Title
Managing novel forest ecosystems: understanding the past and present to build a resilient future

Author
Krasnow, Kevin

Publication Date
2012

Peer reviewed|Thesis/dissertation

Managing Novel Forest Ecosystems:
Understanding the Past and Present to Build a Resilient Future

By

Kevin P. Krasnow

A dissertation submitted in partial satisfaction of the

Requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Scott L. Stephens, Chair
Professor Joe McBride
Professor David Ackerly

Fall 2012

Abstract

Managing Novel Forest Ecosystems:
Understanding the Past and Present to Build a Resilient Future

By

Kevin P. Krasnow

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Scott L. Stephens, Chair

Unprecedented anthropogenic global changes challenge the ability of societies to sustain desirable features of the environment. Some argue that we have entered a new global epoch where human activity is the major driver of environmental change. This is resoundingly true for American western forests, which have seen dramatic changes in disturbance regimes, species composition, and hydrologic and nutrient cycles due to fire suppression, air pollution, land use change, and climate change. These novel stressors have resulted in unprecedented conditions that may require new adaptive approaches to management focused on building resilience. The following research examines novel approaches to revitalizing a disturbance-dependent foundation tree species in the Sierra Nevada and reconstructs temporal and spatial components of historical fire regimes in the Sierra Nevada. These research threads help us understand how Sierran ecosystems functioned before Euro-American management, how these ecosystems are behaving today, and give insight into how we can manage for ecological resilience in the century to come.

Aspen (*Populus tremuloides*) comprises only a small fraction (1%) of the Sierra Nevada landscape, yet contributes significant biological diversity to this range. There is currently a high level of concern in the Western United States about declining vigor in mature aspen stands that often lack sufficient regeneration to ensure their long-term persistence. It is also highly uncertain if aspen will be able to accommodate the rapid climate changes predicted for the next century via migration through seedling establishment. I the first two studies following, I report on the efficacy of aspen revitalization management strategies, post-wildfire regeneration dynamics, experimental human assisted migration, and recent aspen seedling establishment in the Lake Tahoe Basin and eastern Sierra Nevada. I find substantial evidence that greater disturbance severity yields increased aspen sprout density and growth rates. I also find compelling evidence that post-fire aspen ramets are robust transplant material, having higher transplant survival rates than ramets from unburned stands as well as greenhouse-grown seedlings.

Fire is a key ecological process in dry mixed-conifer forests that historically burned frequently. Many of these forests on the western slope of the Sierra Nevada have been highly altered by a century of fire suppression, mining, logging, and land-use change, which have homogenized forest structure over large areas. Historical spatial and temporal patterns of fire can be used to inform current and future disturbance-based management seeking to restore ecosystem heterogeneity and resilience that had been supported by frequent low to moderate-severity fires prior to the twentieth century. Temporal patterns of historical fire are well known in these forests, but there is a high degree of uncertainty regarding the spatial dynamics of the pre-settlement fire regime. In the final study presented here, I reconstruct the spatial and temporal dynamics of wildfire from 1750-1900 in a 3000 ha mixed-conifer forest in the southern Sierra Nevada using data from 118 fire scared tree samples. Fire was once common in these forests that have not burned for 80-100 years, with mean fire return intervals from both spatially explicit and non-spatial temporal reconstructions ranging from 3-11 years. A vast majority of fires in this area (97%) occurred late in the growing season or during tree dormancy, and no significant controls on fire frequency were identified by slope aspect. Spatially explicit fire frequency reconstructions can aid in landscape-scale disturbance-based management aimed at increasing forest resilience and reducing fire risk.

Acknowledgments

I would like to thank many people for making this work possible. First and foremost, I would like to extend my eternal gratitude to my wife, Ingrid. Your unconditional support and encouragement have been so important during this process. This product (as well as my sanity and happiness) would certainly not have been possible without you. Another important thank you is to my parents who have always supported me, even if I choose to be in school for most of my life. A huge thank to my advisor, Scott Stephens, for making this research possible and for guiding me through the process. Danny Fry has helped me "just keep up" and has shared his time and expertise generously. Joe McBride has been an inspiration as a teacher, scientist, and mentor to me.

A huge thank you to Anne Halford for welcoming a graduate student as a collaborator and for supporting this research with BLM monitoring grants. Thanks to David Burton for initial contacts and project encouragement; to Dale Johnson and Martin Oliver for logistical support, and Perry de Valpine for statistical advice. Thanks to the SNAMP research team and funders for making the fire history project possible. Thanks to the many land managers who welcomed my research and with whom I have collaborated: Victor Lyon, Raul Ramirez, Dan Shaw, Gail Durham, Annamaria Echeveria, and Leeann Murphy. Thanks to Suzie Kocher and Daylin Wade for a great collaboration with the California Tahoe Conservancy. And lastly, a heartfelt thank you to all those who worked in the field and/or lab to gather or process data: Ingrid Daffner Krasnow, Tim Kline, Gary Roller, Antja Thompson, Meg Krawchuck, Big Johnny, Tight Steve, Mike Rollins, Zak Thomas, Robby Andrus, Timbo Stillinger, Stephanie Nale, Pablo Beimler, Chris McCoy, Ariel Thompson, Julien Vollerang, Lisa Rosenthal, Carlin Starrs, Brad Kerr, Paul Cheng, Ben Weise, and Karla King.

Chapter 1: Aspen restoration in the Eastern Sierra Nevada: effectiveness of prescribed fire and conifer removal

INTRODUCTION

Aspen (*Populus tremuloides*) 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. 2006b). 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). As a result of their easily edible foliage, as well as their high water use efficiency, aspen stands support a unique assembly of understory plants, insects, birds, and mammals (DeByle and Winokur 1985a). Compared to conifer forests, aspen stands also provide increased water yield, and ecosystem resiliency to fire (Shepperd et al. 2006b).

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 in the next century (Rehfeldt *et al.* 2009). The limited aspen stands in California are in particular danger of being replaced by more shade tolerant conifers due to their rarity, small average stand size (Potter 1998, De Woody *et al.* 2009), and long disturbance-free intervals due to Euro-American management. Though the historic 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 1800's due to widespread fires, dam building, mining, and logging. This may have been the last major window of regeneration for Sierran aspen, as the 20th 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. 2006b).

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), but similar data is currently lacking from the bulk of the Sierra Nevada ecoregion. Bates *et al.* (2006) found that mechanical removal of *Juniperus occidentalis* (Western juniper) 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 and others (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 documenting aspen restoration treatments in the Eastern Sierra Nevada. The goals of this study are to monitor and evaluate aspen restoration in this area, providing critical information for adaptive management of this important species. Our research goals are 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, CA began a *Populus tremuloides* (quaking aspen) restoration and monitoring program focused on increasing the vigor and regeneration of declining aspen stands in the Eastern Sierra Nevada. Three stands along Virginia creek with heavy *Pinus contorta* (lodgepole pine) encroachment were selected for conifer removal (Virginia Creek 1-3, referred to hereafter as VC1, VC2 and VC3), and two stands in sagebrush steppe with very little aspen regeneration, for prescribed fire treatment (Green Creek 1-2, referred to hereafter as GC1 and GC2). This study aims to evaluate the efficacy of both treatment types in stimulating aspen asexual regeneration.

The Eastern 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 2,440 – 2,740 m (8,000 – 9,000 ft) in the Conway summit region, where the current study sites are located, most precipitation occurs as snow, and averages 35-45 cm/year (14-18 inch/yr) according to remote automated weather station readings from 2000-2010 at Bridgeport (38.26°N, 119.22°W), Walker (35.67°N, 118.06°W), Gaylor Meadow (37.52°N, 119.19°W), and Markleeville (38.42°N, 119.47°W). Average yearly, January, and July temperatures were approximately 2, -5.5, and 11° Celsius respectively during this period (35.5, 22, and 52.5 ° F). 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, though 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). The aspen stands in this study are described below prior to treatment:

Study Sites

All stands are on level to gently sloping north facing slopes (10-20%) at elevations of 2,710, 2,573, 2,523, 2,506, and 2,446 meters respectively (8,890, 8,443, 8,276, 8,222, and 8,025 ft.). 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, dominant vegetation is comprised of an overstory of *Pinus contorta* (lodgepole pine) with *Populus tremuloides* (aspen) scattered within small openings throughout the sites. In these stands, understory dominants along the fringes consist of *Artemisia tridentata* ssp. *vaseyana*, (mountain big sagebrush), *Purshia tridentata* (bitterbrush), *Ribes cereum* (squaw currant), *Leymus cinereus* (Great Basin wild rye), *Achnatherum nevadensis* (Nevada needlegrass) and *Lupinus lepidus* (Pacific lupine). The prescribed fire sites had an aspen overstory with similar understory species interspersed throughout the stand.

Campbell and Bartos (2001) identified the following five risk factors indicating an aspen clone is at risk of loss: 1) when conifer canopy cover is >25% canopy, 2) aspen canopy cover is <40%, 3) dominant aspen trees are >100 years of age, 4) aspen regeneration 5-15 feet tall is <500 stems/acre, and 5) sagebrush cover is >10%. The conifer removal study sites exhibited factors 1, 2 (except VC2), 4 and 5. Additionally, though 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, 6.9, and 2 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. Starting with VC1, we treated one stand each year from 2004-2006 between August 1 and October 1 by removing lodgepole pines growing in and around aspen stems by hand felling, and followed with mechanical hauling to a landing outside of the aspen stand. We sold removed timber larger than 10 cm in diameter as fire-wood and chipped and scattered residual materials on site (we limited depth to less than 5 cm). The wood volume removed from VC1, VC2, and VC3 was 85, 59, and 156 m^3/ha respectively (24, 16, and 43 cords/ha).

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 re-ignition within the aspen stands was necessary. Ten hour fuels moistures were 10-12%, relative humidity averaged 20-30%, air temperatures were between 10-16 °C (50-60 °F) with 3-8 kph (2-5 mph) winds from the west / southwest. Average flame lengths were 0.5-1 m (1.5-3 ft), 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 x 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 four size classes (SC) before treatment and up to 5 years after treatment: SC1 = height less than .45 m, SC2 = height .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 (sensu 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 5 years (though not measured in 2008) and measured prescribed fire sites before treatment and annually for 3 years after treatment. We measured canopy cover by tree species with a site tube at 10-foot intervals along each transect and took photos from both ends of each transect. In 2007, we observed new stem mortality in some of the treatment transects, so we recorded dead stems in each size class thereafter.

Control Transects

One to two control transects were established in adjacent, untreated aspen forest in four sites, and in one site (VC2) no controls 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 a t-post with a treatment transect in VC1 (thus experiencing obvious edge effects from the treatment) and 2) 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 treatment 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 are appropriate for the current analysis.

