

RESEARCH ARTICLE

QUAKING ASPEN REGENERATION FOLLOWING PRESCRIBED FIRE IN LASSEN VOLCANIC NATIONAL PARK, CALIFORNIA, USA

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ABSTRACT

Prescribed fire is commonly used for restoration, but the effects of reintroducing fire following a century of fire exclusion are unknown in many ecosystems. We assessed the effects of three prescribed fires, native ungulate browsing, and conifer competition on quaking aspen (*Populus tremuloides* Michx.) regeneration in four small groves (0.5 ha to 3.0 ha) in Lassen Volcanic National Park, California, USA, over an 11 yr period. The effects of fire on aspen regeneration density and height were variable within and among sites. Post-fire aspen regeneration density generally decreased with greater conifer basal area ($r_s = -0.73$), but there was a wide range of aspen regeneration densities (4000 to 36667 stems ha⁻¹) at transects with no live conifers post-fire. The height of aspen regeneration increased as a function of increasing years-since-fire (1 yr to 11 yr), but heavy browsing by mule deer (*Odocoileus hemionus* Rafinesque) may alter future growth trajectories. Median percent of aspen regeneration browsed was high in burned (91%) and unburned (81%) transects. Only

RESUMEN

Las quemas prescritas son utilizadas cada vez más asiduamente en proyectos de restauración ecológica, aunque los efectos de su reintroducción después de un siglo de políticas de exclusión del fuego son desconocidos en numerosos ecosistemas. En este trabajo determinamos los efectos de tres quemas prescritas junto al ramoneo de ungulados nativos, y la competencia de coníferas, en la regeneración del álamo temblón (*Populus tremuloides* Michx.) en cuatro pequeños rodales (de 0.5 ha a 3.0 ha) en el Lassen Volcanic National Park de California, EEUU, durante un período de 11 años. Los efectos del fuego en la densidad y altura de la regeneración del álamo temblón fueron variables dentro y entre los rodales analizados. La densidad de la regeneración post-fuego del álamo temblón decreció de manera general con el aumento del área basal de las coníferas circundantes ($r_s = -0.73$), pero mostró un amplio rango de regeneración en áreas post-fuego en las que había coníferas vivas. La altura de la regeneración del álamo temblón se incrementó en función del incremento de los años transcurridos desde el fuego (de 1 años a 11 años), aunque el ramoneo intenso por parte del ciervo mulo (*Odocoileus hemionus* Rafinesque) podría alterar las trayectorias de crecimiento futuro. El percentil medio de regeneración ramoneada del álamo temblón fue alta, tanto en transectas

7% (282 stems ha⁻¹ to 333 stems ha⁻¹) of post-fire aspen regeneration in 11-year old burns exceeded the height necessary to escape mule deer browsing (150 cm). Browsing may also be altering aspen growth form, such that multi-stemmed aspen regeneration was positively associated with proportion of aspen regeneration browsed. These four case studies indicate that the effects of prescribed fires on quaking aspen in the southern Cascade Range of northern California were highly variable and, when coupled with biotic factors (such as deer browsing and competing vegetation) and varying fire severity, fire may either benefit or hasten the decline of small aspen groves.

quemadas (91 %) como en no quemadas (81 %). Solo el 7% (282 tallos ha⁻¹ a 333 tallos ha⁻¹) de la regeneración del álamo temblón en quemadas de 11 años excedieron la altura necesaria (150 cm) para escapar del ramoneo del ciervo mulo. El ramoneo ha podido alterar también la forma de crecimiento del álamo temblón, tanto que su regeneración con tallos múltiples se asoció positivamente con la proporción del ramoneo. Estos cuatro estudios de caso indican que los efectos de las quemadas prescritas en pequeños rodales de álamo temblón en el sur del cordón Cascade del norte de California fueron altamente variables y, acoplados a factores bióticos (como el ramoneo de ciervos mulos y la competencia de vegetación) y variaciones en la severidad del fuego, pueden tanto beneficiar la regeneración como acelerar la declinación de pequeños rodales de álamo temblón.

Keywords: browse, California, Cascades, fire effects, *Populus tremuloides*, prescribed burning, restoration

