and recruitment. Only fires that contained aspen prior to the disturbance were included in this study. Presence of aspen was visually assessed by 1) post-fire satellite imagery for aspen stems that had not burned completely and had since fallen, which appeared white or grey in the images; and 2) pre- and post-fire aerial photos for aspen regeneration, which appeared as bright green patches in Summer or yellow patches in Fall. Elevation was also applied as another parameter in the selection process. Although aspen can survive at lower elevation, major aspen stands in Utah are usually found at 1800 m or above. Therefore, any fires below 1800 m were excluded from this study. Twenty six fires were originally selected based on our methodology, but one of them was excluded from the study because aspen was not found upon ground-truthing in the field. Elevations of our sites ranged from 2170 m to 3301 m with stand slopes ranged from 1 to 39 degrees.

Field measurements

Using satellite imagery, we randomly generated potential transects points across aspen patches within fires. Field measurements were taken using 50 m belt transects. We had a total of 149 transects in this study. The number of transects within each fire was determined and constrained by the size of pre-fire aspen stands within each burned patch. Final transect points were selected based upon groud-truthing in the field for actual observance of pre-existing aspen before fire. Transects were located at least 50 m from the fire burned edge, at least 50 m within an aspen stand, and were separated by at least 100 m. At each transect, the Universal Transverse Mercator (UTM) coordinates, elevation, aspect, slope, and cardinal direction from the starting point were recorded. All post-fire aspen saplings were counted in the 2 m by 50 m belt transect and divided into three categories: live saplings less<2 m, live saplings>2 m, and dead saplings of any height. In this study, we defined aspen recruitment as live saplings>2 m because aspen begin to escape upper level browsing at this height. We measured trees with DBH ≥ 10 cm along the same belt transect using the point quarter method (Pollard 1971) to estimate for density and composition of the pre-existing forest stand. Pre- and post-fire mortality status of the trees were recorded and used for calculating the fire severity of the stand in this study. To evaluate ungulate activity, we counted the occurrences of pellet-groups from herbivores along the belt transect to estimate for herbivore density (Neff 1968). Pellet-group was classified by species. The presence of a single pellet or pat was counted as one pile group. Deer and elk pellets located within the same 50 cm diameter were counted as the same pile group. These field data were collected between June 3rd and August 30th in 2013.

Image analysis

We accessed the size of pre- and post-fire aspen forest cover area within each fire site by performing multi-temporal supervised classification on Landsat Thermatic Mapper (TM) 5 satellite images using ENVI software (ENVI Version 5.0 ITT Industries Inc., 2012, Boulder, CO, USA) based on methods used by Wolter et al. (1995) and Sankey (2009). At each site, one summer season image and one fall season image were collected for the calendar year prior to each fire to classify pre-fire aspen; and 2011 summer and fall images were used to classify post-fire aspen. We selected images with the least shadow and cloud cover to procure consistent results. Prior to the classification, all images were corrected for atmospheric conditions using FLASSH module (Fast Line-of-Sight Atmospheric Analysis of Spectral Hypercubes) in ENVI software. We amplified the unique change in aspen spectral response during senescence for our classification by compositing bands 2 (0.52–0.60 μm), 3 (0.63–0.69 μm), 4 (0.76–0.90 μm), and 5 (1.55–1.75 μm) of the summer image with bands 2 and 3 of the fall season image. This is possible because of seasonal changes in aspen pigments of anthocyanins, carotenoids, tannins, and xanthophylls as the canopy turns from green to yellow. These changes result in increasing reflectance levels in the green (0.52–0.60 μm) and red (0.63–0.69 μm) portions of the aspen spectral response in the visible electromagnetic spectrum (Sankey 2009). The supervised classification consisted clusters of aspen, no-aspen vegetation, bare ground, and water for a total of four classes. A minimum of 20 training sets was collected for each class by manually digitizing polygons around desired plant canopy or terrain type. Accuracy assessment was performed using a total of 1000 stratified random sample points generated in ENVI 5.0, with 250 random points assigned to each class. In this assessment, we calculated total overall accuracy, producer's and user's accuracy of each class, and the overall kappa statistic (Congalton 1991).

Statistical analysis

We performed simple regression analyses to evaluate the individual direct relationship of fire size, as well as fire severity, against aspen regeneration, recruitment, percent change in aspen cover area, saplings mortality rate, and pellet-group counts. Fire size data was log-transformed for normality. We used multiple regression models to test for the combined effects of fire size and severity on aspen regeneration and recruitment. We generated a simple slopes interaction plot when a significant interaction effect was detected using the methods of Preacher et al. (2006).

We used model selection to identify best approximating models with variables and interactions that likely affect aspen regeneration and recruitment. Since the number of predictor variables is large, the modeling process was automated using the stepwise function in JMP version 10 (SAS Institute, Cary, NC, USA). Variables included in the modeling procedure were aspect, slope, elevation, fire size and severity, pre-fire aspen forest area, and stand density and basal area of aspen and conifer. The best approximating model for each response variable was based on minimization of Akaike Information Criterion value corrected for sample size (i.e., AICc; Burnham and Anderson 2002). After finding the best model, we calculated the strength and direction of estimates of the variables in the model. We were especially interested in whether fire size and severity were in the best models; and if so, what the effect size was.

Prior to the analyses, we checked for multicollinearity and correlations among the variables. None of the collinearity between the variables was high enough to warrant exclusion of a variable. The highest collinearity was found between fire size and pre-fire aspen cover area with a variance inflation factor of 2.12. All values that appear in this paper are adjusted R^2. Statistical analyses were performed in R 2.15.1 (R Core Team 2012) and JMP version 10 statistical software. We used car package (Fox and Weisberg 2011) and lmSupport package (Curtin 2012) in R.

RESULTS

Image analysis

The multi-temporal supervised classification had 90.8% overall accuracy (kappa=0.877). The producer's and user's accuracy were 92.2% and 84.8% respectively for aspen class (Table 1).