Post Treatment Aspen Overstory Mortality

During the measurements in 2009, we observed significant overstory aspen mortality in 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. This data was 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 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 4 treatment transects and 2 control transects, for a total of 18 transects. Each transect in the conifer removal sites was measured 5 times (year zero through year five, without measurement in 2008), for a total of 90 observations among all three sites. The prescribed fire study consists of 2 sites with a total of 8 treatment transects and 5 control transects (13 total transects) measured yearly for 4 years (year zero 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 treatment 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 1-3.

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 (Figure 1 & 2). Figure 3 shows a treatment transect in VC2 before treatment, immediately after treatment, and 5 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 years after treatment ($p > .2$ 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 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 1). 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 hectare). 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 and Winokur 1985a). Further supporting this hypothesis, we found that the basal area of conifers removed on the southern side of each residual aspen tree that died was significantly higher than for those still alive in 2010 ($p = 0.028$, Figure 4). Furthermore, the aspen stems that were dead in 2010 were also significantly older than those that were still alive ($p = 0.015$, Figure 5). Figure 6 is a photo of the overstory mortality observed in VC3 in 2010.

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 7 & 8). These sites did not show a significant increase in SC3 stem density by the third year after treatment ($p = 0.94$). Significant stem mortality was observed 2 and 3 years after treatment in the prescribed fire sites, especially GC2, which exhibited mortality of over 40% of post treatment stems 3 years after treatment (of the dead stems, approximately 50% showed evidence of herbivory, most likely from sheep). In fact, 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 increases in SC2 ($p=0.456$) and SC3 ($p = 0.774$) stem density compared to the controls.

DISCUSSION

Conifer Removal

Results from the conifer removal sites indicate that this is a viable means of stimulating aspen asexual regeneration in 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 experiencing 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/or experienced more severe conifer thinning on their southern side (acute stress from sudden increase of incident solar radiation) than those that survived. However, all stems that were aged in VC3 were over 100 years old, indicating that the entire stand was of advanced age, which alone likely makes restoration activities more risky, as older stands are likely less resilient to disturbance (Grewal 1995). 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 – 50% of the yearly average total precipitation in 2007). Consequently, stand age, degree of conifer encroachment, and potential for stress due to climate factors should be carefully considered before restoration attempts are made.

Prescribed Fire

Results from GC1 and GC2 indicate that prescribed fire has the potential to be an effective restoration tool for aspen regeneration, 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 SC3. Two and three years post fire, a concerning amount of stem mortality has 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. GC2 has instead showed significant mortality of SC1 stems, which is likely a result of a combination of grazing pressure and water stress (2007 and 2008 were drought years in this area).

Herbivory

As many studies have demonstrated, herbivory can be a major challenge to successful aspen regeneration (DeByle and Winokur 1985a, Baker *et al.* 1997). Post burn environments are known to attract herbivores, and we observed this here as both the treatment and controls transects in the prescribed fire sites experienced more damage from herbivores and stem mortality than did those in the conifer removal sites. The scale of the fires are likely important too, as larger (over 30 ha) stands in this area that have burned in wildfires show considerably lower herbivory (Krasnow, personal observation). Small stands, such as those treated in this study, may require post-treatment fencing to protect the aspen regeneration.

Prescribed Fire Intensity

The low-moderate fire intensity produced by the prescribed fires in this study did not effectively eliminate the competing vegetation (*Artemisia tridentata* ssp. *vaseyana*), yet almost completely top-killed the fire-sensitive aspen. High intensity fire that effectively reduces vegetative competition has been shown to produce higher densities of post-fire aspen stems (Fraser *et al.* 2004a, Keyser *et al.* 2005). If the goal is to regenerate aspen, managers should aim for high intensity prescribed fires. Disturbance based forest 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 typically are much smaller in extent than managed wildfire.

The Future Of Aspen In The Sierra Nevada:

In an era where the future environment is likely to be different from the present, understanding the impact of management actions is of paramount importance (Millar *et al.* 2007b). The above findings emphasize the importance of setting up management actions as experiments, with proper controls and post treatment monitoring. 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.* 2008a, De Woody *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 disperser in North America. As a result of working in recently burned areas, we have found 5 different sites of seedling establishment and hundreds of aspen seedlings in the Sierra Nevada (confirmed by digging up 3-5 in each site, 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.* 2001b, Millar *et al.* 2007b, Stephens *et al.* 2010b) by simply allowing wildfires to burn, or more directly through out-planting seedlings, transplanting ramets, or merely dispersing seed to viable microsites after disturbance.

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

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 Class 1-3 in the Eastern Sierra Nevada, California, 2004-2011

	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 and 5 years after treatment

Figure 1: Mean aspen stem density (stems/ha) 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 years following treatment. Note differences in y-axis scale.

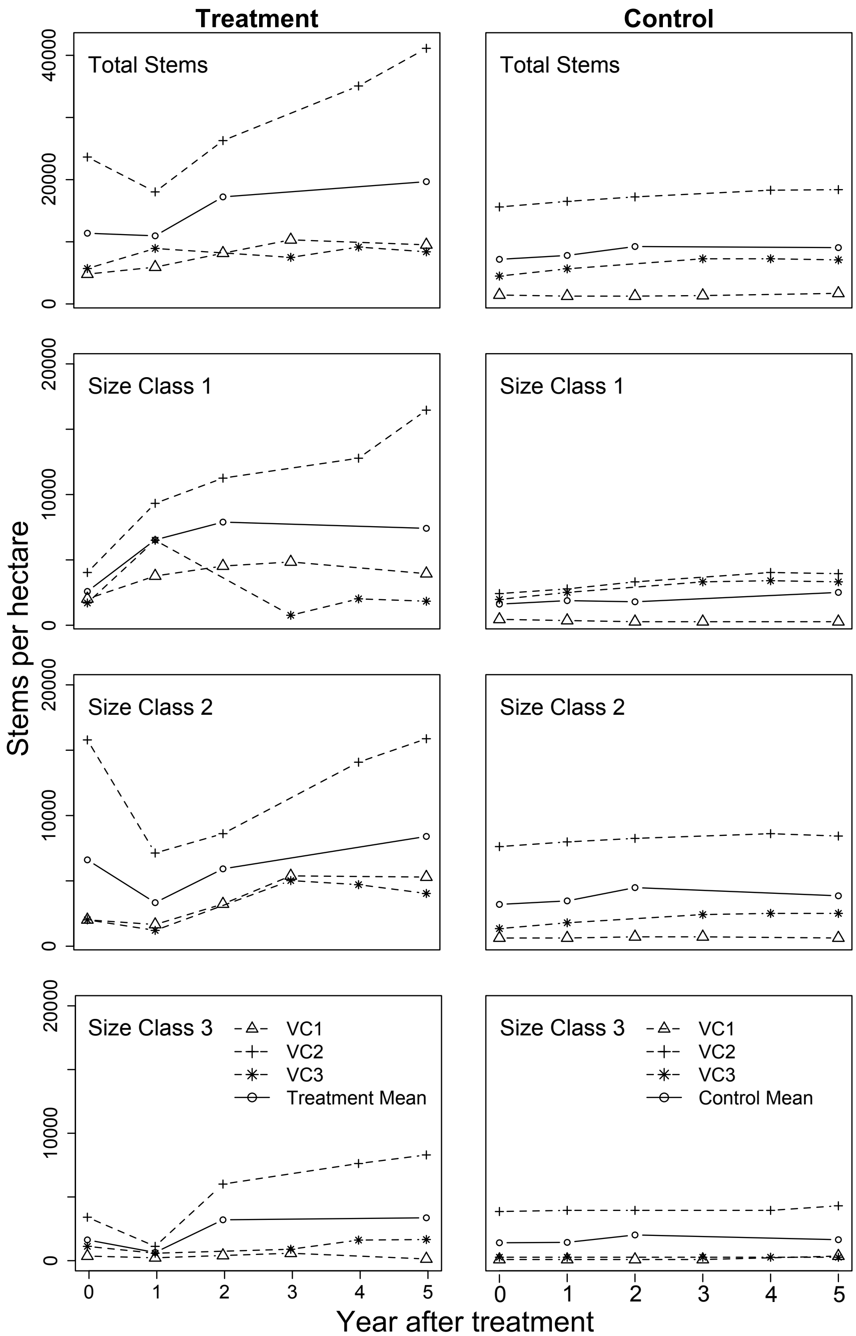


Figure 2: Generalized linear mixed effects model predictions of aspen density in size class 1 (SC1), 2 (SC2), and 3 (SC3), over time for conifer removal and control treatments for all conifer removal sites.

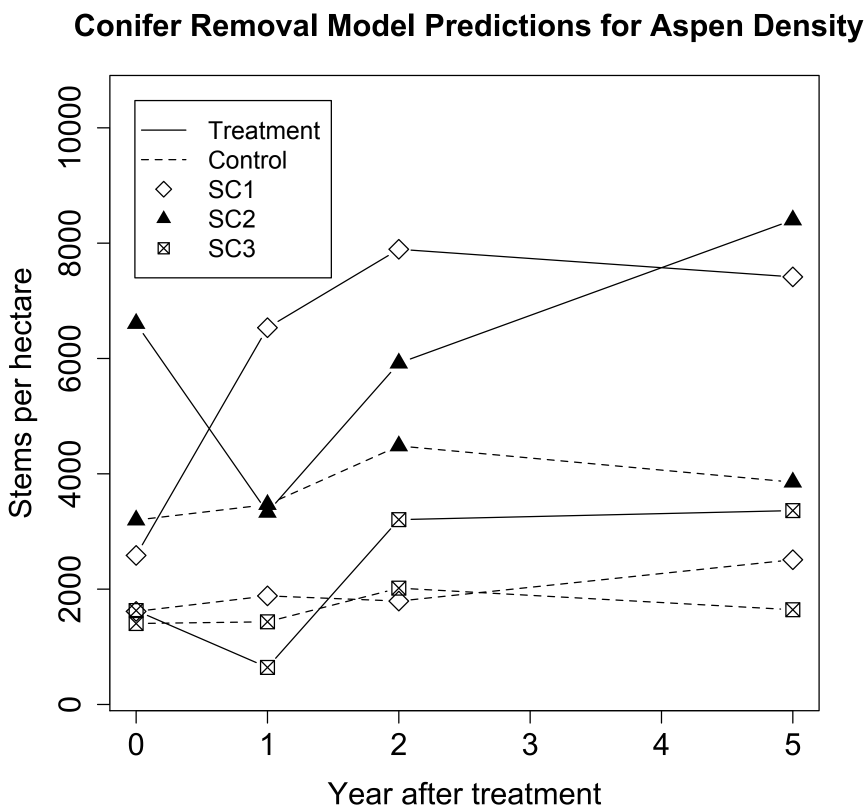


Figure 3: Pictures of a single transect in VC2 (a) before treatment, (b) immediately after treatment, and (c) 5 years after treatment.

