Research Article

Aspen Restoration in the Eastern Sierra Nevada: Effectiveness of Prescribed Fire and Conifer Removal

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ABSTRACT

Aspen (*Populus tremuloides* Michx.) comprises only a small fraction (1 %) of the Sierra Nevada landscape, yet contributes significant biological diversity to this range. In an effort to rejuvenate declining aspen stands, the Bureau of Land Management conducted conifer removal in three sites (2004 to 2006) and prescribed fire in two sites (2007). The goal of this study was to evaluate the efficacy of these treatments. In each site, aspen densities in three regeneration size classes were measured in treated and untreated transects before and up to five years post-treatment. Five years after treatment, two of the three conifer removal sites showed significant improvement over controls in the density of total stems and two of three regeneration size classes. The third site did not show significant gains over controls in any size class and experienced significant aspen overstory mortality three years after treatment, which was attributed to sunscald and advanced age at the time of treatment. Three years after treatment, the two prescribed fire sites showed significant increases in total stem density and two regeneration size classes, but also exhibited significant stem mortality, which was likely due to a combination of herbivory and drought. Overall, both treatments can be effective, but future treatments should incorporate methods to reduce post-treatment mortality of residual aspen and new sprouts.

Keywords: aspen, effectiveness monitoring, generalized linear mixed effects regression, *Populus tremuloides*, prescribed fire, Sierra Nevada

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INTRODUCTION

Aspen (*Populus tremuloides* Michx.) is the most widely distributed tree in North America (Little 1971), yet comprises only a small fraction (1%) of the Sierra Nevada landscape (Shepperd *et al*. 2006). As one of the few broadleaf deciduous trees in a conifer dominated landscape, aspen is considered a foundation species and contributes significant biological diversity in an otherwise relatively low diversity landscape (Kay 1997). Aspen stands support a unique assembly of understory plants, and their edible foliage attracts diverse insects, birds, and mammals (DeByle and Winokur 1985). Compared to Sierran conifer forests, aspen stands also provide increased water yield and ecosystem resiliency to high-severity fire (Shepperd *et al*. 2006).

Currently, aspen populations in the American West are declining in vigor due to fire suppression, drought, and ungulate browsing (Di Orio *et al*. 2005, Worrall *et al*. 2008). In the Rocky Mountains, rapid and widespread mortality, referred to as "Sudden Aspen Decline," is occurring as a result of moisture stress and hydraulic impairment (Worrall *et al*. 2010, Anderegg *et al*. 2012). This mortality is projected to continue as the climate envelope for aspen diminishes with a warming climate in the next century (Rehfeldt *et al*. 2009). The limited aspen stands in the Sierra Nevada are in particular danger of being replaced by more shade-tolerant conifers due to their rarity, small average stand size (Potter 1998, DeWoody *et al*. 2009), and long disturbance-free intervals due to modern-day fire suppression. Although the historical extent of aspen in the Sierra Nevada is unknown, Rogers *et al.* (2007) hypothesize that there was a large pulse of aspen regeneration in the late 1800s due to widespread fires, dam building, mining, and logging. This may have been the last major window of regeneration for Sierran aspen, as the twentieth century marked the onset of fire suppression and reduced human disturbance. As a result, the aspen stands in the Sierra Nevada today are often of advanced age and in the process of succession to conifers (Potter 1998). For example, of 542 aspen stands inventoried since 2002 in the Lake Tahoe Basin, 70% of the stands have been classified as moderate to highest risk of being lost (Shepperd *et al*. 2006).

Aspen stands represent diversity hotspots to land managers and are increasingly being targeted for restoration. West of the Rockies, aspen restoration studies have been conducted in the northern Great Basin (Bates *et al*. 2006) and Lassen National Forest (Jones *et al*. 2005), which lies in the southern Cascade Range and the northern extent of the Sierra Nevada Range, but similar data is currently lacking from the bulk of the Sierra Nevada ecoregion. Bates *et al.* (2006) found that mechanical removal of western juniper (*Juniperus occidentalis* Hook.) in the northern Great Basin followed by prescribed fire in the fall was more effective in stimulating aspen regeneration than was spring prescribed fire. Jones *et al*. (2005) found conifer removal to be an effective strategy to stimulate aspen regeneration in the Lassen National Forest and observed a significant increase in aspen stems above browse height 4 years after treatment.

Currently, no published studies exist that document aspen restoration treatments in the eastern Sierra Nevada. The goals of this study were to monitor and evaluate aspen restoration treatments in this area, providing critical information for adaptive management of this important species. Our research goals were to:

1) Evaluate the efficacy of conifer removal and prescribed fire treatments to stimulate aspen asexual regeneration.
2) Identify challenges to successful restoration and examine possible causes to inform future management.

METHODS

Study Area

In 2003, the Bureau of Land Management office in Bishop, California, USA, began an aspen restoration and monitoring program focused on increasing the vigor and regeneration of declining aspen stands in the eastern Sierra Nevada. We selected three aspen stands along Virginia Creek with heavy lodgepole pine (*Pinus contorta* Douglas ex Loudon) encroachment for conifer removal (Virginia Creek 1 to 3, referred to hereafter as VC1, VC2, and VC3), and two aspen stands in sagebrush (*Artemisia tridentata* Nutt.) steppe with very little aspen regeneration, for prescribed fire treatment (Green Creek 1 to 2, referred to hereafter as GC1 and GC2; Figure 1). This study aims to evaluate the efficacy of both treatment types in stimulating aspen asexual regeneration.