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INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx.) communities in the southern Cascades region of the western United States contribute disproportionately to biological diversity relative to associated coniferous forests (Kuhn *et al.* 2011). Concerns about the decline and deterioration of aspen have prompted a number of restoration efforts on federal and state lands in northern California, but very little is known about long-term aspen dynamics and restoration outcomes in this region (Shepperd *et al.* 2006). In contrast to the Rocky Mountains and Intermountain West regions of the US where aspen is more widespread and has been studied intensively, aspen in the southern Cascades and Sierra Nevada differ in several potentially important ways that warrant more lo-

cal research. Examples include very small grove sizes (typically <0.5 ha) and spatial isolation (Rogers *et al.* 2007), association with conifer forests that historically burned with frequent low-severity fire regimes (e.g., Taylor 2000), Mediterranean climate, lack of elk (*Cervus* spp.), and evidence of successful regeneration by seed following relatively recent volcanic eruptions over the last three centuries (McCullough *et al.* 2013). These small, isolated groves may be particularly vulnerable to decline due to increased conifer densities in the absence of fire (Shepperd *et al.* 2006). For example, 82% of the known aspen stands in the Lassen National Forest, California ($n = 542$), were determined to be at high risk of loss due to high browse pressure on regeneration and high conifer densities (see Shepperd *et al.* 2006). In a nearby study in Lassen Vol-

canic National Park, McCullough *et al.* (2013) found that aspen recruitment was negatively associated with percent conifer cover, and that half of the aspen stands had experienced greater than a 10% increase in conifer cover since 1952 (presumably due to lack of fire). Pierce and Taylor (2010) reported similar negative effects of fire suppression and conifer encroachment on aspen recruitment and growth in the Sierra Nevada.

Land managers in the region have recently begun to emphasize aspen restoration due to the high biological diversity and degraded condition of seral aspen communities (Jones *et al.* 2005, Shepperd *et al.* 2006, Krasnow *et al.* 2012). Specifically, where conifer density has increased due to fire exclusion and thereby reduced aspen growth and regeneration potential (see Calder *et al.* 2012), the goal is to remove competing conifers mechanically or through prescribed burning to stimulate asexual regeneration. Jones *et al.* (2005) reported that removing conifers from aspen groves with mechanized equipment increased aspen regeneration density and growth in the southern Cascades, and Krasnow *et al.* (2012) reported similar findings nearby in the Sierra Nevada. Prescribed burning is another logical choice for restoration given the well documented relationship between fire and aspen regeneration (Shepperd *et al.* 2006, Smith *et al.* 2011) and reported successes of fire treatments in other parts of the country (Jones and DeByle 1985). The use of fire may be the only feasible option in wilderness and other protected natural areas where mechanized treatments are not allowed, or in very large landscapes where fire can be more practical and efficient. However, published data on the short- or long-term effects of prescribed burning on aspen regeneration dynamics in coniferous forests in the Sierra Nevada or Cascades are lacking (see Shepperd *et al.* 2006). The only published study, which occurred in a sagebrush steppe in the southern Sierra Nevada, suggests that prescribed fire can increase overall aspen stem density, but it

is uncertain whether post-fire aspen regeneration will attain sufficient height to escape browsing by mule deer (*Odocoileus hemionus* Rafinesque) and replace the overstory (Krasnow *et al.* 2012). Most studies of post-fire dynamics come from Rocky Mountain and Intermountain West ecosystems where aspen is more extensive and dominated by high severity fire regimes (see Jones and DeByle 1985, Smith *et al.* 2011, Rogers and Mittanck 2013, Seager *et al.* 2013). Additionally, elk are a major source of browse on aspen regeneration following fire in the Rocky Mountains and Intermountain West (Seager *et al.* 2013), but are absent in the southern Cascades. The long-term effects of reintroducing prescribed fires in very small, isolated aspen stands following a century of fire suppression and associated increases in conifer density and surface fuels in California are poorly understood, and it is highly uncertain whether prescribed burning can be successful (Di Orio *et al.* 2005).

The goal of this research was to examine effects of prescribed fire on regeneration of small aspen groves in the Lassen Volcanic National Park wilderness in an effort to address a key information gap regarding the effectiveness of restoration efforts in the southern Cascades. These study sites represented some of the only prescribed burned aspen groves in the region that had not been subjected to previous timber harvest or recent livestock grazing. Our specific objectives were to (1) quantify the effects of prescribed fire on aspen regeneration density and height, and (2) test for associations between browsing and conifer basal area with aspen regeneration.

METHODS

Study Area

Lassen Volcanic National Park (LVNP) is located in northern California at the southern terminus of the Cascade Range (40° 33' 39" N, 121° 20' 34" W; Figure 1). The climate is