Aspen regeneration, recruitment, and cover area

Aspen regeneration density was positively related to fire size (R^2=0.27, P<0.001; Fig. 2) and severity (R^2=0.18, P<0.001; Fig. 2). Adding fire severity significantly improved the model (R^2=0.40, P<0.001; Table 3). Interaction effect of fire size and severity on aspen regeneration was significantly positive, and the effect on aspen regeneration is strongest when severity is high (Fig. 3). The best approximating model based on the lowest AICc for aspen regeneration included variables of fire severity, fire size, pre-fire aspen stand density, elevation, and west-facing aspect (R^2=0.45, P<0.001; Table 4). The model revealed that fire severity, size, pre-fire aspen stand density, and elevation had positive influence on aspen regeneration, but west-facing aspect had a negative relationship. Fire severity, fire size, and pre-fire aspen stand density appeared in all of the top 5 models. Fire size (β=0.45) and severity (β=0.32) had the greatest effect on aspen regeneration, i.e., 3.2 and 2.3 times greater than pre-fire aspen stand density (β=0.14) which had the next largest standardized effect size (Table 5).

Aspen recruitment and fire size had a weak but positive relationship (R^2=0.12, P<0.001; Fig. 2). Fire severity had similar relationship with recruitment (R^2=0.13, P<0.001). Putting fire size and severity together significantly improved the model (R^2=0.21, P<0.001), and it had a positive relationship with recruitment; but no interaction effect was found between fire size and severity on recruitment (Table 3). Fire severity, pre-fire aspen stand density, and pre-fire total aspen cover area were the variables in the best model with the lowest AICc (R^2=0.27, P<0.001; Table 4), and were included in all top models. In the best approximating model, all variables were positively related to aspen recruitment, whereas fire size only appeared in the second and third best models (Table 5). Fire severity had the strongest standardized effect size (β=0.37); pre-fire aspen forest cover area (β=0.28) and pre-fire aspen stand density (β=0.21) also demonstrated strong influence on recruitment.

Percent change in aspen cover area and saplings mortality rate showed no relationship with fire size (percent cover change, R^2<0.01, P=0.46; mortality, R^2=0.01, P=0.14).

Ungulate activity

Deer pellet and cattle pat were negatively and weakly related to fire size (deer, R^2=0.06, P<0.01; cattle, R^2=0.07, P<0.001; Table 3). We found a significant interaction effect between fire size and severity on deer pellet (Table 3). In small fires, low severity burned patches had the largest number of deer pellets. As fire size increased, this pattern reversed because with low severity fire having a steep negative slope, whereas the slope of high severity fire stayed relatively flat (Fig. 3). Although fire size and severity had no interaction effect on cattle pats, both displayed significant negative relationship with cattle pats (Table 3). We found no relationship between elk pellet-group and fire size and severity (Table 3).

DISCUSSION

Effects of fire size and severity on aspen

Consistent with our first hypothesis, aspen regeneration and recruitment density increased with fire size and severity across the 25 studied fire sties. The influence of fire size on regeneration aggregated when intermixed with increasing fire severity, i.e., when large fire size and high severity emerged, they produced a synergy that increased aspen regeneration at a rate that was greater than the sum of their individual effect. Although the synergistic interaction effect that fire size and severity had for aspen regeneration was elusive on recruitment density, both fire size and severity showed positive relationship with recruitment. One possible explanation for the pattern we observed is post-fire changes in competition. Because sspen is a shade-intolerant species (Kobe and Coates 1997) they have higher growths rate when there is a reduction in overstory canopy after disturbance (Huffman et al. 1999). Also, it has been shown that intense competition from grass (*Calamagrostis canadensis*) can significantly suppress the growth potential of juvenile aspen (Landhausser and Lieffers 1998). Large and severe fire removes these competitive effects. This can create a favorable environment for the initiation and growth of regenerating aspen (Frey et al. 2003). In the course of time, intraspecific light competition intensifies (Shepperd 1993), and along with interspecific competitive species that starts to return to the landscape can reduce aspen's growth rates (Cavard et al. 2011). Intense browsing on aspen by ungulate herbivores may be another factor that affected recruitment. Aspen has high nutritional value and often attracts ungulates as a forage source (Cook 2002, Jones et al. 2011). Chronic browsing by high densities of elk and deer can suppress density and height of aspen (White et al. 1998, Kay 2001). Moreover, cattle grazing that coincide with wildlife herbivory can cause further damage to aspen growth (Kay and Bartos 2000, Jones et al.

2011), which can then affect recruitment potential (Didion et al. 2009). We suspect that the synergy of fire size and severity was absent from aspen recruitment because competition and chronic herbivory were acting as counterbalancing forces. Further research is needed to verify the accuracy of our speculation.

Aspen cover change

Contrary to our expectations, we did not find convincing evidence to support our second hypothesis of increasing fire size favors aspen expansion. We noticed that 9 out of 13 fires that were<700 ha in burned area recorded a net loss in total aspen cover. For the other 12 fires that were>700 ha, only 3 of them registered a net loss in aspen cover. Paradoxically, the second and third largest fires (i.e., Garden Valley Fire and Dry Canyon Fire) in this study were among these 3 fires, and lost 39% (41.01 ha) and 35% (7.88 ha) of aspen forest cover respectively (Table 2). Therefore, while aspen stands in smaller fires appear to have a higher risk of regeneration failure, evidence is inconclusive as to whether larger fires influence the maintenance of aspen cover in the landscape. Further evaluation of our findings will require long-term studies that focus on the effects of fire size and severity on ecological processes, and their potential interaction with regional and local abiotic (e.g., temperature and precipitation) and biotic (e.g., competition and herbivory) filters.