a

b

c

Figure 4: Basal area (m^2) of conifers removed on the southern side of residual overstory aspen by status in VC3 mapped area in 2010 (n live = 5, n dead = 11). Different letters indicate significant differences in means (p=0.028)

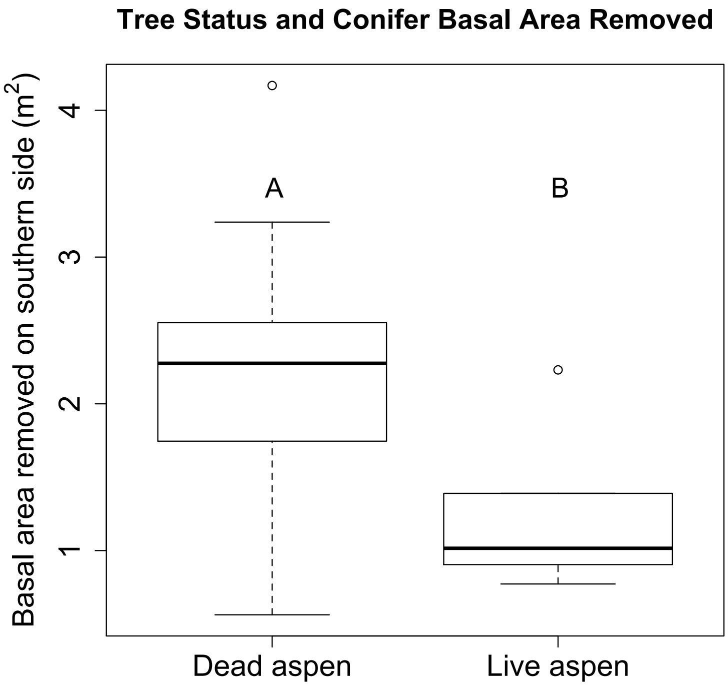


Figure 5: Estimated age of residual overstory aspen in VC3 mapped area by status in 2010 (n live = 5, n dead = 11). Different letters indicate significant differences in means (p = 0.015).

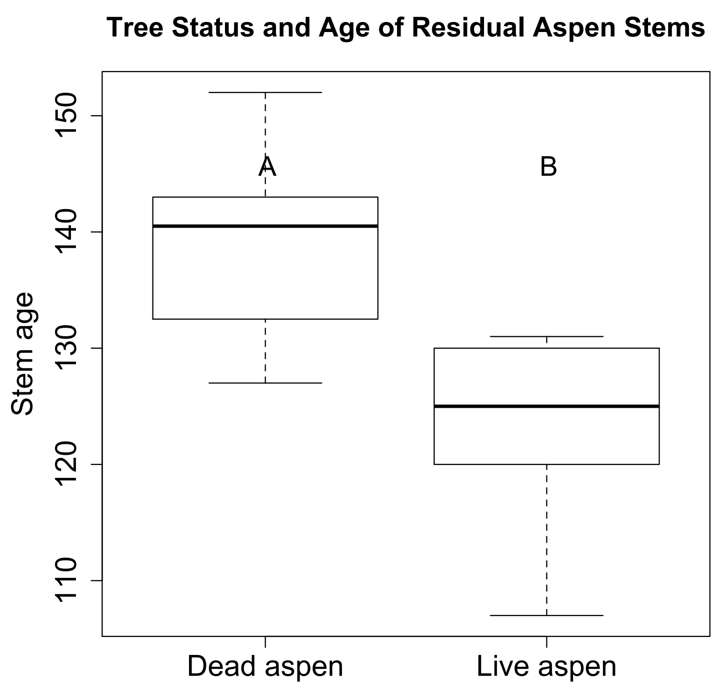


Figure 6: A photo showing observed overstory mortality in VC3 in 2010.

Figure 7: Mean aspen stem density (stems/ha) 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 years following treatment. Note differences in y-axis scale.

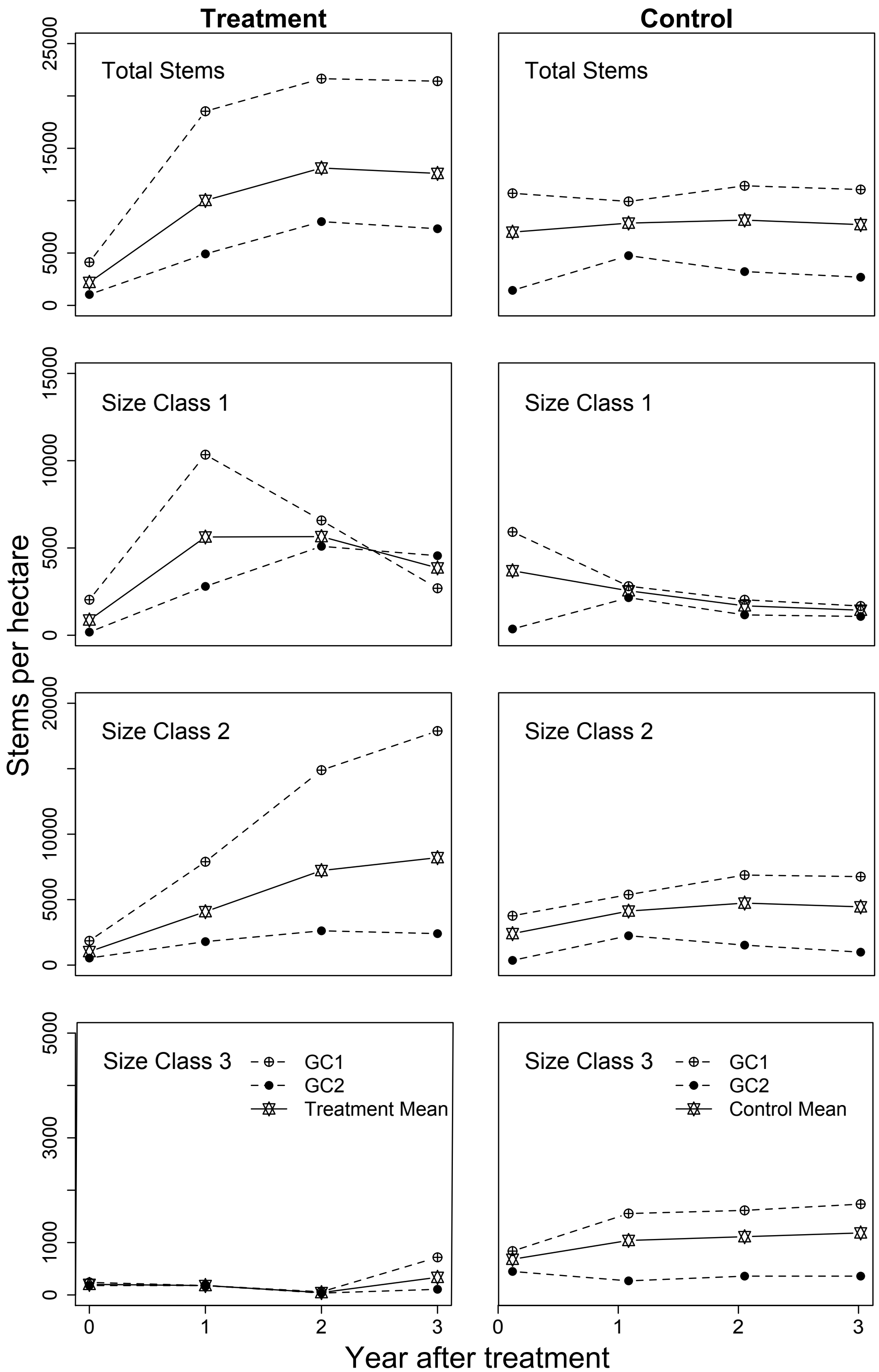
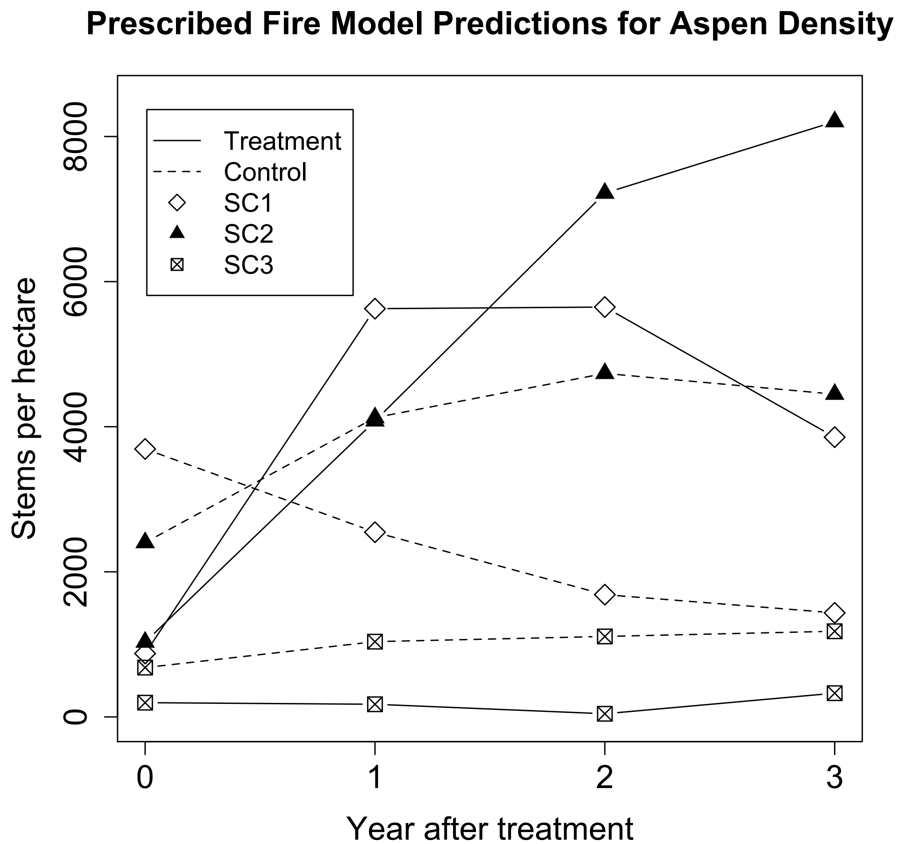


Figure 8: Generalized linear mixed effects model predictions of aspen density in size class 1 (SC1), 2 (SC2), and 3 (SC3), over time for prescribed fire and control treatments for study sites GC1 and GC2.