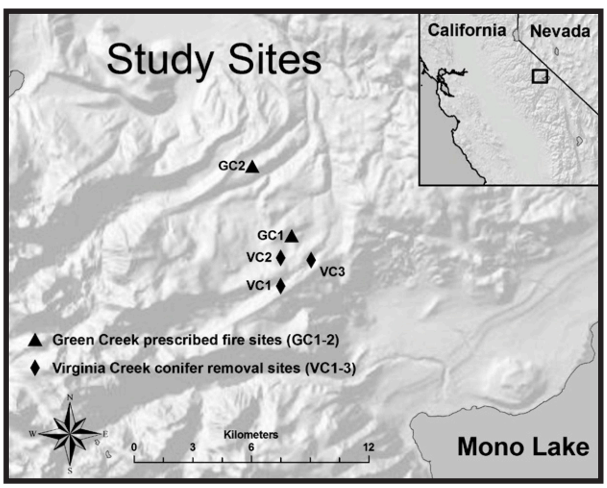

Figure 1. Map of study sites.

The eastern range of the Sierra Nevada lies in the rain shadow of the Sierra Crest, has a steeper elevation gradient, and generally lower average temperature and precipitation than the western slope of the Sierra Nevada. At elevations of 2440 m to 2740 m in the Conway summit region, where the current study sites are located, most precipitation occurs as snow, and averages 35 cm yr^{-1} to 45 cm yr^{-1}. Average yearly, January, and July temperatures are approximately 2 °C, −5.5 °C, and 11 °C, respectively. Soils are weakly developed and well drained decomposed granite Entisols (Potter 1998). Aspen are often associated with riparian areas or mesic sites with low slope angle, although upland stands are also present. Early European settlement in this area occurred after the 1860s and was concentrated in cattle ranches on the valley floor and a few boom-mining areas such as Bodie (25 km from the study sites).

Study Sites

All stands are on level to gently sloping north facing slopes (10 % to 20 %) at elevations ranging from 2446 m to 2710 m. Soils are comprised of granitic parent material in the form of glacial outwash. Soil textures are rocky to gravelly with high drainage capacity. In the conifer removal sites (VC1, VC2, and VC3), dominant vegetation is comprised of an overstory of lodgepole pine with aspen scattered within small openings throughout the sites. In these stands, understory dominants consist of mountain big sagebrush (*Artemisia tridentata* Nutt.), bitterbrush (*Purshia tridentata* [Pursh] DC.), wax currant (*Ribes cereum* Douglas), basin wild rye (*Leymus cinereus* [Scribn. & Merr.] Á. Löve), Nevada needlegrass (*Achnatherum nevadensis* [B.L. Johnson] Barkworth) and Pacific lupine (*Lupinus lepidus* Douglas ex. Lindl.). The prescribed fire sites have an aspen overstory with similar understory species interspersed throughout the stands.

Campbell and Bartos (2001) identified the following five risk factors that indicate that an aspen clone is at risk of loss: 1) when conifer canopy cover is >25 %, 2) aspen canopy cover is <40 %, 3) dominant aspen trees are >100 years of age, 4) aspen regeneration 1.5 m to 4.6 m tall is <1235 stems ha^{-1}, and 5) sagebrush cover is >10 %. The conifer removal study sites exhibited factors 1, 2 (except VC2), 4 (except VC2), and 5. Additionally, although the aspen were not aged at VC1 and VC2, those aged at VC3 were all over 100 years of age. The prescribed fire sites exhibited factors 4 and 5.

Aspen Restoration Treatments

Conifer removal. The stands selected for conifer removal all exhibited significant overstory lodgepole pine encroachment. Total treatment area in VC1, VC2, and VC3 were 2 ha, 6.9 ha, and 2 ha, respectively (total aspen stand sizes were 3 ha, 8.5 ha, and 3 ha, respectively). Average pre-treatment lodgepole pine canopy cover for each site was 97 %, 38 %, and 63 %, respectively. Average pre-treatment aspen canopy cover was 2.5 %, 57 %, and 27 %, respectively. Average pre-treatment aspen stem density for trees over 1.5 m in height and diameter at breast height greater than 2.5 cm was 402 stems ha^{-1}, 494 stems ha^{-1}, and 852 stems ha^{-1}, respectively. Starting with VC1, we treated one stand each year from 2004 to 2006, between 1 August and 1 October, by removing lodgepole pines within and surrounding (up to 10 m) of each aspen stand by hand felling. This was followed by removal of tops and limbs and mechanical hauling to a landing outside of the aspen stand. We sold removed timber larger than 10 cm in diameter as firewood, and chipped and scattered residual materials on site (we limited chip depth to less than 5 cm). The wood volume removed from VC1, VC2, and VC3 was 85 m^3 ha^{-1}, 59 m^3 ha^{-1}, and 156 m^3 ha^{-1}, respectively.

Prescribed fire. We selected two aspen stands in sagebrush steppe with little regeneration for prescribed fire. In the fall of 2007, we applied prescribed fire with strip head-fires using drip torches. Cured grasses and shrub cover were sufficient to carry fire, though reignition within the aspen stands was necessary. Ten hour timelag fuel moistures were 10 % to 12 %, relative humidity averaged 20 % to 30 %, air temperatures were between 10 °C to 16 °C with 3 km hr^{-1} to 8 km hr^{-1} winds from the west and southwest. Average flame lengths were 0.5 m to 1 m, producing a low intensity fire with patches of moderate intensity fire (S. Volkland, Bureau of Land Management, personal communication).