Ungulate community response

Disturbance studies that examine multiple background densities of both domestic and wild ungulate species are rare but much needed (Wisdom et al. 2006). We provided a study that examined post-fire patterns of deer, elk, and cattle populations in mixed aspen-conifer stands that spread across the state of Utah (Fig. 1). A key finding of this study was that ungulates respond to fire size and severity differently depending on species. Although the effects were small, increasing fire size and severity appear to disperse both deer and cattle densities over a larger area. Another interesting pattern was that deer seemed to have a preference for low severity patches when fire size was small, but that preference shifted to avoidance as fire size increased. Also, deer density remained relatively constant when fire severity is high (Fig. 3). We do not understand the exact mechanism behind this pattern, but it is most likely related to the tradeoff between maximizing forage benefits and minimizing risk of predation in habitat selection (Pierce et al. 2004).

On the other hand, elk density was insensitive to changes in fire size and severity in this study. Our results are consistent with previous findings in which elk pellets showed a uniform pattern across sites of different burn severity (H.Y. Wan et al. unpub. results). This pattern could be related to their relatively high adaptability to diverse environment. In general, elk are less selective in their diet than deer (Collins and Urness 1983). They are capable of adapting to a variety of habitats with different forage sources (Pallesen 1979, Baker and Hobbs 1982). While elk are frequently attracted to burned aspen stands for resprouting forages as food source, they can also maintain diets of similar nutritional value in unburned area (Canon et al. 1987).

Although browsing and grazing were not within the scope of this study, we found that fire size and severity interaction appears to modify patterns of deer activity, which provides a premise for future study on whether such interaction also makes a difference to the browse impact of deer on aspen regeneration. Furthermore, many studies documented the fire effects on large ungulates behavior within the first few years after burning (Rowland et al. 1983, Canon et al. 1987, Pearson et al. 1995). Our study further shows that fire history can have legacy effects on ungulate community even 10 to 20 years after fire occurrence. We suggest more research be conducted at larger temporal and spatial extent to characterize the long-term effects of fire size and severity on ungulate community at the landscape level.

CONCLUSION

Recent climate change modeling predicts that fire activity in the Western United States will increase due to warmer temperature and earlier snowmelt (Westerling et al. 2006). Rapid changes in fire regimes can alter forests compositions and structures (Kulakowski et al. 2004), with the potential of jeopardizing the stability of aspen ecosystems in the future (Shinneman et al. 2013). Aspen is one of the most broadly distributed tree species in North America (Little 1971), and provides critical habitats for a wide number of biodiversity (DeByle 1985). Changes in the aspen landscape will lead to immense cascading effects on the many communities that aspen habitats support (Bailey and Whitham 2002). Aspen is a fire driven species, and theoretically, increasing fire activity in the future will likely trigger more aspen regeneration. However, aspen is also susceptible to ungulate herbivory, especially after disturbance. Therefore, to promote aspen ecosystem resilience, detailed examination of the relationship between aspen and ungulate communities in altered fire regimes should be a top research priority.

Fire disturbance produces spatially complex patterns and exerts variable impact on forest and community structures (Turner and Romme 1994). Understanding how variation in post-fire environments influences ungulate community response is necessary when making long-term decisions pertaining to forest management in fire regimes. This is especially important when managing forest systems that are predominantly occupied by highly palatable species to large herbivores such as aspen (Baker et al. 1997, Seager et al. 2013). Both experimental and long-term correlative studies indicate that ungulate herbivory can suppress aspen regeneration (White et al. 1998, Romme et al. 2005, Sankey et al. 2006). Chronic ungulate herbivory after fire can devastate vegetation recovery and possibly result in aspen stand losses (Suzuki et al. 1999, Ripple and Larsen 2000, Hessl 2002, Larsen and Ripple 2003). While fire can be used as a management tool to rehabilitate aspen habitat, it also increases the risk of exposing aspen to ungulate herbivory. In this study, we have identified interaction effects between fire size and severity that strongly influence aspen and ungulate densities. Until we have a better understanding of how this effect is related to browsing and grazing capacity, prescribed fires should be used with precaution. In particular, our results suggest that deer may be more attracted to small and low severity patches. While more studies are needed to identify the potential impact of this pattern, small and low severity disturbance should be avoided especially in areas with high ungulate densities, to prevent the loss of aspen habitat due to potential intense browsing. Considering the recent increase in large and severe fires, we suggest that forest agencies should increase efforts in characterizing post-fire regeneration responses to improve effectiveness in managing forests landscape in the long run.

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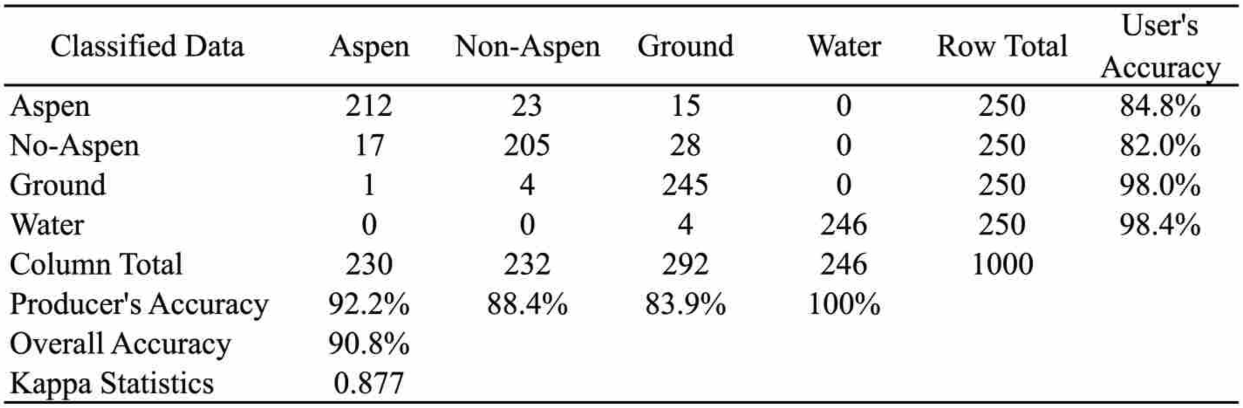
Table 1. Accuracy assessment of image classification results.