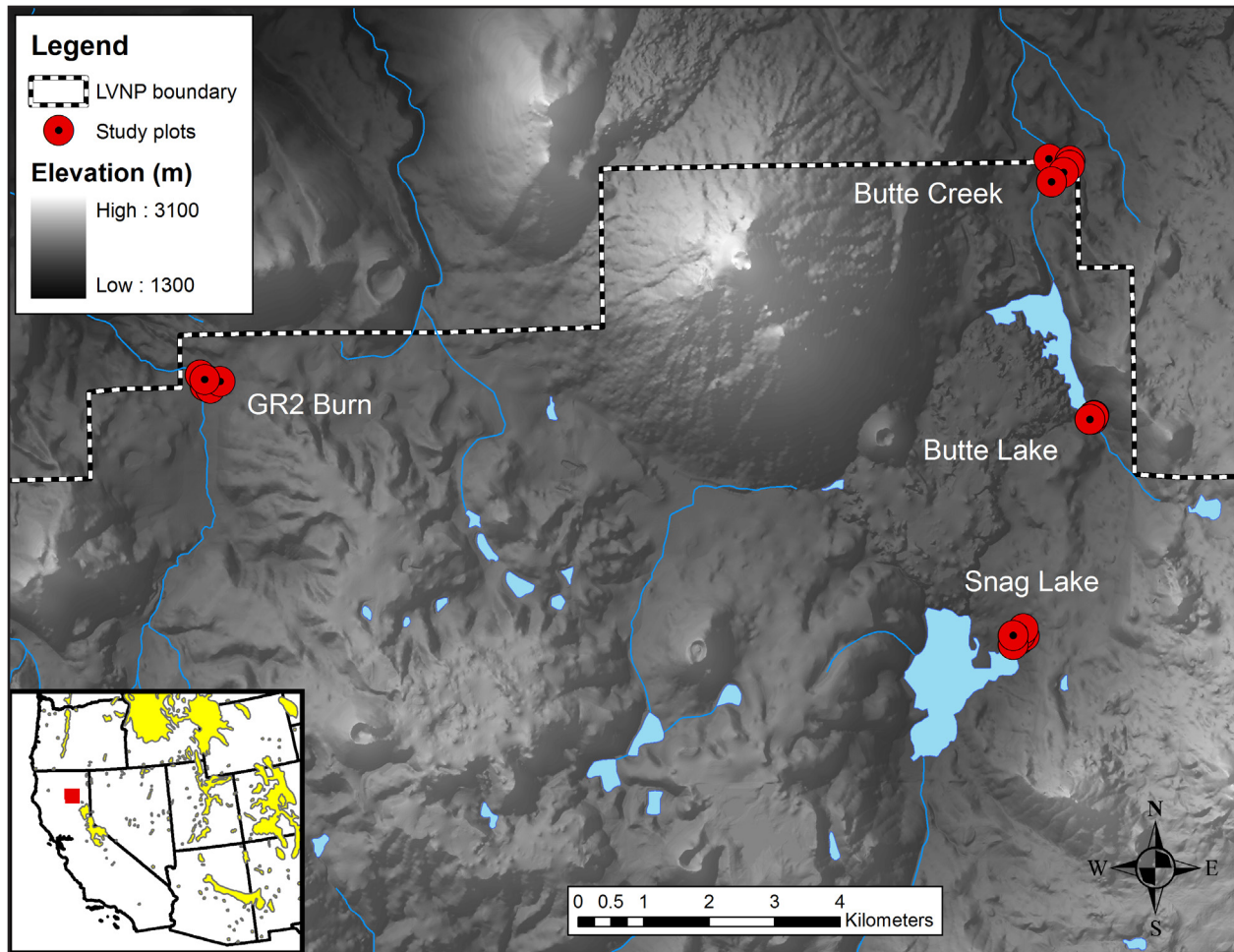


Figure 1. Post-fire quaking aspen regeneration study sites in Lassen Volcanic National Park (LVNP), California, USA. Inset map indicates the isolated location of study area within the range of quaking aspen in the western USA (after Little 1971).

characterized by warm, dry summers and cold, wet winters. Mean monthly temperatures range from 0.1 °C in January to 16.1 °C in July, and 83% of mean annual precipitation (1079 cm) falls between November and May (1971 to 2000, www.prism.oregonstate.edu). Grazing by domestic livestock has not occurred in LVNP since 1916.

We sampled all four seral aspen groves in LVNP burned by management-ignited prescribed fires (Figure 1, Table 1). The prescribed fires were conducted between 1998 and 2008 (i.e., years-since-fire when sampled ranged from 1 yr to 11 yr). Prior to the prescribed fires, none of the four groves had

burned for at least 80 years according to documentary records. All study sites consisted of seral aspen within climax conifer communities, but were relatively close to riparian or meadow communities (classified as Riparian or Meadow Seral following Shepperd *et al.* 2006). Associated conifers in order of abundance at all four sites included: lodgepole pine (*Pinus contorta* Douglas ex Loudon), white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.). Based on data from McCullough *et al.* (2013), who assessed conifer change over time in these four groves and others in the park, overstory conifer cover averaged 66% in

Table 1. Post-fire aspen regeneration site information for Lassen Volcanic National Park, California, USA.

Site name	Elevation (m)	Aspen area (ha)	Date burned	Energy Release Component (percentile)	No. burned transects	No. unburned transects
Butte Creek (BUT)	1778	2.5	1 Nov 2008	50 th	3 ^a	2
GR2 Burn (GR2)	1876	3.0	31 Oct 2006	15 th	3	3
Butte Lake (BLK)	1847	0.5	8 Oct 1998	25 th	2	2
Snag Lake (SL)	1866	3.5	8 Oct 1998	25 th	7 ^a	0

^a Includes pre-fire aspen regeneration density.