Vegetation Measurements

Prior to implementing conifer removal or prescribed fire treatments, we randomly located three to five permanent 30.5 m × 1.8 m belt transects in treatment areas in each site (three sites of conifer removal and two sites of prescribed fire; see Table 1 for details). In each transect, we measured aspen stems in the following size classes (SC) before treatment and up to 5 years after treatment: SC1 = height less than 0.45 m, SC2 = height 0.45 m to 1.5 m, SC3 = height above 1.5 m and diameter at breast height (dbh) less than 2.5 cm, and SC4 = height above 1.5 m and dbh greater than 2.5 cm (Jones *et al.* 2005). Size class three represents the height at which aspen escape pressure from ungulate browsers in this area. We measured conifer removal sites prior to treatment and annually thereafter for five years (except in 2008) and measured prescribed fire sites before treatment and annually for three years after treatment. We measured canopy cover by tree species with a sight tube at 3.03 m intervals along each transect and took photos from both ends of each transect. Shrub cover by species was also assessed in each transect. In 2007, we observed post-treatment sprout mortality in some of the treatment transects, and so thereafter we recorded the total number of stems that were dead as well as those that had the main leader removed by herbivores in each size class.

Control Transects

One to two control transects were established in adjacent, untreated aspen forest in four sites, and in one site (VC2), no controls

Table 1. Summary of treatment and control transects in each study site in the eastern Sierra Nevada, California. Conifer = conifer removal; Rx fire = prescribed fire.

	VC1	VC2	VC3	GC1	GC2
Year established	2004	2005	2006	2007	2007
Treatment type	Conifer	Conifer	Conifer	Rx fire	Rx fire
Number of treatment transects	4	4	4	3	5
Number of original control transects	2	0	1	2	2
Number of original controls retained	1	0	0	2	2
Number of new controls established	1	2	2	1	0
Number of controls used in analysis	2	2	2	3	2

were established at the initiation of the treatment. Two of the initial control transects in the conifer removal sites were problematic due to: 1) sharing an end point with a treatment transect in VC1 (thus experiencing obvious edge effects from the treatment), and 2) being located on a different aspect and of significantly higher aspen density and lower conifer density than the treatment transects in VC3. To remedy this problem, we established new controls transects in the summer of 2010 in adjacent, untreated aspen stands similar to the neighboring treated stands (Table 1). We made identical measurements on each new control transect. In addition, we reconstructed densities of aspen stems in each size class for prior years by using bud scar quantities and heights to age each aspen stem (Craig *et al.* 1989) and to reconstruct the height of each stem in prior years. We determined stem age by counting the growth segments on the main leader, and recorded ages as an integer from one to the age of the treatment or "older than treatment." Additionally, we reconstructed size class totals for years between the treatment and 2010 from the height of each bud scar.

Reconstructions of control transects captured recruitment well but were unable to capture stem mortality because stems that died after treatment but prior to 2010 were absent in the survey in 2010. This potential bias is likely not problematic for this study since it provides a conservative estimate of control transect densities by only allowing a flat or positive slope for change over time, making it more difficult to detect a significant difference between treatment and control stem densities over time (the main objective of this analysis). Furthermore, the control transects that were initiated prior to treatments showed few changes over time with very modest recruitment and mortality; thus, it is expected that the reconstructed stem densities were appropriate for the current analysis.

Post Treatment Aspen Overstory Mortality

During the measurements in 2009, we observed significant overstory aspen mortality (40% of the size class 4 stems) in the eastern half of VC3 (three years after conifer removal). Due to the heavy conifer thinning in this site, it was hypothesized that sunscald may have caused the observed mortality. To examine this possibility, we mapped both live and dead mature aspen stems as well as the stumps of removed conifers in one half of the treated area in 2009 (1 ha). For each stem, we recorded the diameter (at breast height for the aspen and stump height for the removed conifers) and the distance and bearing from trees with known GPS coordinates. For the dead aspen, we recorded any visible damage to the bole and extracted two tree cores to estimate the tree's age at death. At the time of sampling, every dead aspen stem exhibited cracked bark that had peeled away from the tree bole on one side of the tree. We recorded the length of the separated bark at breast height, and the azimuth of the middle of the separated bark section. These data were used to construct a map of live and dead aspen stems and the removed conifers in approximately one half of the treated area in VC3. Using this map, we calculated the basal area of conifers removed on the southern side of each aspen tree (in a 10 m radius) in a geographic information system. We employed two sample t-tests to determine if the live and dead residual aspen were significantly different in stem age or basal area of conifers removed on the southern side.

Data Analysis

The data structure for this study is comprised of multiple measurements of treatment and control transects (the experimental unit) both before and after one of two different treatments (conifer removal or prescribed fire). The conifer removal study is comprised of three sites, each with four treatment transects and two control transects, for a total of 18 transects. Each transect in the conifer removal sites was measured five times (year 0 through year 5, without measurement in 2008), for a total of 90 observations among all three sites. The prescribed fire study consists of two sites with a total of eight treatment transects and five control transects (13 total transects) measured yearly for four years (year 0 through year 3) for a total of 52 observations.

We selected generalized linear mixed effects models to determine the effect of treatment on aspen density (the response variable) because they can account for non-independence of repeated measures (*sensu* Jones *et al.* 2005); can accommodate calendar year differences introduced by treatments implementation in successive years in the conifer removal sites; and allow the use of Poisson distributions for count data (Bolker *et al*. 2009). We constructed separate models for individual sites analyzed alone and all sites combined for total aspen stem density and density of stems in size classes 1 to 3.