Classified Data	Aspen	Non-Aspen	Ground	Water	Row Total	User's Accuracy
Aspen	212	23	15	0	250	84.8%
No-Aspen	17	205	28	0	250	82.0%
Ground	1	4	245	0	250	98.0%
Water	0	0	4	246	250	98.4%
Column Total	230	232	292	246	1000	
Producer's Accuracy	92.2%	88.4%	83.9%	100%		
Overall Accuracy	90.8%					
Kappa Statistics	0.877					

Table 2. A summary of the stand characteristics, pellet-group counts, and aspen cover, regeneration, and recruitment data of the 25 studied fires. Mean±SE are shown.

Fire	Year	*n*	Firesize (ha)	Elevation (m)	Stand density (stems ha-1)		Basal Area (m2 ha-1)		Pre-fire aspen cover (ha)	Post-fire aspen cover (ha)	Pellet-group counts (100 m-2)			Total regeneration (stems ha-1)	Sapling mortality (%)	Mature recruitment (stems ha-1)
					aspen	conifer	aspen	conifer			deer	elk	cattle			
Sanford	2002	18	33124.98	2970 ± 35	618 ± 100	417 ± 73	223 ± 21	384 ± 33	1048.04	1191.92	1.6 ± 0.4	2.0 ± 0.5	0 ± 0	29856 ± 3243	16.0 ± 2.1	8478 ± 1257
Garden Valley	2002	11	5764.68	2848 ± 42	173 ± 26	348 ± 64	308 ± 70	518 ± 71	103.87	62.86	4.5 ± 1.0	2.3 ± 0.5	0 ± 0	19882 ± 3121	12.8 ± 4.2	2255 ± 791
Dry Canyon	1994	3	4640.68	2228 ± 10	312 ± 207	203 ± 104	192 ± 17	308 ± 154	22.34	14.46	0.7 ± 0.3	2.3 ± 1.2	4.0 ± 3.1	2667 ± 1067	4.2 ± 4.2	1100 ± 862
Mollie	2001	3	3176.82	2675 ± 13	119 ± 76	117 ± 10	424 ± 46	1243 ± 283	102.65	132.14	2.0 ± 1.0	0.3 ± 0.3	1.3 ± 0.9	5667 ± 4667	13.1 ± 4.6	3900 ± 3302
Pole Creek	1996	10	2390.48	3135 ± 210	392 ± 75	473 ± 93	358 ± 61	628 ± 108	108.52	216.37	4.3 ± 0.9	2.8 ± 0.8	0.5 ± 0.3	24140 ± 3568	16.8 ± 2.7	11260 ± 1502
Edgar Canyon	1994	6	1723.80	2338 ± 15	483 ± 108	329 ± 120	142 ± 10	685 ± 105	140.76	173.26	1.3 ± 0.5	3.2 ± 1.2	3 ± 1.5	2000 ± 648	6.2 ± 3.7	933 ± 600
Price Canyon	2002	5	1261.87	2481 ± 17	420 ± 101	1 ± 1	300 ± 26	31 ± 31	25.64	31.34	8.2 ± 3.4	7.0 ± 3.2	5.2 ± 1.6	12720 ± 3397	8.7 ± 2.7	2980 ± 1328
Willow Basin	1994	8	1177.57	2438 ± 20	300 ± 57	196 ± 44	496 ± 65	782 ± 98	26.37	75.85	3.8 ± 1.4	4.5 ± 0.8	4.8 ± 1.2	2788 ± 1771	20.7 ± 6.9	12.5 ± 12.5
South Hollow	2001	7	935.89	2555 ± 86	445 ± 107	91 ± 84	380 ± 43	313 ± 163	146.00	167.65	3.6 ± 0.9	0.7 ± 0.4	2.9 ± 0.9	3886 ± 1348	25.2 ± 5.5	1686 ± 1000
Dry Fork	2000	7	912.00	2611 ± 3	1157 ± 426	35 ± 21	257 ± 23	286 ± 154	22.01	16.49	3.1 ± 1.0	15.0 ± 1.8	16.1 ± 6.9	10414 ± 2632	12.1 ± 2.9	3971 ± 1272
Huff	2002	2	890.34	2183 ± 13	225 ± 8	0 ± 0	291 ± 7	0 ± 0	8.11	34.50	2.0 ± 0	2.0 ± 0	15.0 ± 2.0	17100 ± 1500	37.5 ± 8.0	6000 ± 1300
Johnstarr	1999	6	848.15	2622 ± 9	836 ± 236	339 ± 142	193 ± 24	510 ± 73	1.10	5.76	4.8 ± 1.7	17.3 ± 5.8	0 ± 0	2383 ± 808	11.0 ± 3.3	0 ± 0
Bruin Point	2000	5	688.62	2943 ± 10	240 ± 120	492 ± 97	403 ± 61	416 ± 40	31.11	7.34	3.2 ± 1.3	11.4 ± 2.5	0.6 ± 0.6	4640 ± 1508	5.2 ± 1.8	1620 ± 1101
Johnson	2002	6	682.54	2823 ± 22	64 ± 23	251 ± 129	232 ± 65	439 ± 63	8.61	3.59	3.7 ± 1.4	3.8 ± 1.2	2.3 ± 0.6	11217 ± 4305	3.0 ± 1.7	3533 ± 2100
Cottonwood	2002	5	553.64	3268 ± 21	78 ± 27	140 ± 49	190 ± 24	317 ± 66	19.17	2.75	6.6 ± 3.1	14.8 ± 8.6	0 ± 0	15260 ± 5998	5.2 ± 3.5	60 ± 40
Flat Canyon II	1993	9	409.86	3102 ± 18	108 ± 30	254 ± 38	422 ± 55	844 ± 62	35.02	3.46	2.9 ± 0.8	1.8 ± 1.1	3.2 ± 1.0	3133 ± 998	32.6 ± 12.8	1100 ± 540
Oldroyd	2000	7	385.23	2888 ± 16	459 ± 109	330 ± 92	276 ± 38	284 ± 75	15.20	0.26	2.6 ± 1.4	8.6 ± 1.3	1.7 ± 0.2	6171 ± 3318	52.9 ± 17.6	0 ± 0
USFS RX	2001	8	379.86	2485 ± 42	551 ± 125	25 ± 10	249 ± 19	328 ± 160	25.24	76.72	3.0 ± 1.2	0.5 ± 1.1	4.9 ± 2.4	6288 ± 4188	17.0 ± 4.1	3338 ± 3083
New Canyon I	1999	3	281.98	2373 ± 56	373 ± 147	239 ± 48	305 ± 114	663 ± 118	24.05	32.22	0.3 ± 0.3	2.0 ± 2.0	0.7 ± 0.7	6333 ± 4615	0 ± 0	3600 ± 3250
Flat Canyon IV	1993	3	95.44	3018 ± 69	440 ± 108	574 ± 220	204 ± 17	395 ± 42	10.29	4.55	0 ± 0	1.7 ± 0.9	6.7 ± 0.9	16467 ± 3200	7.9 ± 1.6	7700 ± 624
Flat Canyon VI	1993	4	34.10	2923 ± 20	357 ± 218	398 ± 92	276 ± 95	612 ± 108	3.97	1.12	2.3 ± 1.6	0.3 ± 0.3	6.3 ± 1.3	3075 ± 1608	33.0 ± 22.4	475 ± 382
Flat Canyon I	1993	6	33.78	2941 ± 6	255 ± 108	483 ± 114	201 ± 29	453 ± 53	6.11	3.78	7.3 ± 2.3	1.7 ± 0.8	4.8 ± 1.6	7433 ± 1824	10.8 ± 2.9	3300 ± 818
New Canyon II	1999	2	27.24	2416 ± 12	460 ± 123	37 ± 22	347 ± 194	1291 ± 371	0.71	2.31	1.5 ± 1.5	1.0 ± 1.0	2.0 ± 0	11500 ± 5000	7.6 ± 1.5	3700 ± 2300
Flat Canyon V	1993	2	25.08	3139 ± 18	53 ± 32	262 ± 76	586 ± 66	737 ± 186	0.37	0.02	1.5 ± 1.5	0.5 ± 0.5	4.0 ± 3.0	900 ± 900	52.8 ± 47.2	0 ± 0
Flat Canyon III	1993	3	11.05	2801 ± 2	189 ± 30	41 ± 41	199 ± 11	78 ± 78	2.71	2.73	25.3 ± 11.8	4.0 ± 2.1	10.3 ± 3.8	2800 ± 874	22.0 ± 7.3	833 ± 219