2008 compared to just 22 % in 1955. The aerial extent of the sampled aspen stands ranged from <1 ha to approximately 3 ha, and elevations ranged from 1830 m to 1890 m (Table 1).

The prescribed burns ranged from 200 ha to 630 ha in area and were ignited between mid-October and early November following early fall precipitation events (Table 1). The burns were part of a restoration program designed to incrementally reintroduce fire as an ecosystem process in the historically low to mixed severity fire regimes that dominate the landscapes (Taylor 2000). Thus, these were first-entry burns conducted under cool conditions with the intent of reducing surface fuel loads while limiting overstory mortality of old growth (in preparation for subsequent burning). The Energy Release Component, an index related to potential energy or heat release in a flaming fire front (Bradshaw *et al.* 1983), ranged from 15th to 50th percentile on the days the aspen sites burned (Table 1). Fire behavior consisted predominantly of creeping, low intensity (flame length <30 cm) surface fires through surface fuels (torching was rare and limited to individual trees). Stand level fire severity mapped from satellite imagery (one year post-fire) was classified as “unchanged/low” for pixels in each grove, indicating little or no conifer overstory mortality at 30 m mapping resolution (Eidenshink *et al.* 2007). Surface fuel consumption varied greatly at finer spatial scales depending on the presence and

amounts of coarse woody debris, which supported higher flame lengths and longer residence times.

Field Sampling and Analysis

We compared the density and height of live aspen regeneration between burned and unburned transects and related this to measures of conifer basal area, browse, and number of years-since-fire. Two sites had pre-fire aspen regeneration density data (Snag Lake [SL] and Butte Creek [BUT]), enabling us to make direct comparisons with post-fire aspen regeneration density (Table 1). There was no pre-fire data at the other two sites (Butte Lake [BLK] and GR2 Burn [GR2]), but we were able to compare burned aspen transects with adjacent unburned aspen transects (i.e., unburned references). All pre-fire and reference sites are hereafter referred to as “unburned.” Data were collected from a total of 22 permanent 2 m × 30 m belt transects that were randomly located within each grove. The total number of transects at each site ranged from four to seven, which was limited by the size of the aspen groves and the amount that had burned (Table 1).

In each transect, we recorded the species and diameter of all live trees (≥5 cm diameter at breast height, dbh), the total number of live aspen regeneration (<5 cm dbh), regeneration height, and whether aspen regeneration was

browsed or not (as indicated by evidence of stems and leaves that had been bitten off). We commonly observed multiple aspen regeneration stems originating from the same root node, particularly when stems were browsed back to near ground level. We defined these groups of aspen regeneration stems as a single aspen regeneration “cluster,” and recorded and analyzed the number of (1) regeneration clusters, (2) individual stems, and (3) stems per cluster.

We tested for effects of fire on aspen regeneration stem density at each site using the Wilcoxon signed-rank test for sites with pre-fire density measurements (BUT and SL) and a Wilcoxon ranked sum test for sites without pre-fire density measurements (i.e., burned vs. adjacent unburned transects, BLK and GR2). We tested for effects of fire on aspen regeneration height at three sites (BLK, BUT, and GR2) using the Wilcoxon ranked sum test (i.e., burned vs. adjacent unburned transects, with no pre-fire measurements). Pre-fire aspen regeneration height measurements at SL did not include stems greater than 1.37 m tall and therefore were not compared with post-fire regeneration heights. Spearman rank correlation (r_s) was used to test for associations between (1) post-fire conifer basal area and aspen regeneration density at burned transects across all sites, (2) years-since-fire and site-level mean regeneration height, (3) site-level mean

percent of regeneration browsed and mean regeneration height, (4) years-since-fire and transect-level mean number of aspen regeneration stems per cluster, and (5) transect-level mean percent of regeneration browsed and the mean number of aspen regeneration stems per cluster. The Anderson-Darling test was used to determine that non-parametric statistical tests were appropriate for all analyses. The α level for all tests was 0.05. All analyses were performed in the R statistical computing environment (R Core Team 2014).

RESULTS

Prescribed burning increased the median density of aspen regeneration by 243 % at SL, decreased regeneration density by 5 % at BLK and 87 % at GR2, and resulted in no change at BUT, compared to unburned transects (Table 2). Due to high within-site variability, the changes in median regeneration density were only statistically significant at SL (Table 2). Some transects had no post-fire aspen regeneration while adjacent transects at the same site (e.g., BUT) had densities greater than 36 000 stems ha^{-1} . Overall median post-fire regeneration densities ranged from 1167 stems ha^{-1} to 21 833 stems ha^{-1} among the four sites (Table 2).