References:

Anderegg, W.R.L., J.A. Berry, D.D. Smith, J.S. Sperry, L.D.L. Anderegg, and C.B. Field. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. Proceedings of the National Academy of Sciences 109: 233-237.

Baker, W.L., J.A. Munroe, and A.E. Hessl. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20: 155-165.

Bates, J.D., R.F. Miller, and K.W. Davies. 2006. Restoration of quaking aspen woodlands invaded by western juniper. Rangeland Ecology & Management 59: 88-97.

Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S.S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24: 127-135.

Campbell, R.B. and D.L. Bartos. 2001. Aspen ecosystems: objectives for sustaining biodiversity. Pages 299-307 in: Shepperd, W. D., D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, ediors. Proceedings from the symposium: sustaining aspen in western landscapes. USDA Forest Service RMRS-P-18, Grand Junction, Colorado.

Craig, T.P., J.K. Itami, and P.W. Price. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. Ecology: 1691-1699.

Crawley, M.J. 2007. The R book. Wiley.

De Woody, J., T.H. Rickman, B.E. Jones, and V.D. Hipkins. 2009. Allozyme and microsatellite data reveal small clone size and high genetic diversity in aspen in the southern Cascade Mountains. Forest Ecology and Management 258: 687-696.

DeByle, N.V. and R.P. Winokur. 1985. Aspen: ecology and management in the Western United States. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-119.

Di Orio, A.P., R. Callas, and R.J. Schaefer. 2005. Forty-eight year decline and fragmentation of aspen (Populus tremuloides) in the South Warner Mountains of California. Forest Ecology and Management 206: 307-313.

Fraser, E., S. Landhäusser, and V. Lieffers. 2004. The effect of fire severity and salvage logging traffic on regeneration and early growth of aspen suckers in north-central Alberta. The Forestry Chronicle 80: 251-256.

Grewal, H. 1995. Parent stand age and harvesting treatment effects on juvenile aspen biomass productivity. The Forestry Chronicle 71: 299-303.

Holling, C. and G. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation biology 10: 328-337.

Jones, B.E., T.H. Rickman, A. Vazquez, Y. Sado, and K.W. Tate. 2005. Removal of encroaching conifers to regenerate degraded aspen stands in the Sierra Nevada. Restoration Ecology 13: 373-379.

Kay, C.E. 1997. Is Aspen doomed? Journal of Forestry 95: 4-11.

Keyser, T.L., F.W. Smith, and W.D. Shepperd. 2005. Trembling aspen response to a mixed-severity wildfire in the Black Hills, South Dakota, USA. Canadian Journal of Forest Research 35: 2679-2684.

Landhäusser, S.M., D. Deshaies, and V.J. Lieffers. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. Journal of Biogeography 37: 68-76.

Little, E.L. 1971. Atlas of United States trees: Vol. 1. Conifers and important hardwoods. Government Printing Office, Washington, D.C.

Manion, P.D. 1981. Tree Disease Concepts. Prentice-Hall, Englewood Cliffs, N.J.

Millar, C.I., N.L. Stephenson, and S.L. Stephens. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications 17: 2145-2151.

Mock, K.E., C. Rowe, M.B. Hooten, J. Dewoody, and V. Hipkins. 2008. Clonal dynamics in western North American aspen (*Populus tremuloides*). Molecular Ecology 17: 4827-4844.

Pinheiro, J. and D. Bates. 2000. Mixed Effects Models in S and S-PLUS. New York: SpringerVerlag.

Potter, D.A. 1998. Forested communities of the upper montane in the central and southern Sierra Nevada. US Dept. of Agriculture, Forest Service, Pacific Southwest Research Station General Technical Report PSW-GTR-169.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rehfeldt, G.E., D.E. Ferguson, and N.L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. Forest Ecology and Management 258: 2353-2364.

Rogers, P.C., W.D. Shepperd, and D.L. Bartos. 2007. Aspen in the Sierra Nevada: regional conservation of a continental species. Natural Areas Journal 27: 183-193.

Romme, W.H., M.G. Turner, G.A. Tuskan, and R.A. Reed. 2005. Establishment, persistence, and growth of aspen (Populus tremuloides) seedlings in Yellowstone National Park. Ecology 86: 404-418.

Saab, V.A., R.E. Russell, and J.G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. The Condor 109: 97-108.

Shepperd, W.D., D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, editors. 2001. Proceedings from the symposium: sustaining aspen in western landscapes. USDA Forest Service RMRS-P-18, 2000 13-15 June, Grand Junction, Colorado, USA.

Shepperd, W.D., P. Rogers, D. Burton, and D.L. Bartos. 2006. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-178.

Stephens, S.L., C.I. Millar, and B.M. Collins. 2010. Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. Environmental Research Letters 5: 9.

Turner, M.G., W.H. Romme, R.A. Reed, and G.A. Tuskan. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. Landscape Ecology 18: 127-140.

Worrall, J.J., L. Egeland, T. Eager, R.A. Mask, E.W. Johnson, P.A. Kemp, and W.D. Shepperd. 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. Forest Ecology and Management 255: 686-696.

Worrall, J.J., S.B. Marchetti, L. Egeland, R.A. Mask, T. Eager, and B. Howell. 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. Forest Ecology and Management 260: 638-648.

Chapter 2: Wildfire, management, and regeneration of quaking aspen in the Sierra Nevada

INTRODUCTION:

Aspen (*Populus tremuloides*) 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. 2006b). 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). As a result of their easily edible foliage, as well as their high water use efficiency, aspen stands support a unique assembly of understory plants, insects, birds, and mammals (DeByle and Winokur 1985b). Compared to conifer forests, aspen stands also provide increased water yield through increased runoff and recharge, and ecosystem resiliency to fire (Shepperd et al. 2006b).

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 in the next century (Rehfeldt *et al.* 2009). The limited aspen stands in California are in particular danger of being replaced by more shade tolerant conifers due to their rarity, small average stand size (Potter 1998, De Woody *et al.* 2009), and long disturbance-free intervals due to Euro-American management. Though the historic 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 1800's due to widespread fires, dam building, mining, and logging. This may have been the last major window of regeneration for Sierran aspen, as the 20th 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).

Aspen stands represent diversity hotspots to land managers and are increasingly being targeted for restoration. As a result, there has been a major effort to assess the conditions of current stands to identify those that are at the highest risk of being lost, indicating they have a high level of conifer encroachment, major component of sagebrush understory (*Artemisia tridentata* ssp. *Vaseyana),* inadequate regeneration, and/or high levels of disease (Burton 2004). 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. 2006b). Similarly, in the Lassen National Forest, 43 of 709 inventoried aspen stands were completely dead, and 532 of 666 living stands (79.3%) were at a high risk of being lost (De Woody *et al.* 2009).

Despite our best efforts to document the conditions of current stands, we still have an incomplete understanding of how these stand conditions will impact the future trajectories of these forests (Frey *et al.* 2003), and many questions still remain, such as: Are these stands really at high risk of being lost? Can they be rejuvenated with prescribed fire and/or mechanical treatment? What will happen if these stands are burned in a wildfire? In an era of changing climate, should our effort be spent restoring existing stands or establishing new ones?

Many studies have examined the impact of fire severity on aspen regeneration, but there is no clear consensus among their findings. Bailey and Whitham (2002) and Fraser (2004b) found that fire severity was positively associated with post fire aspen sprout density. Horton and Hopkins (1965) and Wang (2003) found a negative relationship, and Brown and Debyle (1987) and Bartos et al. (1994) found no clear relationship between fire severity and post fire aspen regeneration. Due to aspen's ability to store and protect reproductive capacity in underground root networks (DeByle and Winokur 1985b), their ability to produce abundant root sprouts when apical dominance is interrupted (Frey *et al.* 2003), and their poor competitive ability compared to later seral conifers, I hypothesize that post-fire sprout density and growth will be positively correlated with the amount of living aspen present before the fire and the percentage of competing vegetation killed by the fire. I expect to see increased post-fire aspen density and growth in more severely burned areas due to the elimination of conifer competition and greater availability of growing resources.

In this family of studies, I seek to address current knowledge gaps by

- Comparing post-fire aspen regeneration dynamics to those observed after revitalization treatments (conifer removal and prescribed fire)
- Examining how post-fire aspen regeneration is mediated by fire severity and pre-fire stand composition
- Experimenting with a novel form of post fire restoration / human assisted migration
- Discussing the importance and likelihood of successful aspen sexual reproduction

METHODS:

Study sites:

Study sites were located in the Lake Tahoe Basin and the eastern Sierra Nevada (Figure 1). Sample plots and transects were located in six different study areas, each of which contained aspen forests that had been burned in a wildfire or had been subject to conifer removal or prescribed fire revitalization treatments (Table 1).

Eastern Sierra Nevada

The Eastern 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 2,150 – 2,740 m (7,050 – 9,000 ft), the elevation of the current study sites in the Eastern Sierra, most precipitation occurs as snow, and averages 35-45 cm/year (14-18 inch/yr) according to remote automated weather station readings from 2000-2010 at Bridgeport (38.26°N, 119.22°W), Walker (35.67°N, 118.06°W), Gaylor Meadow (37.52°N, 119.19°W), and Markleeville (38.42°N, 119.47°W). Average yearly, January, and July temperatures were approximately 2, -5.5, and 11° C respectively during this measurement period (35.5, 22, and 52.5 ° F). 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, though 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 which is 25 km from the Virginia Creek and Green Creek study sites (for aspen revitalization treatment stand description, see Chapter 1). The Silver Creek study area is comprised of mixed aspen, conifer forest, and is comprised primarily (90% of stems) of two species: aspen and Jeffery pine (*Pinus Jefferii*). Thirty percent of the aspen stems are dead, whereas only one percent of the Jeffery pine are dead, indicating a possible difference in age at the Silver Creek site.

Lake Tahoe Basin:

This basin is located between the crest of the Sierra Nevada to the West and the Carson Range to the East. It is characterized by warm, dry summers and cold, wet winters. Most precipitation falls as snow during the winter, with mean monthly temperatures in South Lake Tahoe (38.92°N, 119.95°W) ranging from -1 ° in January to 16 ° C in July, and mean annual precipitation of 74 cm during the period from 2000-2010. The forests around Lake Tahoe have a diverse history of human use. The Lake Tahoe basin was used by the Washoe, who migrated from the Great Basin during the summer (Beaty and Taylor 2008). Euro-Americans first traversed the Tahoe region in 1844 but large numbers of Euro-Americans did not settle in the Lake Tahoe basin until the 1860s (Elliott-Fisk *et al.* 1997). Beginning in the 1870s, nearly 70% of the Lake Tahoe watershed was logged to provide wood for silver mines in Virginia City, Nevada. Aspen forests here are commonly found in riparian or mesic areas, and the Angora aspen stand in this study is situated on at the edge of Angora Creek on level ground.