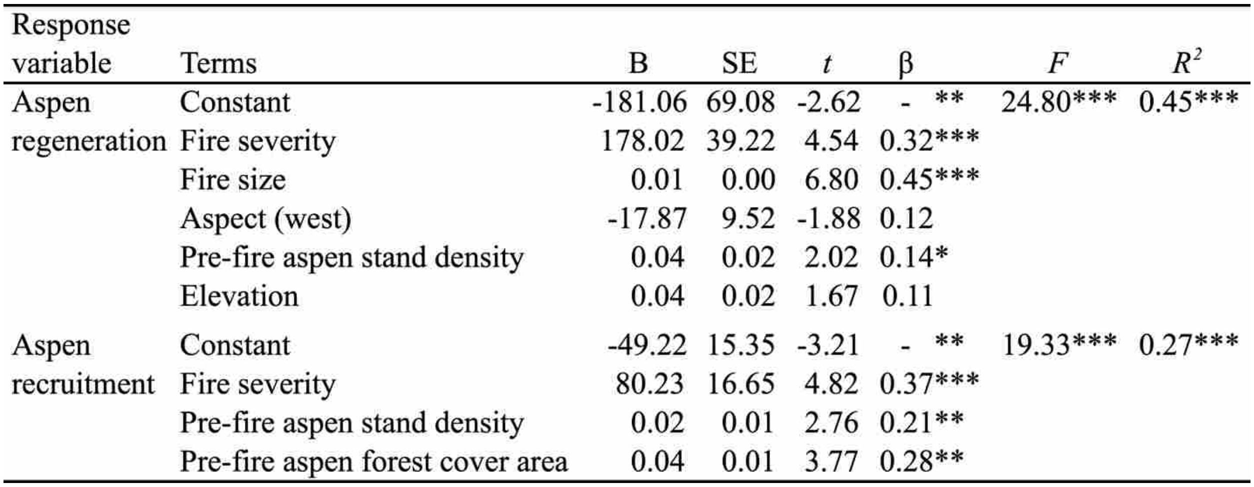
Table 3. Summary of multiple regression analysis shows main and interaction effects of fire severity and fire size for predicting aspen regeneration, recruitment, and ungulate pellet-group counts. Unstandardized coefficient (B), standard error (SE), t-statistic (*t*), and standardized coefficient (β) for each term, and *F*-statistics and R^2 for each model are presented. Change of R^2 (ΔR^2) was calculated between either model 1 or 2 (whichever has the biggest R^2) and model 3; and between model 3 and model 4. Statistical significant terms are marked with asterisks (*P<0.05, **P<0.01, ***P<0.001).