Post-fire live conifer basal area ranged from 0 $\text{m}^2 \text{ha}^{-1}$ to 143 $\text{m}^2 \text{ha}^{-1}$ among burned

Table 2. Quaking aspen regeneration density (stems ha^{-1}) from burned and unburned transects at four sites in Lassen Volcanic National Park, California, USA. Note: burned and unburned regeneration densities were compared with the Wilcoxon rank sum (BLK and GR2) and Wilcoxon signed-rank tests (BUT and SL).

Site	Median		<i>W</i> statistic	<i>P</i> -value
	unburned	burned		
BUT	5 167 ^a	5 167	2	1.00
GR2	12 667	1 667	2	0.40
BLK	21 833	20 750	1	0.67
SL	1 167 ^a	4 000	27	0.03

^aUnburned density from pre-fire measurements.

transects. Post-fire aspen regeneration density generally decreased with greater conifer basal area ($r_s = -0.73$, $P = 0.002$). However, there was a wide range of aspen regeneration densities (4000 to 36667 stems ha^{-1}) at transects with no live conifers post-fire (Figure 2).

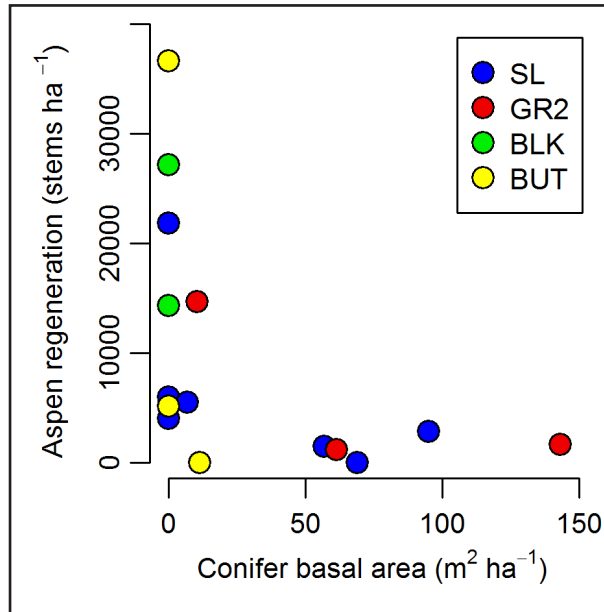


Figure 2. Post-fire quaking aspen regeneration density as a function of post-fire live conifer basal area ($n = 15$ burned transects across four sites). Aspen regeneration density generally decreased with high post-fire conifer basal area, although aspen regeneration varied widely at transects with no live conifers post-fire.

Prescribed burning increased the median height of aspen regeneration by 12 % at BLK, and decreased regeneration height by 65 % at BUT and 45 % at GR2, compared to unburned transects (Table 3). Due to high within-site variability, the changes in median regeneration height were not statistically significant (Table 3). The number of years-since-fire had a stronger association with post-fire aspen regeneration heights ($r_s = 0.95$, $P = 0.05$) than percent browse ($r_s = 0.40$, $P = 0.75$). The sites with the greatest years-since-fire (11 yr) had the tallest aspen regeneration and the site that was measured one year post-fire had the shortest regeneration heights (Table 3). Only 7 % ($n = 15$) of all aspen regeneration in the 11-year old burned transects have reached heights of greater than 150 cm, and these were present in only two transects (see Table 3). The mean density of aspen regeneration greater than 150 cm at the two 11-year old burn sites was 282 stems ha^{-1} (SL) and 333 stems ha^{-1} (BLK) (Table 3). No regeneration reached 150 cm in height at the two more recent burns (BUT and GR2).

The median percent of aspen regeneration browsed was 81 % in the burned transects and 91 % in the unburned reference transects. At all sites, we observed multi-stemmed aspen regeneration clusters (Figure 3). There was no relationship between the mean number of stems per cluster in a transect and the number

Table 3. Quaking aspen regeneration height from burned and unburned transects at four sites in Lassen Volcanic National Park, California, USA. Note: sites are ordered by ascending number of years-since-fire. Burned and unburned regeneration heights were compared with the Wilcoxon rank sum test.

Site	Years-since-fire	Median height (cm)		<i>P</i> -value (<i>W</i>)	>150 cm (%)	>150 cm density (ha^{-1})
		unburned	burned			
BUT	1	95.0	33.3	0.33 (0)	0.0	0
GR2	3	72.7	40.3	0.40 (2)	0.0	0
BLK	11	57.7	64.9	0.67 (3)	4.8	333
SL ^a	11	5.5	57.2		8.1	282

^a SL was the only site with pre-fire height data, but stems greater than 1.37 m tall were not measured and therefore could not be compared to the burned aspen heights at this site.