Vegetation dynamics following wildfire and revitalization treatments:
Wildfire sampling:

Areas in four recent wildfires that burned aspen stands were samples 1 to 6 years after burning. The Angora (2007) and Silver Creek (2008) fire areas were sampled 1, 2, and 3 years post-fire, whereas the Black Mountain (2006) and Wet Meadow (2003) fire areas were sampled 4 and 6 years post fire, respectively (Table 1). In each fire area, burned plots were randomly located at least 40 meters apart in areas that contained aspen cover prior to the wildfire in a GIS. In the two study areas where wildfires burned aspen forests at variable severities (Silver Creek and Wet Meadow), sample plots were stratified by severity as classified by the differenced Normalized Burn Ratio (dNBR) algorithm (Eidenshink *et al.* 2007). In the two study areas that had unburned aspen stands within 200 meters of the fire perimeter (Silver Creek and Wet Meadow), control plots were randomly located at least 40 meters apart using a GIS. In each circular 50 m^2 sample plot (4 m radius) regenerating aspen stems were counted in a randomly determined half of the plot, live and dead tree stems were measured for species and diameter at breast height (dbh) or basal diameter if it did not extend to breast height. Composite burn index (Key and Benson 2006), which assesses burn severity on five different strata (substrates, herbs and shrubs, tall shrubs and small trees, intermediate trees, and dominant trees), was visually assessed and the five strata were averaged to get an overall composite burn index on each plot. Additionally, aspect was measured in degrees from true north with a compass, slope was measured with a clinometer, and the cover of bare rock and ground scorch were visually estimated. To estimate the average ramet basal diameter and height in each plot, a measuring tape was laid along the diameter of each circular plot at a random azimuth and the first 15 ramets the tape intersected in each direction from the plot center were measured for basal diameter and height. In a subset of the control plots, the two largest aspen and Jeffery pine trees were cored at the base to estimate the age of the oldest individuals for these two species (5 plots in the Silver Creek Fire and 4 plots in the Wet Meadow area). In and around the Silver Creek and Angora fire areas, The USDA Forest Service had also conducted a “loss-risk” evaluation in the aspen stands in 2005-2007 prior to the wildfires (Annamaria Escheveria, personal communication, August 10, 2009). This assessment incorporates measures of aspen canopy cover, regeneration, understory composition, degree of conifer encroachment, disease, and browsing pressure to categorize the degree of decline (termed "risk of loss") of each aspen stand (loss-risk levels: none, low, moderate, high, or highest) (Burton 2004).

Aspen revitalization treatment measures – conifer removal and prescribed fire:

In 2003 the Bureau of Land Management office in Bishop, CA, began an aspen restoration and monitoring program focused on increasing the vigor and regeneration of declining aspen stands in the Eastern Sierra Nevada. Three stands along Virginia creek with heavy lodgepole pine (*Pinus contorta*) encroachment were selected for conifer removal (Virginia Creek 1-3, referred to hereafter as VC1, VC2 and VC3), and two stands in sagebrush steppe with very little aspen regeneration, were selected for prescribed fire treatment (Green Creek 1 & 2, referred to hereafter as GC1 and GC2). Three to five permanent 30.5 m x 1.8 m belt transects were established in treatment areas and two-three transects were established in untreated control in each study site. In each transect, aspen stems were measured in the following four size classes (SC) before treatment and up to 5 years after treatment: SC1 = height less than .45 m, SC2 = height .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). Conifer removal sites were measured prior to treatment and annually thereafter for 5 years (though not measured in 2008) and prescribed fire sites were measured before treatment and annually for 3 years after treatment (for a complete description of sampling methods, see Chapter 1).

Human assisted migration:

The Angora Fire (a high intensity fire that burned 1,250 ha and 254 homes in the Lake Tahoe Basin in the summer of 2007) burned through a one ha aspen stand on US Forest Service property (Lake Tahoe Basin Management Unit), top-killing all of the existing trees, but initiating vigorous re-sprouting after the fire. Adjacent to the Forest Service property, the California Tahoe Conservancy (CTC) manages 32 ha that were partially burned. Through a collaborative agreement between the US Forest Service, the CTC, and UC Berkeley, I received permission to harvest aspen stems from the regenerating post-fire aspen stand on Forest Service property as well as similar sized stems from an unburned stand just outside the burn perimeter on CTC land. The harvested stems were used to conduct an experimental transplantation into a riparian area on the CTC land that burned in the fire, but did not contain aspen prior to the fire.

In the fall of 2008 (during leaf fall and the beginning of aspen dormancy), eight paired 3m x 3m permanent plots were established in the regenerating aspen stand on Forest Service property. Paired plots contained a harvest and a control plot separated by 3 m. In each plot, every ramet above 3 mm in basal diameter was tagged, and the basal diameter and height were recorded (832 total ramets were tagged and inventoried) for longitudinal measurement.

In order to build a statistical model to predict aboveground sprout biomass from basal diameter and height, 50 random sprouts were collected for destructive sampling. A meter tape was run 5 metes away from and parallel to the experimental plots. At every meter mark (for 25 meters), the closest sprout on each side of the tape was cut at the root collar, tagged and retained for analysis. In the lab, leaves were removed from each sample and stem and branch material was oven dried at 100 °C. The mass of dry stem and branch material was recorded for each sample to inform statistical models of aboveground dry mass.

The resulting model was used to calculate the total above-ground dry biomass in each study plot in the Angora Fire area (where all ramets were measured yearly for basal diameter and height). The same equation was employed to estimate the above-ground biomass of study plots in the Silver Creek Fire area by calculating a mean basal diameter and height from 30 random ramets measured in each plot, calculating the mean dry biomass and multiplying by the number of ramets in each plot.

Each harvest plot was subdivided into six 1.5m x 1m quadrants, in each of which the middlemost stem (or stem clump) was harvested for transplantation. One of two plug sizes (30cm or 15cm diameter around the central stem axis, 20 cm deep, including soil) was assigned alternately to each transplant starting from the north-east quadrant and working counter clockwise, producing three transplants of each plug size from each harvest plot. The eight harvest plots yielded 24 total transplants (12 of each plug size).

Twelve transplants were also harvested from an unburned aspen stand approximately 1500 m from the Angora fire perimeter. Stems of a similar size range to those from the burned site were randomly selected by running a line transect through the stand and selecting the nearest stem or clump of stems of appropriate size (height range: 25 – 260 cm, basal diameter range: 0.3 – 3.2 cm) every five meters. All unburned transplants were 30 cm plugs.

Once harvested, the roots and soil of each transplant were kept moist and planted on the CTC land within one hour. Prior to transplantation, each planting site was determined by vegetative indicator species of soil moisture to be appropriate for aspen (these plants had established in the year since the fire) and by similar soil moisture readings from a FieldScout time domain reflectometry (TDR) soil moisture probe which measures the dialectic constant of the soil, and has a strong positive correlation to the volumetric water content (Topp *et al.* 1980). The transplant sites all had TDR readings between 52 – 65, indicating a volumetric soil water content of between 0.6 – 0.65 according to calibration curves developed for TDR measurements (Topp *et al.* 1980). Once planted, competing vegetation was clipped within a 15 cm radius around the edge of each transplant. All transplants were revisited every fall for the following 3 years to make measurements of basal diameter, height growth, and to assess for mortality.

One year after transplantation, I noticed a significantly higher mortality rate of ramets harvested from the unburned stand (n dead = 5) than the post-fire stand (n dead = 0). To investigate if this trend was associated with root to shoot ratio differences between the two transplant sources, ten new stems or clumps of stems from each transplantation source site were randomly chosen for destructive sampling using the same transect method described above. The basal diameter and height of each stem was measured before removal from the ground as 30 cm plugs. In the field, soil was carefully removed from the roots and any root material that was separated in the process was retained for analysis. The bare-root samples and separated roots were placed in individual garbage bags, labeled, and brought back to the lab. In the lab, samples were air-dried. Once dry, leaves were removed and the stem was separated from the roots at the root collar. Dry soil was carefully brushed off of roots, and lastly, roots were washed over a tub to remove any remaining soil. Once washed, any separated root material in the tub was cleaned and retained for drying. Once clean, the roots of each sample were dissected and separated into three diameter classes: fine roots (< 1.5 mm), medium roots (1.5-8 mm), and large roots (>8 mm) (Landhäusser and Lieffers 2002). Stem, branch, and root material was then oven dried at 100 °C. The mass of dry shoot (stem and branch) material and each root diameter size were recorded and root to shoot ratios were calculated for all roots together and each root diameter size class for each sample.

Aspen sexual reproduction:

One result of working in recently burned aspen forests has been the discovery of five sites of recent aspen seedling establishment in severely burned areas of the Silver Creek fire. All sites were in and around pre-fire aspen stands, and seedlings were identified by their growth morphology, which differed from sprouts growing from existing roots. The seedlings were generally smaller than the sprouts, and were all growing individually rather than in clumps. Additionally, all the seedling sites were on south-facing aspects in concave microsites or small drainages that retained high soil moisture throughout the summer. To confirm seedling status, four suspected aspen seedlings in each seedling site were carefully removed from the soil to determine that they were not connected to any lateral roots, which none were. A total of 125 suspected aspen seedlings in three of the five sites were identified and tagged to monitor survival and growth.

Statistical methods

Sprout density by treatment by time (Figure 2):

Data from the BLM aspen revitalization treatments, (prescribed fire and conifer removal, Chapter 1) is shown with data from two recent wildfires that I surveyed 1, 2, and 3 years post fire (Angora Fire, and Silver Creek Fire, Table 1). Year zero sprout values for the wildfires were the mean new sprout totals from the unburned controls minus any 1 year old spouts (as they were surveyed 1 year post fire). Points in Figure 2 indicate the mean ramet density among plots and whiskers represent the exact 95% Poisson confidence intervals calculated using the pois.exact method in the R Epitools statistical package (Aragon 2010).

Sprout basal diameter by severity over time (Figure 3):

Years 1-3 are comprised of measurements from the Silver Creek and Angora Fire plots. Year 4 is comprised of measurements from the Black Mountain fire plots (aspen burned only at high severity in this fire); and year 6 measurements are from the Wet Meadow Fire plots. Measurements of the basal diameter of 30 randomly selected ramets from each plot in each study site were used to calculate the mean and 95% confidence intervals among plots in each fire severity class.