		Model 1 Fire size				Model 2 Fire severity				Model 3 Fire size + Fire severity				Model 4 Fire size + Fire severity + Size x Severity			
Response variable	Term	B	SE	*t*	β	B	SE	*t*	β	B	SE	*t*	β	B	SE	*t*	β
Aspen regeneration	Constant	-11863	3245	-3.66	- ***	-8021	3536	-2.27	- *	-24618	388	-6.34	- ***	-24124	3839	-6.28	- ***
	Fire size	7792	1042	7.48	0.53***					6847	978	7.00	0.46***	5943	1052	5.65	0.40***
	Fire severity					23476	4102	5.72	0.43***	18732	3625	5.17	0.34***	20832	371	5.62	0.38***
	Size x Severity													13395	6188	2.16	0.15*
	Model *F*				55.94***				32.76***				46.21***				33.15***
	R^2				0.27***				0.18***				0.38***				0.40***
	ΔR^2				-				-				0.11***				0.02*
Aspen recruitment	Constant	-2495	1398	-1.78	-	-3242	1415	-2.29	- *	-7176	1713	-4.19	- ***	-7083	1717	-6.28	- ***
	Fire size	1970	449	4.39	0.34***					1623	432	3.76	0.28***	1455	471	5.62	0.25**
	Fire severity					7999	1641	4.87	0.37***	6874	1601	4.29	0.32***	7266	1660	5.65	0.34***
	Size x Severity													2495	2768	2.16	0.07
	Model *F*				19.25***				23.75***				19.99***				13.58***
	R^2				0.12***				0.13***				0.21***				0.21***
	ΔR^2				-				-				0.08***				0.00
Deer pellet	Constant	8.77	1.58	5.55	- ***	4.96	1.67	2.96	- **	8.95	2.05	4.36	- ***	36.42	8.43	4.32	- ***
	Fire size	-1.67	0.51	-3.28	-0.26**					-1.65	0.52	-3.18	-0.26**	-11.40	2.95	-3.86	-0.37***
	Fire severity					-1.41	1.94	-0.72	-0.06	-0.27	1.92	-0.14	-0.01	-31.06	9.37	-3.31	0.06**
	Size x Severity													10.83	3.23	3.35	0.38**
	Model *F*				10.73*				0.53				5.34*				7.55***
	R^2				0.06***				-0.00				0.06***				0.12***
	ΔR^2				-				-				0.00				0.06**
Elk pellet	Constant	5.40	2.10	2.57	- *	5.84	2.15	2.71	- **	6.36	2.73	2.33	- *	6.18	2.73	2.26	- *
	Fire size	-0.29	0.67	-0.42	-0.04					-0.22	0.69	-0.31	-0.03	0.12	0.75	0.17	0.02
	Fire severity					-1.57	2.5	-0.63	-0.05	-1.42	2.55	-0.56	-0.05	-2.21	2.64	-0.84	-0.07
	Size x Severity													-5.03	4.40	-1.14	-0.10
	Model *F*				0.18				0.39				0.24				0.60
	R^2				-0.01				0.00				-0.01				-0.01
	ΔR^2				-				-				0.00				0.00
Cattle pellet	Constant	9.06	1.76	5.14	- ***	8.49	1.83	4.65	- ***	12.57	2.25	5.59	- ***	12.59	2.26	5.57	- ***
	Fire size	-1.94	0.57	-3.43	-0.27***					-1.68	0.57	-2.97	-0.24**	-1.72	0.62	-2.78	-0.24**
	Fire severity					-6.31	2.12	-2.98	-0.24**	-5.15	2.10	-2.45	-0.19*	-5.06	2.18	-2.32	-0.19*
	Size x Severity													0.57	3.64	0.16	-0.01
	Model *F*				11.75***				8.90***				9.08***				6.02***
	R^2				0.07***				0.05***				0.10***				0.10***
	ΔR^2				-				-				0.03*				0.00

Table 4. Top 5 models with the smallest AICc in forward stepwise modeling for aspen regeneration and recruitment respectively. The following predictor variables were used for constructing the models: year of fire, terrain features (aspect, slope, elevation), fire characteristics (fire size, fire severity), and pre-fire stand characteristics (aspen stand density, conifer stand density, aspen basal area, conifer basal area, aspen forest total cover area).

Response variable	Model	AICc	R^2
Aspen regeneration	Fire severity + Fire size + Aspen stand density + Elevation + Aspect (W)	1780.59	0.45
	Fire severity + Fire size + Aspen stand density + Aspect (W)	1781.28	0.44
	Fire severity + Fire size + Aspen stand density + Elevation	1782.02	0.44
	Fire severity + Fire size + Aspen stand density + Elevation + Aspect (W) + Aspen forest cover	1782.06	0.44
	Fire severity + Fire size + Aspen stand density + Elevation + Aspect (W) + Aspen basal area	1782.27	0.44
Aspen recruitment	Fire severity + Aspen stand density + Aspen forest cover	1538.53	0.27
	Fire severity + Aspen stand density + Aspen forest cover + Fire size	1538.60	0.28
	Fire severity + Aspen stand density + Aspen forest cover + Fire size + Aspect (W)	1539.73	0.28
	Fire severity + Aspen stand density + Aspen forest cover + Aspect (W)	1539.93	0.27
	Fire severity + Aspen stand density + Aspen forest cover + Conifer basal area	1540.09	0.27

Table 5. Strength and direction of estimates from best approximating model of predicting aspen regeneration and recruitment. Statistical significance is marked with asterisks (*P<0.05, **P<0.01, ***P<0.001).