Figure 3. Photograph of an exceptional example of repeatedly browsed, multi-stemmed aspen regeneration 11 years post-fire that is less than 25 cm tall. Photo credit: Ellis Q. Margolis.

of years-since-fire ($r_s = -0.14$, $P = 0.618$). At 21 of 22 transects, there was a strong positive correlation between the transect-level mean number of stems per cluster and percent of regeneration browsed ($r_s = 0.75$, $P < 0.001$). The one outlier transect had an average of 4 stems per cluster, but low percent browse and was in the most recently burned site (BUT).

DISCUSSION

The density of aspen regeneration following prescribed fire in LVNP was highly variable within and among sites, although the overall density range among individual transects (0 stems ha^{-1} to 36 667 stems ha^{-1}) was similar to that reported three years after prescribed fire in the Sierra Nevada (Krasnow *et al.* 2012) and four years after mechanical removal of conifers on the Lassen National Forest adjacent to LVNP (Jones *et al.* 2005). These aspen densities are slightly lower than the range of 8000 stems ha^{-1} to 40 000 stems ha^{-1} reported five years following mechanical thinning in the Sierra Nevada (Krasnow *et al.* 2012). Interestingly, aspen regeneration densities from the few studies in the southern Cascades and the Sierra Nevada (including our study) are at the low end of the range of regen-

eration densities reported following fire or clear-cutting in the Rocky Mountains (e.g., 35 800 stems ha^{-1} four years following high severity fire in spruce-fir in New Mexico, 30 000 stems ha^{-1} to 150 000 stems ha^{-1} following fire in western Wyoming, and 76 600 stems ha^{-1} following a clear cut in Colorado; Jones and Debye 1985, Schier *et al.* 1985). It is possible that aspen regeneration densities at LVNP will continue to increase in the burned transects in the future, but total aspen regeneration tends to stabilize or decline in the first two years following disturbance (Shepperd 1993).

Post-fire conifer basal area was negatively associated with post-fire aspen regeneration density among transects (Figure 2). This is consistent with many studies throughout the western USA, indicating that increased conifer competition is one cause of deteriorating aspen stands and reduced regeneration (St. Clair *et al.* 2013). Although the highest post-fire aspen regeneration densities at LVNP occurred in transects with no conifers post-fire, other transects with no post-fire conifers had low regeneration (e.g., SL and BUT; Figure 2). This suggests that lack of conifer shading and competition is important, but not sufficient by itself to result in high post-fire aspen regeneration density. Pre-treatment aspen density (of all size classes) has been shown to be positively associated with post-treatment regeneration response in the adjacent Lassen National Forest, California (Jones *et al.* 2005). Low pre-fire total aspen density could possibly explain some of the low regeneration response at LVNP where there was seemingly a suitable post-fire regeneration environment (i.e., low post-fire conifer density), but these data were not available for our sites.

Although aspen regeneration density is an important component of aspen stand dynamics, this metric alone can potentially be misleading if regeneration is in poor condition. Height growth and vigor of aspen regeneration will ultimately determine the potential to replace a declining aspen overstory, particularly

when there is heavy browse pressure (Jones *et al.* 2005, Shepperd *et al.* 2006). In aspen stands with heavy browsing pressure, a height of greater than 150 cm is considered a conservative estimate for the tops of the trees to escape browsing by deer (*Odocoileus* spp.), and are therefore deemed “successful” in terms of having a high probability of recruitment into the overstory (assuming subsequent growth is not inhibited by conifer competition) (Muegler and Bartos 1977). The small percentage (5% at all sites and 7% at 11-year post-fire sites) and low density (282 stems ha⁻¹ to 333 stems ha⁻¹) of aspen regeneration greater than 150 cm tall in burned sites at LVNP suggests that browsing is greatly reducing the number of stems that reach sufficient height to replace the declining aspen overstory (Table 3). It is possible that regeneration at recently burned sites (BUT, 1-year post-fire, and GR2, 3-years post-fire) may not have had sufficient time to reach 150 cm height (e.g., Jones *et al.* 2005). However, asexual aspen regeneration are commonly observed growing greater than 150 cm within one or two years after disturbance because of large clonal root system reserves (Jones and Schier 1985), which would be expected at mesic sites associated with springs and streams in our study areas. Moreover, low numbers of aspen regeneration greater than 150 cm at the two sites (SL and BLK) that were 11 years post fire suggest that browsing is preventing the post-fire regeneration from recruiting into the overstory (Figure 3, Table 3). These results are consistent with Jones *et al.* (2009), who found that simulated browsing and the presence of overstory conifers reduced aspen regeneration height growth in three aspen stands on the adjacent Lassen National Forest. This is also consistent with experimental observations in the Rocky Mountains (Calder *et al.* 2011). Thus, in the absence of elk, which can significantly affect aspen regeneration in the Rocky Mountains (Seager *et al.* 2013), mule deer browsing within small groves at LVNP is likely effectively reducing

aspen regeneration height and the potential for recruitment into the overstory.