In these analyses, fixed effects included treatment type, year after treatment, pre-treatment aspen density, and the interaction of treatment and year after treatment. We treated individual transects as random effects to account for co-dependence of repeated measures (Bolker *et al*. 2009), and when the conifer removal sites were analyzed together, we included calendar year as a random effect to account for treatment implementation in successive years (Saab *et al*. 2007). We fit models using the GLMER function in R (R Development Core Team 2010), employing the Laplace approximation of parameter estimates, the log-link function, and a Poisson error distribution for count data (Crawley 2007). Model simplification followed Crawley (2007) using the Akaike information criterion (Pinheiro and Bates 2000). We used control treatments as the baseline category for all regression models. We interpreted significant treatment by year interaction terms as true differences in aspen stem density over time between treatment and controls.

RESULTS

Conifer Removal

When analyzed together, the conifer removal sites showed significant increases in stem density in total stems ($P < 0.001$), SC1 ($P = 0.011$), and SC3 ($P = 0.013$) compared to control transects by year 5 after treatment, as indicated by the significant treatment by year 5 interaction terms (Table 2). These sites did not show a significant increase in SC2 stem density ($P = 0.92$) at this time due to a combination of mortality from the initial treatment (mechanical damage from conifer removal, especially in VC2) as well as recruitment of SC2 stems into SC3 size class (Figures 2 and 3; year 0 is pre-treatment). Figure 4 shows pho-

Table 2. Results of generalized linear mixed effects models to determine the effects of conifer removal and prescribed fire treatments on total aspen stem counts and stem counts in size classes 1 to 3 in the eastern Sierra Nevada, California, 2004 to 2011.

	Total stems		Size class 1		Size class 2		Size class 3	
Model term	**Value[a]**	***P****	**Value**	***P***	**Value**	***P***	**Value**	***P***
Conifer removal sites (VC1, VC2, and VC3)								
Intercept (control baseline)	2.26	<0.001	1.32	<0.001	1.59	<0.001	−0.32	0.549
Conifer removal	0.28	0.223	0.53	0.179	0.55	0.021	−0.23	0.695
Year 1 [b]	0.08	0.348	−0.26	0.194	0.23	0.227	0.02	0.918
Year 5 [b]	0.23	0.007	0.33	0.254	0.45	0.017	0.16	0.429
Year 0 total aspen density	0.02	<0.001	0.01	0.001	0.02	<0.001	0.03	<0.001
Treatment by year interaction								
Removal by year 1	−0.12	0.240	0.94	<0.001	−0.79	<0.001	−0.95	<0.001
Removal by year 5	0.31	<0.001	0.52	0.011	0.01	0.949	0.57	0.013
Prescribed fire sites (GC1 and GC2)								
Intercept (control baseline)	2.48	<0.001	2.12	<0.001	1.04	0.023	0.52	0.279
Prescribed fire	−0.81	0.058	−1.04	0.021	−0.63	0.201	−0.85	0.146
Year 1	0.12	0.238	−0.37	0.015	0.54	<0.001	0.42	0.153
Year 2	0.15	0.120	−0.78	<0.001	0.67	<0.001	0.49	0.093
Year 3	0.10	0.323	−0.95	<0.001	0.62	<0.001	0.55	0.056
Year 0 total aspen density	0.03	<0.001	0.02	0.010	0.03	<0.001	0.02	0.044
Treatment by year interaction								
Fire by year 1	1.40	<0.001	2.23	<0.001	0.84	<0.001	−0.54	0.347
Fire by year 2	1.63	<0.001	2.65	<0.001	1.27	<0.001	−1.99	0.018
Fire by year 3	1.65	<0.001	2.43	<0.001	1.46	<0.001	−0.04	0.936

[a] Value of the coefficient for each model term.
* *P*-value for each model term.
[b] All conifer removal sites were measured 1 yr and 5 yr after treatment.

tos of a treatment transect in VC2 before treatment, immediately after treatment, and five years after treatment.

When analyzed individually, only one site, VC3, did not show a significant increase in density of any size class in the treated transects 5 yr after treatment ($P > 0.2$ for treatment by year 5 interaction terms for total stems and all size classes; data not shown). Although this site showed a significant initial increase in SC1 density one year after treatment ($P = 0.001$), by the third year after treatment (2009), many of these stems had died (or had been recruited to SC2), and this site showed a significant decrease in SC1 stem density in treatment transects compared to controls ($P < 0.001$; Figure 2). In 2009, we noticed significant aspen overstory mortality in VC3 and initiated the mapping, coring, and measurement of residual aspen and removed conifers in half of this site (n = 16 [11 dead trees, 5 live trees]; total mapped area was 1 ha). For this particular site, each overstory aspen that died had the bark peeling back on the southwest side of the tree (average azimuth = 215 degrees), indicating sunscald as a possible mechanism of mortality (DeByle