Predicting post-fire sprout density from pre-fire stand composition and fire severity:

The two-year post-fire aspen sprout density in the Silver Creek and Angora fires was predicted from the live and dead pre-fire aspen basal area, total aspen stems killed by the fire, the conifer basal area alive before the fire, fire severity, and the stand loss-risk level assessed by the Forest Service prior to the fires. A generalized linear model was employed because it can incorporate a Poisson distribution for count data. The data structure was composed of 74 burned plots (58 in the Silver Creek Fire and 16 in the Angora Area, Table 1). Model simplification followed Crawley (2007) using the Akaike information criterion (Pinheiro and Bates 2000). Low loss-risk level was used as the baseline category and all other variables were continuous.

RESULTS

Stand composition from unburned controls

According to measurements from the unburned control plots at the Silver Creek and Wet Meadow sites there are some major differences in the size, age, and past mortality of aspen and

Jeffery pine in these two sites (818 trees measured in Silver Creek control plots, 176 trees measured in Wet Meadow plots, 20 trees of each species cored for age estimates at each site). The average diameter at breast height for aspen and Jeffery Pine at the Silver Creek site is 20 and 27 cm, respectively, and at the Wet Meadow site, 19 and 30 cm, respectively. Though, on average, the pine are larger, they are also younger (56-80 years at Silver Creek and 64-86 years at Wet Meadow) than the aspen (98-140 years at Silver Creek and 88 – 143 at Wet Meadow).

Aboveground biomass prediction model:

Using measurements from 50 destructively sampled ramets, the following statistical model was built to predict ramet dry mass from basal diameter and height measurements ($r^2 = .98$, $p < .001$).

Log(Mass (g)) = 1.16 + .806 Log(Height (m)) + 1.91 Log(Basal Diameter(cm))

Aspen regeneration after wildfire and revitalization treatments:

Results indicate clearly that greater disturbance severity yields increased aspen sprout density (Figure 2). Aspen forests that burned at high severity produced significantly higher ramet densities than forests that burned at moderate or low severity (Figure 2). Two years following prescribed fire treatments, aspen ramet density was similar to aspen forests that burned at low severity. Three years following conifer removal, those areas showed a significant increase in ramet density compared to untreated controls (Figure 2), but also showed significantly lower ramet density compared to areas that burned. Untreated controls did not show significant increases in ramet density over 5 years (Figure 2).

Similarly, greater fire severity yielded increased aspen sprout growth rate (Figure 3). Sprouts had the largest basal diameter after high severity wildfire, followed by moderate severity, and then low severity. These differences were significant 2 years following wildfire and persisted for at least 6 years after wildfire (Figure 3).

Pre-fire stand composition and post fire aspen regeneration:

As discussed above, the generalized linear model results support the finding that fire severity was the most significant predictor of post-fire ramet density 2 years post-fire in the sampled stands (Table 2), clearly showing that stands that burned at higher severity contained greater post-fire sprout density. However, various components of the pre-fire stand condition also impact post-fire sprout density. The basal area of aspen alive prior to the fire and total number of aspen stems killed by the fire had significant positive relationship to post-fire sprout density. The two most important pre-fire stand factors that were negatively correlated to post-fire sprout density were the amount of live conifer and dead aspen basal area. Similarly, stands that had been classified as moderate or high risk of loss before the fire exhibited decreased post-fire sprout density. And lastly, the non-growable percentage (percent occupied by bare rock or severely scorched bare mineral soil) was negatively associated with post-fire sprout densities (all terms were significant at $P<0.001$ level).

As a result of greater flammability of conifers compared to aspen, and the increased basal density of conifers in the high loss-risk stands, these stands burned at a significantly higher severity than did the low loss-risk stands (Figure 5), whereas moderate loss-risk stands burned at an intermediate severity. This relationship helps to explain the roughly equal densities of post fire ramets in each loss-risk category (Figure 6) because stands with little pre-fire conifer encroachment showed similar post-fire sprout density as those that had a high level of pre-fire conifer competition that was eliminated by a high severity fire. This illustrates the primary importance of the change in resource availability to predict post-fire aspen dynamics. In this case, even heavily encroached aspen stands responded vigorously when competing conifers were eliminated by the fire and ample resources were available in the post-fire environment.

Having plots located in the same fire area, I felt it important to understand the possible impact of pseudoreplication (Hurlbert 1984) in my study design and results (Bailey and Whitham 2002). In an effort to make my sample units as independent as reasonably possible, sample plots were set at a minimum distance of 40 meters apart, and were often separated by a break in pre-fire aspen cover. Given the small size and multi-genet nature of aspen stands in this area (Hipkins and Kitzmiller 2004, De Woody *et al.* 2009), plots were likely to be composed of different genets, which should reduce the possibility of pseudoreplication, as genetic factors have been shown to be important in post disturbance aspen sprout density (Zasada and Schier 1973).

To investigate the potential influence of spatial autocorrelation on my regression model results, I examined empirical semivariograms of the dependent variable (sprout density 2 years post-fire), each predictor variable, and the model residuals. Legendre and others (2002) have shown that spatial autocorrelation must be present in both the dependent and independent variables in order for inflation of Type 1 errors due to lack of independence among samples in a regression analysis. Empirical semivariograms showed evidence of spatial autocorrelation in the composite burn index and minor evidence of spatial structure in both the non-growable percentage and total aspen stems killed by fire. The dependent variable, aspen sprout density, showed no evidence of spatial structure nor did the other predictor variables. Similarly, the residuals of the final model did not contain recognizable spatial autocorrelation (Figure 4), thus I can be confident type 1 errors were not inflated for this generalized linear model. This is not surprising as a recent study of subsamples from six fires in the Sierra Nevada found little evidence for strong spatial autocorrelation on various measures of forest conditions either before or after burning (van Mantgem and Schwilk 2009).

Survival and growth of aspen ramet transplants and impact to source stand:

Three years after transplantation, a binomial proportion test showed no significant difference in cumulative mortality rates between the two plug sizes (Table 3), but did detect a significant difference in survival between the two transplant sources ($P = 0.01$) as the transplants from the unburned source were over five times more likely to die after 3 years. Of the surviving transplants in 2011 (3 years after transplantation), there was no detectable difference in growth rate between plug sizes or transplant source. Destructively sampled ramets from the burned stand had a significantly higher mean fine root to shoot ratio, whereas samples from the unburned stand had a significantly higher mean large root to shoot ratio (Table 4). Additionally, the burned harvest plots showed no significant difference in mean ramet mortality rate, mean relative growth rate, or total plot above-ground biomass accumulation from the paired un-harvested control plots.

Aspen Seedlings:

Three years after the Silver Creek fire, seedling sites 1, 2, and 3 exhibited cumulative mortality rates of 100, 12, and 10 percent, respectively (Table 5). Seedling site 1 was in a depression that was inundated with water during peak snowmelt in the spring of 2010 and 2011, which killed all of the seedlings by the fall re-measurement in 2011.

DISCUSSION:

Aspen regeneration after wildfire and revitalization treatments:

As an early seral species, aspen are poor competitors but have the ability to capitalize quickly on available resources (DeByle and Winokur 1985b). These life history traits of aspen are clearly shown through the strong positive relationship between burn severity and post fire ramet density. In mixed conifer aspen forests, such as those surveyed here, competition is most effectively eliminated by fires with enough intensity to kill the neighboring conifers (Kurzel *et al.* 2007). Though an interruption of the flow of auxin from shoots to roots is necessary for vegetative regeneration in aspen (Schier *et al.* 1985), it is not sufficient for re-sprout vigor and long-term survival, which also requires a resource rich growth environment (and protection from possible herbivores) (Shepperd *et al.* 2006a).

In the present analysis, it is clear that ramet density and growth rates were greater with increased fire severity, as has been shown in Arizona (Bailey and Whitham 2002) and Alberta (Fraser *et al.* 2004b). One important caveat to this is in the presence of heavy course woody debris within an aspen stand. I did not have a direct measure of large heat pulses from heavy downed fuels, but rather used indirect evidence such as heavily scorched bare mineral soil with a layer of white ash on top. Presence of this type of smoldering and/or flaming combustion, which often contributes to much longer and deeper lethal soil temperatures, had a negative relationship to post-fire sprout density as it likely heat-killed aspen roots. Brown and DeByle (1987) showed that post-fire depth of sprout origin was positively related to fire severity, hypothesizing that more superficial roots, responsible for most post-fire sprouts (Schier and Campbell 1978) were heat-killed by the fire.

In this vein, prescribed fires can be problematic for aspen revitalization because they are often burned under moderate environmental conditions with reduced fire severity, compared to naturally occurring wildfires that burn under more extreme conditions (lower fuel moistures and higher wind speeds). If aspen regeneration is a management goal, it will likely be better met by allowing wildfires to burn for resource benefit rather than attempting to conduct a prescribed fire (unless it is a high-intensity prescribed fire). In areas where allowing wildfires to burn may not be socially acceptable, revitalization treatments such as conifer removal and prescribed fire can also be effective (Jones *et al.* 2005, Bates *et al.* 2006).

Pre-fire stand composition and post fire aspen regeneration:

I propose that there are two major determinants of post-fire aspen sprout density and growth rate:

1. The growing resources available after the fire (e.g. radiation, water, soil nutrients), which are reduced by competing vegetation.
2. The quantity of belowground resources stored and protected from fire

Post fire growing environment is listed first because my data indicate that fire severity, which directly reduces post fire biotic competition and indirectly increases abiotic factors such as soil moisture, soil temperature, and solar radiation (DeByle and Winokur 1985b), is the most important predictor of post fire aspen sprout density and growth. Though I did not measure resources directly, I assert that the link between fire severity and post-fire aspen density and growth is mediated through post-fire resource availability. As a result of aspen's ability to quickly take advantage of released resources, it appears that as long as there are *some* underground resources available for the initiation of sprouting, aspen can quickly occupy available growing space. This is evident in that even high loss-risk stands produced high sprout densities and growth after high severity fire released growing space.

Below ground resources, which are likely a combination of live root mass (DesRochers and Lieffers 2001, Shepperd *et al.* 2001a) and root non-structural carbohydrate reserves (Anderegg *et al.* 2012), are positively associated with aspen sprout density and growth (Landhäusser and Lieffers 2002). Aspen vegetative regeneration is a clear example of the storage effect (Chesson and Huntly 1989) in which over time, stands are often outcompeted by later seral competitors while simultaneously building a reserve of stored reproductive potential underground. All that is required to shift the competitive balance is a disturbance that knocks back the competition and releases the stored reproductive energy.