Heavy browsing pressure at all four sites may also be influencing aspen growth form. We found the ubiquitous presence of multi-stemmed aspen regeneration clusters (e.g., Figure 3) to be in contrast to the structure of the overstory aspen, which were single-stemmed, tall “trees.” In the Intermountain West, aspen has been observed to regenerate in clusters from a single point on a root, but most clusters self-thin to a single dominant stem by 5 to 10 years after the regeneration event (Schier *et al.* 1985). We found no relationship between the number of stems per cluster and years-since-fire, which suggests that self-thinning is not occurring at LVNP. At the two sites that burned over 11 years ago (SL and BLK), the mean number of stems per cluster is still high (1.5 to 3). We hypothesized that another potential cause of multi-stemmed regeneration could be persistent browsing, such that as the apical meristem is repeatedly removed by browsing additional stems are produced. The positive correlation between browsing and the number of aspen stems per cluster at all but one transect supports this hypothesis. Multi-stemmed aspen “bushes” associated with repeated mid- to late-summer mule deer browse has been observed in the nearby northern Sierra Nevada (Shepperd *et al.* 2006). The possible link between browsing and a trend toward change in aspen vegetative structure should be a topic of further research.

Prescribed Fire

Although the four aspen groves in this study all burned, fire intensity and severity varied at fine-scales between (and even within) individual transects, which has important implications for these very small groves. These three prescribed burns were not designed specifically for restoration of aspen groves with high intensity fire, as is typically recommended in the Rocky Mountains or In-

termountain West (e.g., Keyser *et al.* 2005). Rather, they were initial (first-entry) burns during cool conditions aimed at restoring low severity fire regimes that historically burned in surrounding coniferous forests (Taylor 2000), and limiting old-growth conifer mortality. We did not have access to data on pre-fire overstory density or transect-scale fire severity. However, we observed that overall fire intensity in many of the aspen stands and transects was high enough to girdle and kill fire-sensitive overstory aspen stems, but too low to kill most conifers with thicker bark. Thus, after the fire, the few regenerating shade-intolerant aspen

stems were still in an unfavorable environment, shaded by conifers and heavy coarse woody debris (e.g., Figure 4, top panels). This is consistent with our observed general trend of lower aspen regeneration density with increasing post-fire conifer basal area (i.e., lower fire severity; Figure 2). The main mechanism to stimulate aspen regeneration is an event that alters the auxin-cytokinin balance and induces sprouting from the roots (e.g., high severity crown fire that top-kills aspen stems) (Schier *et al.* 1985). It has been shown that increased soil temperature (e.g., from increased solar radiation following reduced canopy cover) can