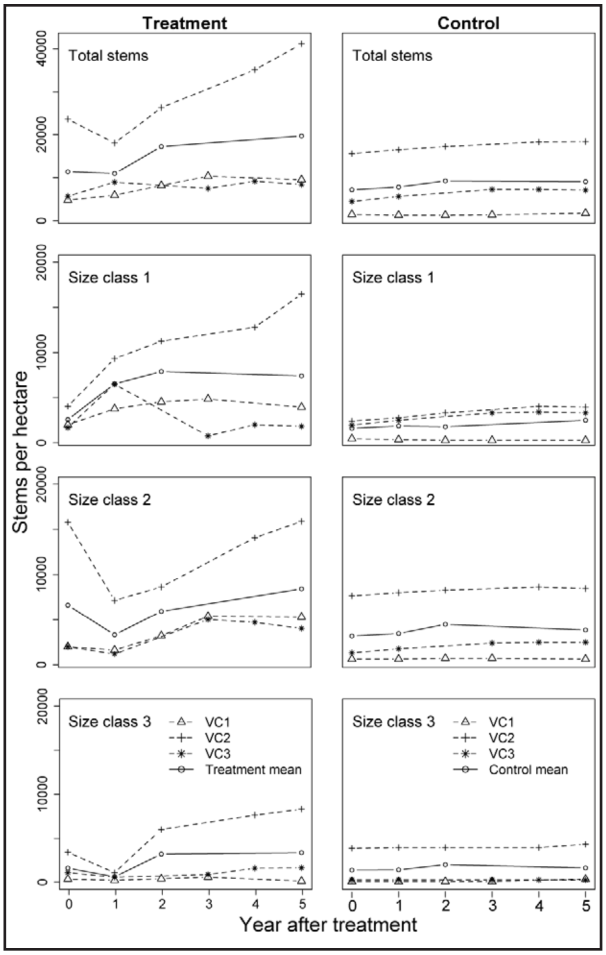

Figure 2. Mean aspen stem density (stems ha^{-1}) for control (no conifer removal) and treatment (conifers removed) transects for aspen stem size classes 1 (SC1), 2 (SC2), and 3 (SC3), and total stems by site (VC1, VC2, and VC3) before (year 0) and during the 5 yr following treatment. Note differences in *y*-axis scale.

and Winokur 1985). Further supporting this hypothesis, we found that the basal area of conifers removed on the southern side (within a radius of 10 m) of each residual aspen tree that died was significantly higher than for those still alive in 2010 ($P = 0.028$; Figure 5). Furthermore, the aspen stems that were dead in 2010 were also significantly older than those that were still alive ($P = 0.015$; Figure 6). Figure 7 is a photo of the overstory mortality observed in VC3 in 2010.

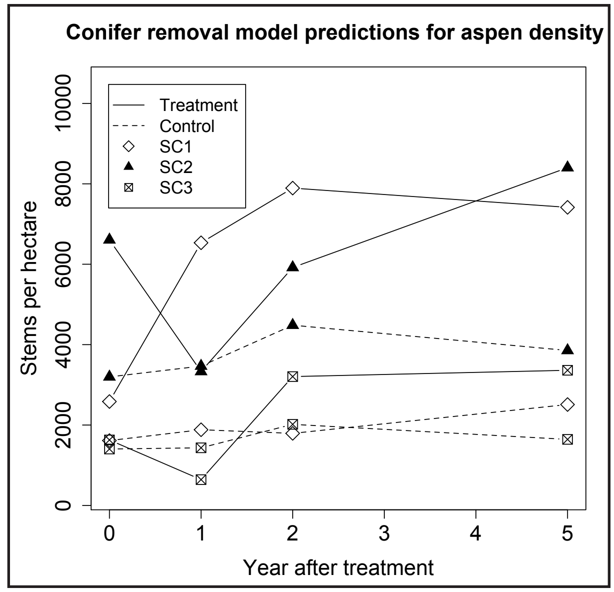

Figure 3. Generalized linear mixed effects model predictions of aspen density in size classes 1 (SC1), 2 (SC2), and 3 (SC3), over time for conifer removal and control treatments for all conifer removal sites.

Prescribed Fire

By year 3 after treatment, prescribed fire sites, when analyzed together, showed significant increases in total stem density ($P < 0.001$), SC1 density ($P < 0.001$), and SC2 density ($P < 0.001$) compared to control transects, as indicated by the significant treatment by year 3 interaction terms (Table 2, Figure 8 and Figure 9). These sites did not show a significant increase in SC3 stem density by the third year after treatment ($P = 0.94$). Significant SC1 and SC2 stem mortality was observed two and three years after treatment in the prescribed fire sites, especially in GC2, which exhibited mortality of over 40% of post treatment SC1 and SC2 stems three years after treatment (of the dead stems, approximately 50% showed evidence of herbivory). When analyzed separately, three years after treatment, GC2 showed significant increases in total stems ($P < 0.001$) and SC1 ($P = 0.003$), but failed to show significant differences in SC2 ($P = 0.456$) and SC3 ($P = 0.774$) stem density compared to the controls.