Response variable	Terms	B	SE	*t*	β	*F*	R^2
Aspen regeneration	Constant	-181.06	69.08	-2.62	- **	24.80***	0.45***
	Fire severity	178.02	39.22	4.54	0.32***		
	Fire size	0.01	0.00	6.80	0.45***		
	Aspect (west)	-17.87	9.52	-1.88	0.12		
	Pre-fire aspen stand density	0.04	0.02	2.02	0.14*		
	Elevation	0.04	0.02	1.67	0.11		
Aspen recruitment	Constant	-49.22	15.35	-3.21	- **	19.33***	0.27***
	Fire severity	80.23	16.65	4.82	0.37***		
	Pre-fire aspen stand density	0.02	0.01	2.76	0.21**		
	Pre-fire aspen forest cover area	0.04	0.01	3.77	0.28**		

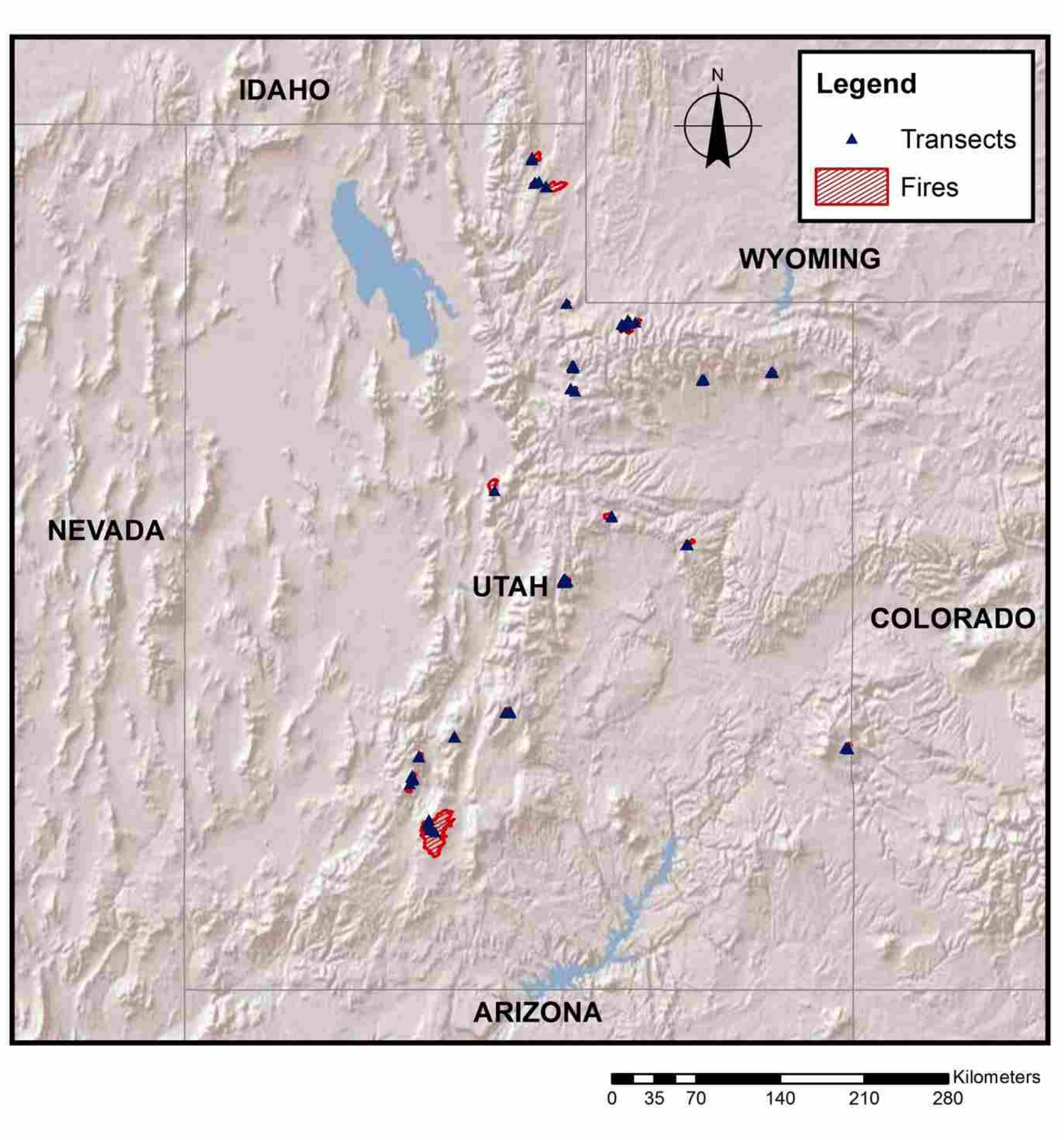


Fig. 1. Fire site and belt transect locations. A total of 25 fire sites and 149 transects were studied.