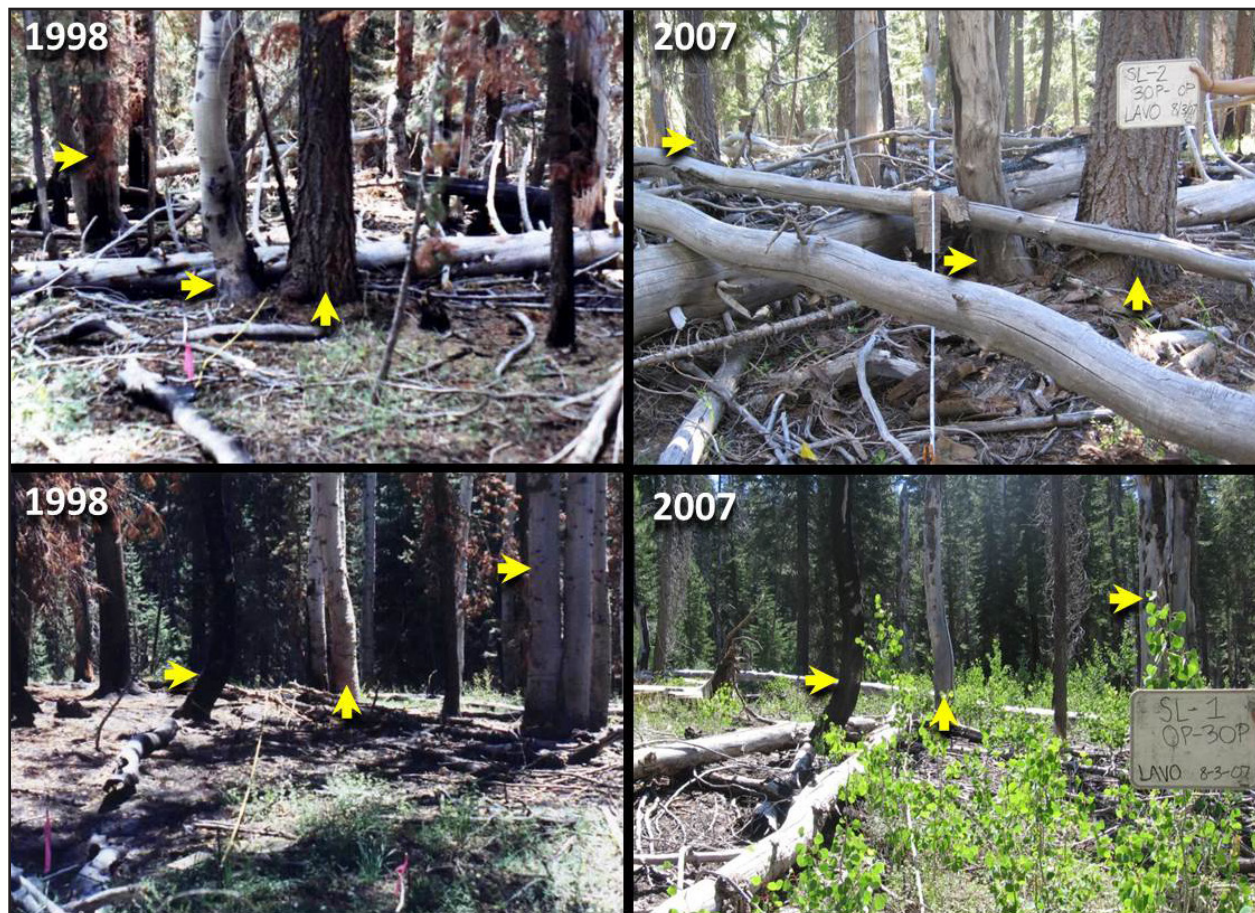


Figure 4. Photographs from two transects at Snag Lake (SL) taken 1 year post-fire (1998) and 9 years post-fire (2007), illustrating variability in post-fire aspen regeneration associated with spatial variability in fire intensity. Top: suboptimal, shaded, regeneration conditions associated with low intensity burning that lethally girdled live aspen but did not kill established conifers (note post-fire dead and down aspen stems). Bottom: transect with higher fire intensity that killed most conifers and reduced canopy cover, which is associated with the maximum aspen regeneration numbers and heights among transects within the site. Photo credit: Calvin A. Farris.

also increase cytokinin levels in roots, which signals regeneration (Schier *et al.* 1985). Thus, low intensity fire that killed dominant aspen, but did not sufficiently reduce shading from live conifers or forest floor cover, would likely not be beneficial for aspen regeneration and could possibly explain the poor post-fire response in some transects (e.g., SL and GR2 transects with high conifer basal area and low aspen regeneration density; Figure 2). This pattern would be consistent with Keyser *et al.* (2005), who found higher levels of suckering in high severity burns compared to unburned or low severity burns. After our study was completed, a large wildfire (2012 Reading Fire) burned the GR2 transects and additional aspen groves in LVNP with varying severity, so continued monitoring and research of those sites will help quantify effects of fire severity on aspen regeneration in the region.

Although fire of higher intensity and severity may be important for successful aspen regeneration, localized high heat loads associated with long flame residence times appear to have occurred at some sites (e.g., BUT) where large logs were present and probably contributed to lower post-fire aspen regeneration. We observed that, where fire consumed the duff layer, aspen roots were exposed, burned, and killed, and thus were unable to regenerate post-fire; whereas, areas within the same transect (<10 m apart) with intact duff had successful aspen regeneration. This could not be observed or quantified for the older burns, so we could not analyze this systematically. However, on the adjacent Lassen National Forest, Jones *et al.* (2005) observed a similar absence of post-fire aspen regeneration in areas where slash piles were burned, possibly because the fire intensity and residence time

killed the aspen roots. In declining, small aspen groves with heavy fuel loading, mechanical treatment (including removal of activity fuels) may be beneficial prior to burning, and regeneration may need initial protection from browse until stems reach heights of greater than 150 cm.

The prescribed burns we studied may have benefited quaking aspen in some individual transects by increasing mean regeneration density or heights relative to untreated or pre-fire numbers (although only one site had statistically significant changes). However, heavy post-fire mule deer browsing is reducing the number of aspen regenerations that reach sufficient height (>150 cm) to replace the declining aspen overstory, and may even be producing multi-stemmed trees or aspen “shrubs.” Low intensity burning followed by heavy browsing could ultimately lead to reduced aspen regeneration density, as was observed at two sites. Fires likely need to be intense enough to kill conifers that are out-competing the shade-intolerant aspen regenerations, or aspen stands may decline further. In areas where aspen restoration is the primary goal, multiple risk factors should be considered (e.g., numbers of live aspen regeneration, conifer cover, and browse pressure) for prioritizing and designing restoration treatments (Bartos and Campbell 1998). Additional research is needed to improve our understanding of the interactions of fire severity, competing vegetation and browsing on aspen in this understudied region. This is especially the case in small, declining groves where low intensity fires are being implemented that are consistent with historical fire intensity, but may be ineffective at reducing conifer density or regenerating aspen under current conditions.

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