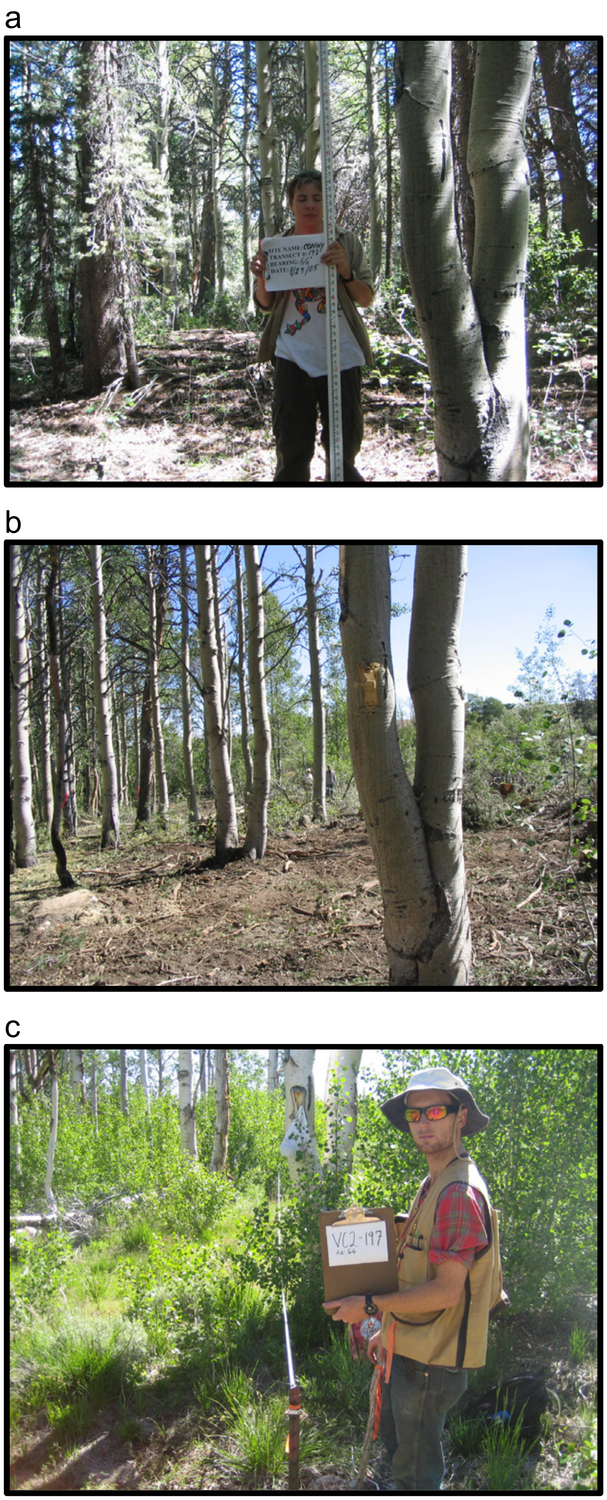

Figure 4. Photographs of a single transect in VC2 (a) before treatment, (b) immediately after treatment, and (c) 5 yr after treatment.

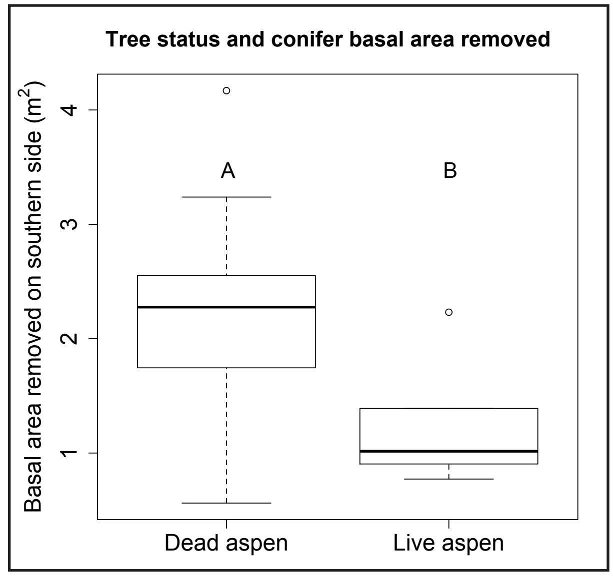

Figure 5. Basal area (m^2) of conifers removed on the southern side of residual overstory aspen (in a 10 m radius) by tree status in VC3 mapped area in 2010 (n live = 5, n dead = 11). Different letters indicate significant differences in means (P = 0.028).

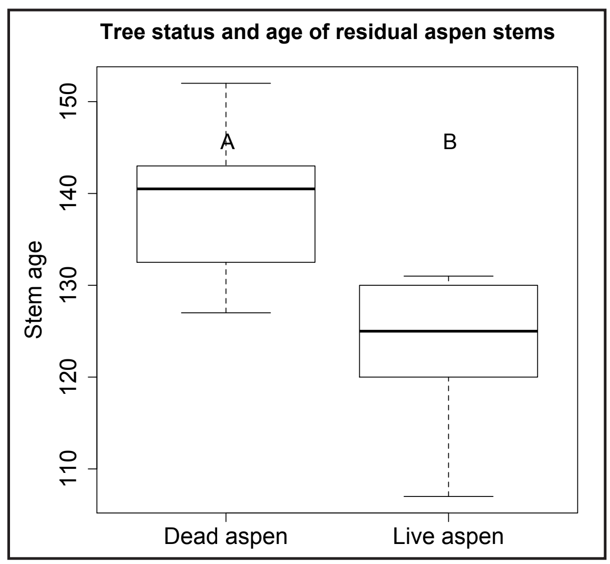

Figure 6. Estimated age of residual overstory aspen in VC3 mapped area by tree status in 2010 (n live = 5, n dead = 11). Different letters indicate significant differences in means (P = 0.015).

Figure 7. A photograph showing observed overstory mortality in VC3 in 2010.