The covariates other than composite burn index in my statistical model likely impact post fire sprout density indirectly by modulating the amount of underground resources stored in each stand. My results indicate that the basal area of live aspen is positively related to post fire sprout density, which I attribute to increased underground resources. DesRochers and Lieffers (2001) found that that basal area of aboveground aspen is a good indication of the amount of live roots belowground but Shepperd and others (2001a) found no difference in root mass between stands that differed in aboveground biomass and growth rate. It is well known that when apical dominance is interrupted by the death of the above-ground aspen biomass (such as being top-killed by a fire), auxin production and transport to the roots is halted (Schier 1972). Auxin acts to suppress sprouting in roots, but when the flow of auxin from the stem is interrupted, root sprouting initiates (Eliasson 1971, Wan *et al.* 2006). Though hormonal control of sprouting has been well studied, more research is needed to investigate aboveground-belowground biomass relationships and how they are related to sprouting response.

Our results also indicate that conifer encroachment (measured as conifer basal area) has a negative influence on post fire sprout density, as does the pre-fire basal area of dead aspen. Not surprisingly, I found these two variables to be positively correlated in the untreated controls. Both of these factors likely indicate reduced aboveground and belowground vigor of aspen.

Our statistical model was significantly improved by the addition of the loss-risk category assigned prior to the fire. This categorical variable likely improved the model predictions because it more accurately assessed the condition of the pre-fire understory (eg the presence of sagebrush) and level of stand decline, which was not always evident after the fire.

Human assisted migration:

Our transplant data indicates that human assisted migration is a viable alternative to ensure that this important species is able to migrate with its preferred climate envelope. A few key findings include: transplantation of post-fire ramets show improved survival over ramets from unburned stands as well as out-planted greenhouse grown seedlings (Shepperd and Mata 2005) and harvest from a post fire stand does not negatively impact the residual stems' mortality or growth rate.

Though source-sink relationships are not well understood in aspen (Frey *et al.* 2003), the results of my destructive sampling suggest that the sprouts that were harvested from the mature, unburned stand were a carbohydrate sink on the parent stand. The high large root to shoot ratio and low fine root to shoot ratio may indicate that the large roots of these ramets are used primarily for nutrient transport from overstory trees rather than water and nutrient absorption, which is likely the role of the fine roots. The significantly higher mortality rate of the ramets from the unburned source was likely caused by the inability of these ramets to absorb adequate underground resources with so few fine roots.

Post fire ramet transplantation to initiate a new aspen stand may represent a novel opportunity for service learning, and community-based forestry and post-fire restoration. Additionally, it could potentially allow for the intentional initiation of aspen stands in and around human communities in high fire hazard areas as a low flammability fire break (Fechner and Barrows 1976).

Aspen sexual reproduction:

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 (Mueggler 1988, Romme *et al.* 2005). However, recent studies have shown that aspen stands contain much more genetic diversity than once assumed (Mock *et al.* 2008b, De Woody *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 disperser in North America.

The numerous seedlings found after the Silver Creek Fire indicate to me that aspen sexual reproduction does, in fact, occur more often than once assumed. Furthermore, the high survival rate in two of the seedling sites is a promising sign for successful seedling establishment in this area. Both of these sites were situated on south-facing benches with concave microtopography (Landhäusser *et al.* 2010), and retained high soil moisture well into the summer dry season. However, it is important to note that the regeneration niche (Grubb 1977) of aspen is extremely small in both spatial and temporal extent, and most often created by high severity fire. DeWoody et al. (2009) explain the “patchy and isolated nature of the small, monoclonal stands” in the southern Cascade Mountains to be the product of small scale disturbance. I contend that the origin of these small stands is not necessarily a small disturbance, but more likely small patches, within a larger disturbance, that provide for the exacting requirements for aspen seedling establishment. In fact, I hypothesize that aspen stand size is generally smaller in the Sierra Nevada than in the intermountain west due to the reduced size of high severity patches in natural fire regimes, and the low frequency of high soil moisture areas within these severely burned patches. Though it is still debated, Collins and Stephens (2010) estimate that high severity fire comprised only 15% of fire areas in upper elevation mixed conifer forests in the Illilouette Creek Basin, Yosemite National Park.
Regardless of the historic patterns of high severity fire, successful sexual regeneration and long distance dispersal of aspen in the future will depend heavily on the occurrence of high severity fire and the availability of a seed source.

Aspen management in uncertain futures:

Future climate change will present both challenges and opportunities for aspen. Increased temperatures and severity of drought will likely stress existing populations (as is currently being observed in the intermountain west). But increased high severity fire in forested areas (Miller *et al.* 2009), may open the door for successful aspen migration and novel genets to establish that may better tolerate future climates than current stands.

Forestalling the impacts of conifer encroachment to highly valued aspen stands is often the primary strategy resource agencies have to maintain the important biological diversity supported by this foundation species. This is a 'resistance' to change strategy (Millar *et al.* 2007a, Stephens *et al.* 2010b), which should be one of many strategies considered or used in tandem. I suggest that resilience and response strategies should also be considered, such as creating conditions for the establishment of new stands by simply allowing desirable wildfires to burn, or more directly though out-planting seedlings, transplanting ramets, or merely dispersing seed to viable microsites after disturbance.

Table 1: Data acquisition summary: Treatment type, transect/plot totals, aspen stand extent, and measurement year details by study site. Low severity plots had a composite burn index (CBI) below 1.5, moderate severity plots had a CBI from between 1.5 and 2.5, and high severity plots had a CBI over 2.5 ("…" indicates no data for that cell).

Site name	Treatment Type	Treatment Transects	Control Transects / Plots	Low Severity Plots	Moderate Severity Plots	High Severity Plots	Post Treatment / disturbance Years Measured	Extent of Aspen Stand(s) (ha)	Calendar Years Measured
Angora	Wildfire	...	...	...	...	16	1, 2, 3	1	2008, 2009, 2010
Silver Creek	Wildfire	...	20	18	20	20	1, 2, 3	33	2009, 2010, 2011
Black Mountain	Wildfire	...	…	...	...	10	4	5	2010
Wet Meadow	Wildfire	...	4	4	4	4	6	7	2010
Virginia Creek 1	Conifer removal	4	2	...	...	...	0, 1, 2, 3, 5	2	2004, 2005, 2006, 2007, 2009
Virginia Creek 2	Conifer removal	4	2	...	...	...	0, 1, 2, 4, 5	7	2005, 2006, 2007, 2009, 2010
Virginia Creek 3	Conifer removal	4	2	...	...	...	0, 1, 3, 4, 5	2	2006, 2007, 2009, 2010, 2011
Green Creek 1	Prescribed fire	3	3	6	4	...	0, 1, 2, 3	1	2007, 2008, 2009, 2010
Green Creek 2	Prescribed fire	5	2	6	13	1	0, 1, 2, 3	8	2007, 2008, 2009, 2010

Table 2: Results of generalized linear regression analysis to determine the effects of pre-fire stand composition and fire severity on post-fire aspen ramet density, listed in decreasing order of standardized parameter estimates ("…" indicates no data for that cell).

Model term	Estimate	Standardized Estimate	Z-value	P-value
Intercept	4.811	…	129.38	< 0.001
Composite Burn Index	0.496	0.0018	38.40	< 0.001
Aspen basal area alive before fire	5.204	0.0012	33.21	< 0.001
Total aspen stems killed in fire	0.006	0.0004	10.51	< 0.001
Risk : high	-0.276	-0.0005	-9.08	< 0.001
Percent non-growable area in plot	-0.012	-0.0007	-18.71	< 0.001
Risk : moderate	-0.631	-0.0014	-22.57	< 0.001
Aspen basal area dead before fire	-80.177	-0.0015	-7.83	< 0.001
Conifer basal area alive before fire	-2.151	-0.0015	-35.82	< 0.001

Table 3: Transplant summary: Heights (m) and basal diameters (cm) reported are the mean measurements made prior to transplantation in 2008 ± standard deviations. Different letters following values in the same row indicate significant differences (ANOVA used to test differences in height and diameter among the three groups and binomial proportion test used to test for differences in mortality rates among groups).

	Burned Source		Unburned Source
	15 cm plug	30 cm plug	30 cm plug
Number of transplants	12	12	12
Transplant mean height (m)	1.19 ± 0.43	1.27 ± 0.71	1.15 ± 0.47
Transplant mean basal diameter (cm)	0.97 ± 0.40	1.24 ± 0.77	1.46 ± 0.70
Three-year cumulative mortality (%)	8^{a}	0^{a}	50^{b}

Table 4: Destructive samples summary: Heights (m) and basal diameters (cm) reported are the mean measurements made prior to removal from the ground in 2009 ± standard deviations. Different letters following means in the same row indicate significant differences (ANOVA used to test differences in means for height and diameter and Wilcoxon's signed rank test used for root to shoot ratios) ("…" indicates no data for that cell).

	Burned Source		Unburned Source
	15 cm plug	30 cm plug	30 cm plug
Number of samples	…	10	10
Sample mean height (m)	…	1.50 ± 0.50^{a}	1.06 ± 0.41^{b}
Sample mean basal diameter (cm)	…	1.40 ± 0.50^{a}	1.39 ± 0.58^{a}
Mean fine root to shoot ratio	…	0.05 ± 0.03^{a}	0.01 ± 0.02^{b}
Mean medium root to shoot ratio	…	0.17 ± 0.12^{a}	0.12 ± 0.17^{a}
Mean large root to shoot ratio	…	0.29 ± 0.09^{a}	1.08 ± 1.24^{b}

Table 5: Aspen seedling data by site – Sample quantities, mortality rates, and mean height and basal diameter of seedlings ("…" indicates no data for that cell).