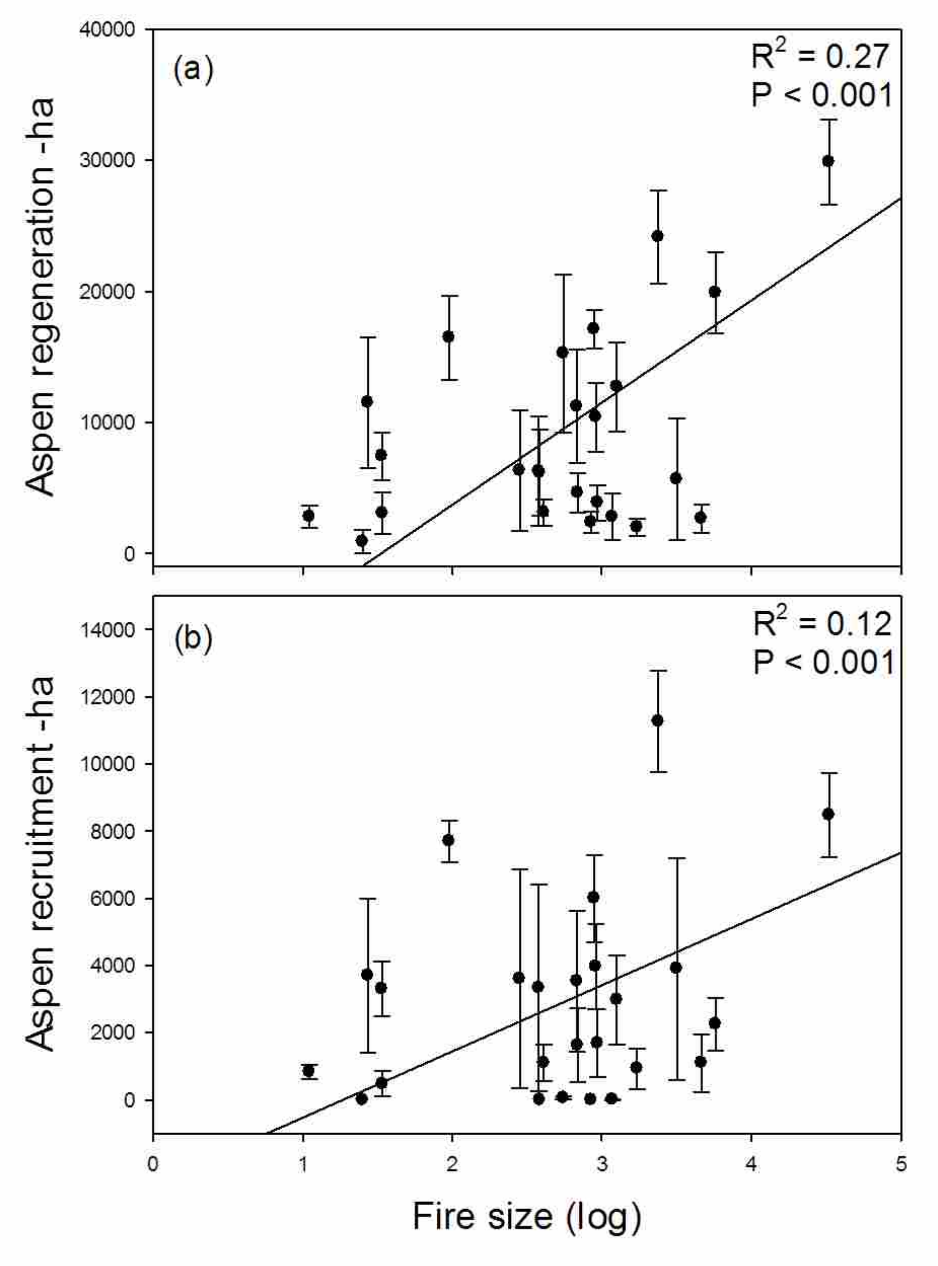


Fig. 2. Linear regression analyses indicating positive effects of fire size on (a) aspen regeneration and (b) aspen recruitment across 25 fire sites. Fire size in hectare (x-axis) is shown in log scale. Each point represents the stem mean±SE at each fire.

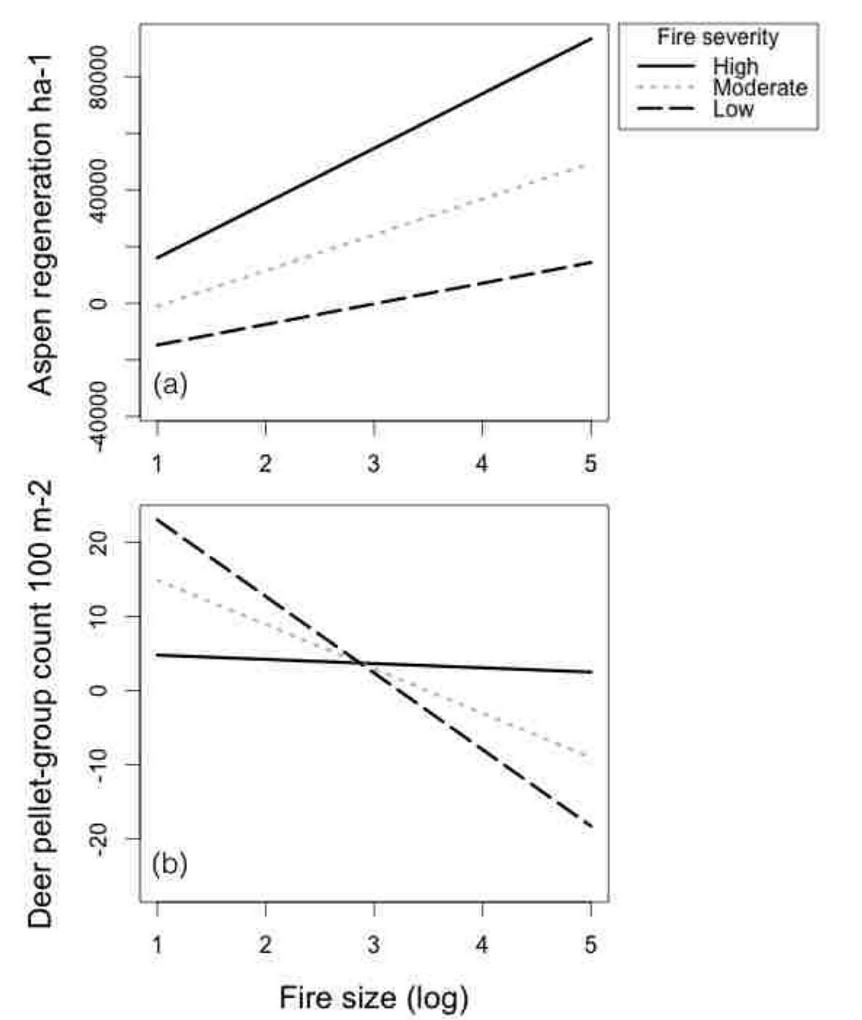


Fig. 3. Simple slopes interaction plot showing the interaction effect between fire size and fire severity on aspen regeneration. High, moderate, and low fire severities are defined at 100% (maximum observed value), 50%, and 10% (minimum observed value) severity respectively. Fire size in hectare (x-axis) is shown in log scale. (a) Regeneration response increases with fire size across all fire severities, and the strongest positive association (i.e., steepest slope) occurs for high severity fires. (b) Deer pellet generally decreases as fire size increases, but this response is most sensitive to changes in fire size when severity is low.