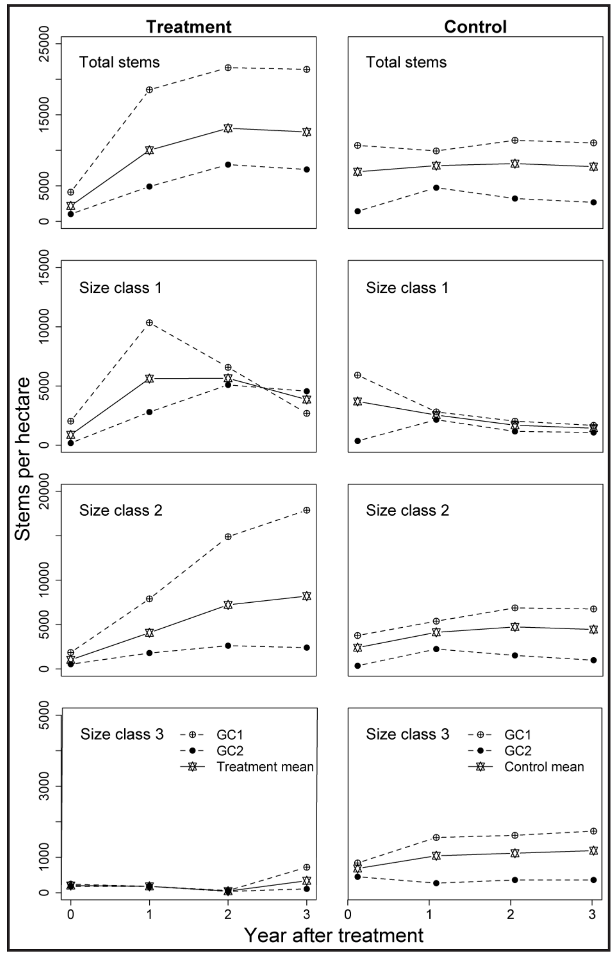

Figure 8. Mean aspen stem density (stems ha^{-1}) for control (unburned) and treatment (prescribed fire) transects for aspen stem size classes 1 (SC1), 2 (SC2), and 3 (SC3), and total stems by site (GC1 and GC2) before (year 0) and during the 3 yr following treatment. Note differences in *y*-axis scale.

Mitigation of Risk Factors for Aspen Stands

Conifer removal mitigated two of the risk factors identified by Bartos and Campbell (2001) by reducing conifer canopy cover below 25 % and sagebrush cover to below 10 % (treated stands had a mean conifer canopy cover of 0 % and sagebrush cover of 4 % five years after treatment). The other pre-treatment risk factors present in VC1 and VC3 persisted five years after conifer removal (aspen canopy cover <40 % and aspen regeneration 1.5 m to 4.6 m tall is <1235 stems ha^{-1}).

Prescribed fire reduced sagebrush cover below 10 % in GC2 but did not effectively reduce sagebrush cover below 10 % in GC1 (post-treatment sagebrush cover was 3 % and 15 %, respectively). Aspen regeneration 1.5 m to 4.6 m tall remained <1235 stems ha^{-1} three years after prescribed fire treatment in both GC1 and GC2.

DISCUSSION

Conifer Removal

Results from the conifer removal sites indicated that this is a viable means of stimulating aspen asexual regeneration in conifer-encroached stands (Shepperd *et al.* 2001, Jones *et al.* 2005). Lack of treatment success in VC3 is likely due to a variety of factors that caused overstory death of the residual aspen stems after conifer removal. Tree death typically occurs as a result of many interacting long- and short-term stressors, and those trees experienc-

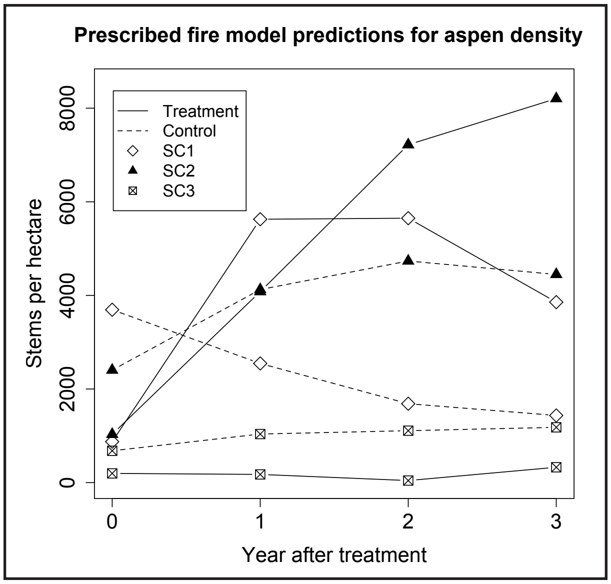

Figure 9. Generalized linear mixed effects model predictions of aspen density in size classes 1 (SC1), 2 (SC2), and 3 (SC3), over time for prescribed fire and control treatments for study sites GC1 and GC2.

ing more long-term stress are more vulnerable to mortality from acute stress (Manion 1981), such as a large increase in incident radiation (as experienced by aspen stems after conifer removal). The aspen trees that died in VC3 were significantly older (more long-term stress) and experienced more severe conifer thinning on their southern side (acute stress from sudden increase of incident solar radiation) than those that survived. However, all live and dead stems that were aged in VC3 were over 100 years old, indicating that the entire stand was of advanced age; older stems have been shown to be less resilient to disturbances (Grewal 1995). In addition, VC3 had twice as much conifer volume removed per hectare than VC1, and three times as much as VC2, suggesting that there may be a threshold of optimum thinning intensity. Furthermore, VC3 was the stand at the lowest elevation and likely experienced more water stress than VC1 or VC2, especially in 2007 and 2008, which were drought years in California (nearby RAWS stations recorded only 30% to 50% of the yearly average total precipitation in 2007). Consequently, dominant stem age, potential for moisture stress, and degree of conifer encroachment and thinning all likely interacted to influence aspen vigor and asexual regeneration following conifer removal treatments. In heavily encroached aspen stands, it may be valuable to assess the potential benefits of removing conifers in stages to limit the acute stress from the initial treatment (potentially leaving select conifers to protect residual aspen from sunscald). However, this strategy will introduce the added complication of multiple stand entries, which may disturb regeneration from the initial treatment and increase costs.

The inability of VC1 and VC3 to rebound above 40% aspen canopy cover and >1235 stems between 1.5 m to 4.6 m tall is likely a result of pre-treatment conditions in VC1 and the combination of stressors described above in VC3. VC1 had a pre-treatment aspen canopy cover of only 2.5% and the lowest density of aspen stems of all the conifer removal stands; thus, it will likely require more time for stand recovery. Recovery from these risk factors in VC3 is more uncertain and will require long-term monitoring.

Prescribed Fire

Results from GC1 and GC2 indicate that prescribed fire has the potential to be an effective restoration tool for aspen regeneration within sagebrush communities, but more time will be needed to monitor these treatments to determine if a significant number of post-fire stems grow above browse height. Three years after treatment, both sites analyzed together showed a significant increase in SC1 and SC2 stem density, but not in SC3. Two and three years post fire, a concerning amount of stem mortality had been observed (especially in GC2). Future years will likely see a significant increase in SC3 stems in GC1 as stems recruit from SC2 to SC3, but GC2 has failed to show significant recruitment from SC1 to SC2; therefore, significant future increases in SC3 stem density is uncertain.

Herbivory

As many studies have demonstrated, herbivory can be a major challenge to successful aspen regeneration (DeByle and Winokur 1985, Baker *et al*. 1997). Post-burn environments are known to attract herbivores, and we observed this here as both the treatment and control transects in the prescribed fire sites experienced increased herbivory and stem mortality compared with those in the conifer removal sites. In a simulated browsing study on aspen sprouts in the Eagle Lake Ranger District in the Lassen National Forest, Jones *et al*. (2009) found that protecting aspen terminal leaders from browsing is critically important to enhance aspen regeneration. Additionally, they found that midseason and repeat browsing significantly reduced sucker growth (Jones *et al*. 2009).

The scale of the prescribed fires in this study are likely important as well, as larger (>30 ha) aspen stands in this area that have burned in wildfires show considerably lower herbivory (K. Krasnow, Teton Science Schools, Jackson, Wyoming, USA, personal observation). Small or highly degraded stands, such as those treated in this study, may benefit from post-treatment fencing to protect the aspen regeneration (Campbell and Bartos 2001, Jones *et al*. 2009). In the cases in which fencing may not be viable or economically feasible, Jones *et al*. (2009) recommend grazing practices such as herding-water-supplement distribution, rest-rotation systems, and seasonal grazing strategies to reduce the frequency and intensity of aspen browse by livestock.

Prescribed Fire Intensity

High intensity fire that effectively reduces vegetative competition has been shown to produce higher densities of post-fire aspen stems (Fraser *et al*. 2004, Keyser *et al*. 2005). The low to moderate fire intensity produced by the prescribed fires in this study did not effectively eliminate the competing sagebrush in GC1. If the goal is to regenerate aspen, managers should aim for high intensity prescribed fires. Disturbance-based natural resource management focused on reinstitution of natural processes (Holling and Meffe 1996) such as "wildland fire use" may be a better option for managers than prescribed fires, which cannot often be burned under conditions required for high intensity fire effects and are typically smaller in extent than managed wildfire.

The Future of Aspen in the Sierra Nevada

In an era in which the future environment is likely to be different from the present, understanding the impact of management actions is of paramount importance (Millar *et al*. 2007). The above findings emphasize the importance of monitoring management actions to assess if the goals of the project have been met and to identify any unanticipated outcomes. This is especially true at the edge of species' distributions and in times of increased climatic stress.

Given the paucity of knowledge concerning aspen seedling establishment and their relatively slow rate of asexual clone expansion, it is unclear if aspen will be able to migrate successfully to appropriate locations to accommodate the rapid climate changes predicted in the coming century (Rehfeldt *et al*. 2009). It has often been assumed that aspen sexual reproduction is extremely rare (Romme *et al*. 2005). However, recent studies have shown that aspen stands contain much more genetic diversity than once assumed (Mock *et al*. 2008, DeWoody *et al*. 2009), and numerous aspen seedlings have been found after disturbance in recent years (Turner *et al*. 2003, Landhäusser *et al*. 2010), indicating that seedling establishment may be more common than once thought. Measured by its range alone, aspen could be considered the most successful dispersed tree in North America. As a result of working in recently burned areas, we have found five sites and hundreds of aspen seedlings in the Sierra Nevada (confirmed by carefully excavating 3 to 5 seedlings in each site; K. Krasnow, unpublished data), all occurring in areas severely burned in recent wildfires. Current aspen restoration efforts are focused on rejuvenation of existing stands, but in an era of high uncertainty, it may also be wise to facilitate the establishment of new stands (Shepperd *et al*. 2001, Millar *et al*. 2007, Stephens *et al*. 2010) by allowing wildfires to burn for resource benefit when appropriate, or more directly through out-planting seedlings, transplanting ramets, or merely dispersing seed to viable microsites after disturbance.

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