Seedling Site (SS)	SS1	SS2	SS3
Total seedlings tagged 2009	50	25	50
Cumulative mortality percent in 2010	54	8	6
Mean seedling height 2010 (cm)	11.26	44.59	34.14
Mean seedling basal diameter in 2010 (cm)	0.24	0.47	0.49
Cumulative mortality percent in 2011	100	12	10
Mean seedling height in 2011 (cm)	…	47.4	51.09
Mean seedling basal diameter in 2011 (cm)	…	0.60	0.56

Figure 1: Study sites map

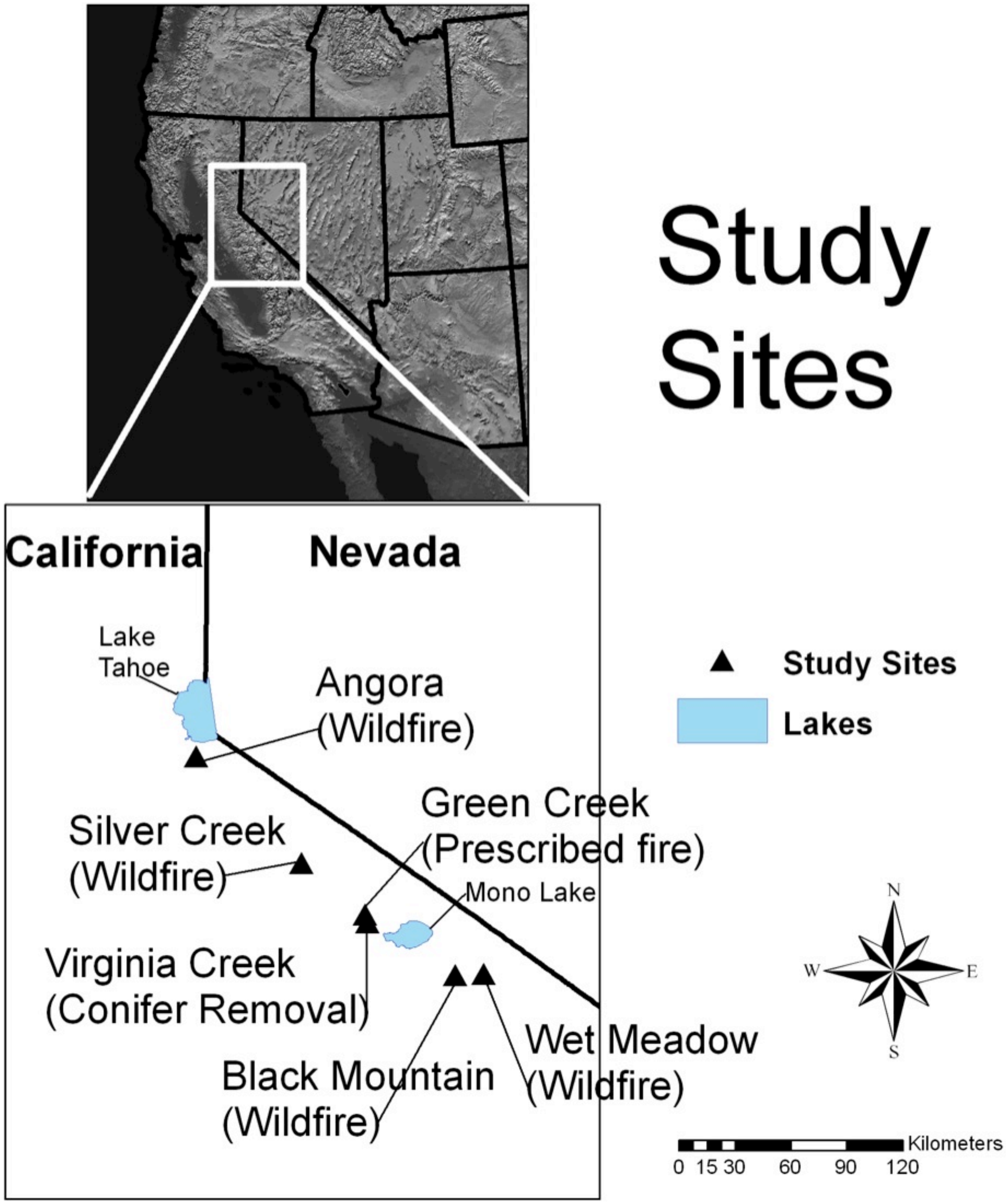


Figure 2: Ramet density is shown over time for prescribed fire, conifer removal, as well as from low, moderate, and high severity wildfire (Angora and Silver Creek Fires). Year zero sprout values for the wildfires were the mean new sprout totals from the unburned controls minus any 1 year old spouts (as they were surveyed 1 year post fire). Points in Figure 2 indicate the mean ramet density among plots and whiskers represent the exact 95% Poisson confidence intervals.

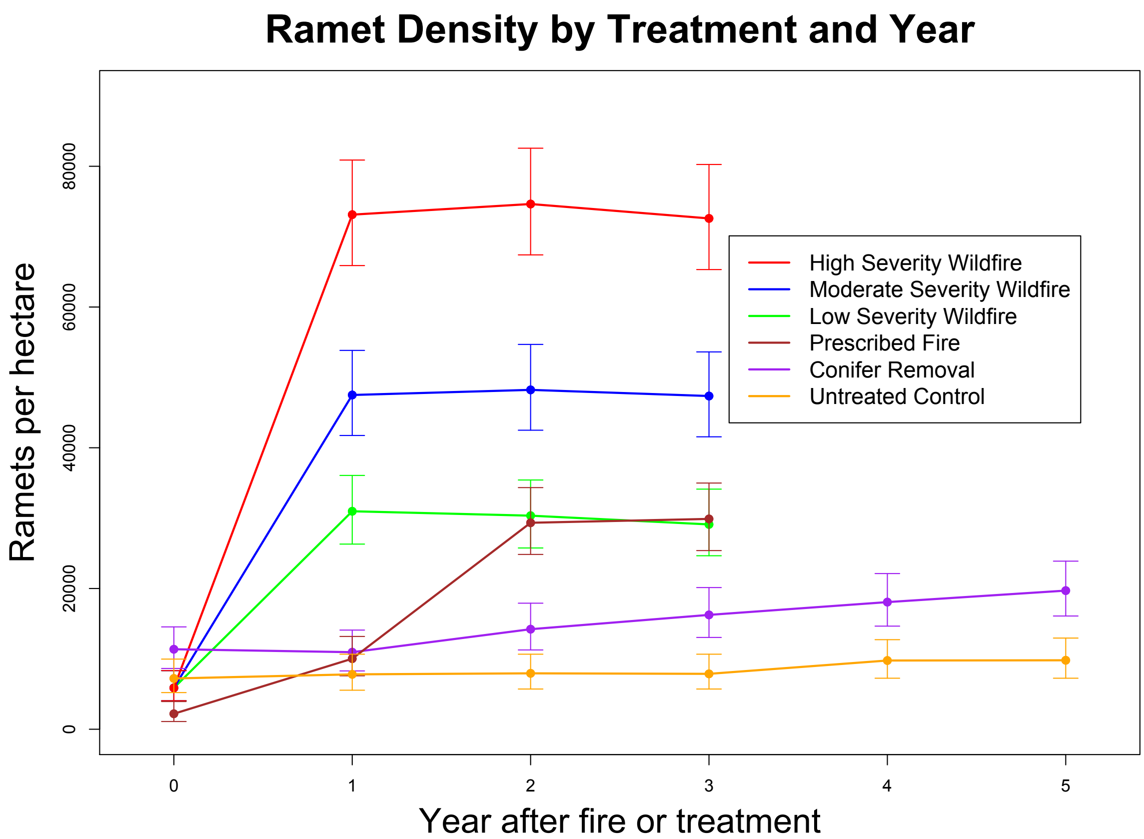


Figure 3: Average ramet basal diameter is show over time by fire severity class. Years 1-3 are comprised of measurements from the Silver Creek and Angora Fire plots. Year 4 is comprised of measurements from the Black Mountain fire plots; and year 6 measurements are from the Wet Meadow Fire plots. Measurements of the basal diameter of 30 randomly selected ramets from each plot in each study site were used to calculate the mean and 95% confidence intervals among plots in each fire severity class.

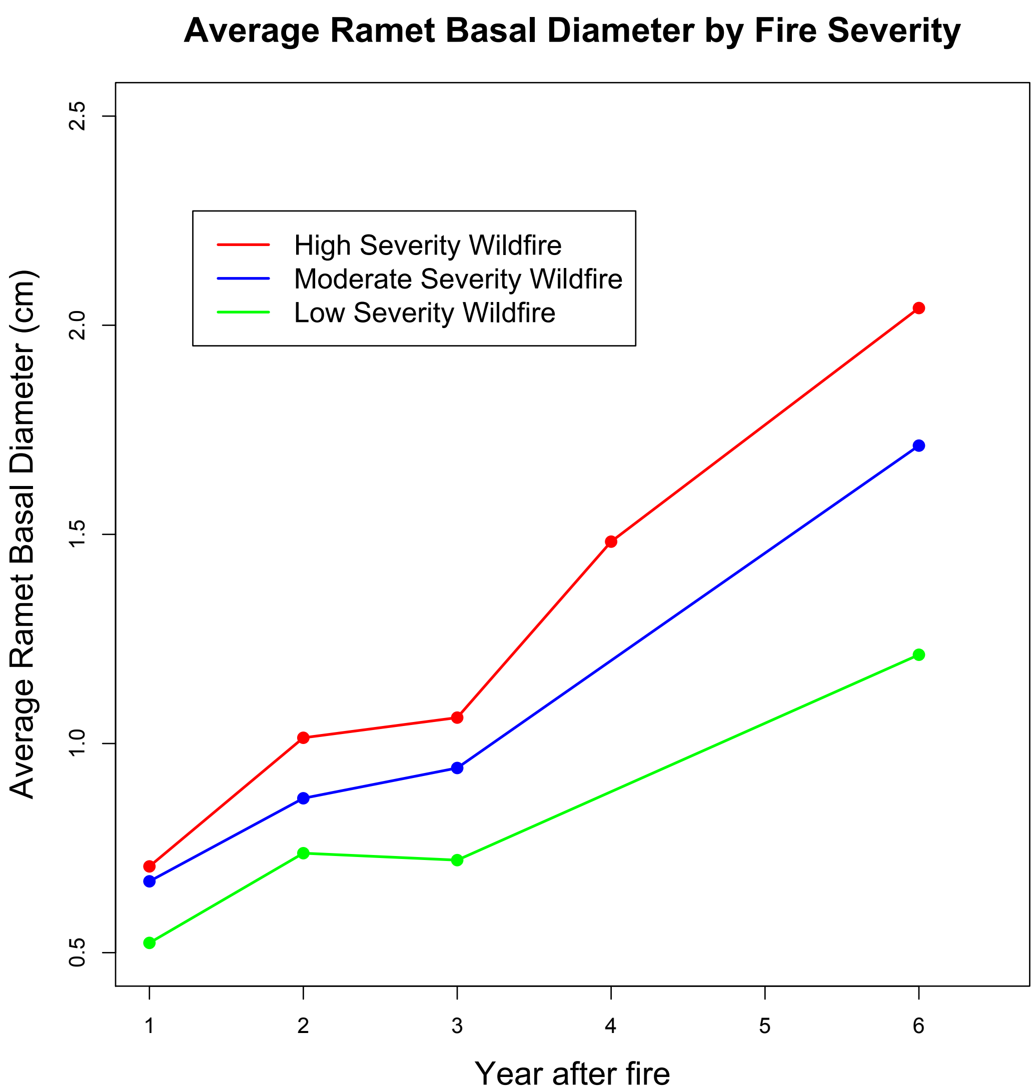


Figure 4: Semivariogram of ramet density prediction generalized linear model errors – the residuals of the final model do not contain recognizable spatial autocorrelation, thus type 1 errors were not inflated due to the spatial structure of the underlying data.

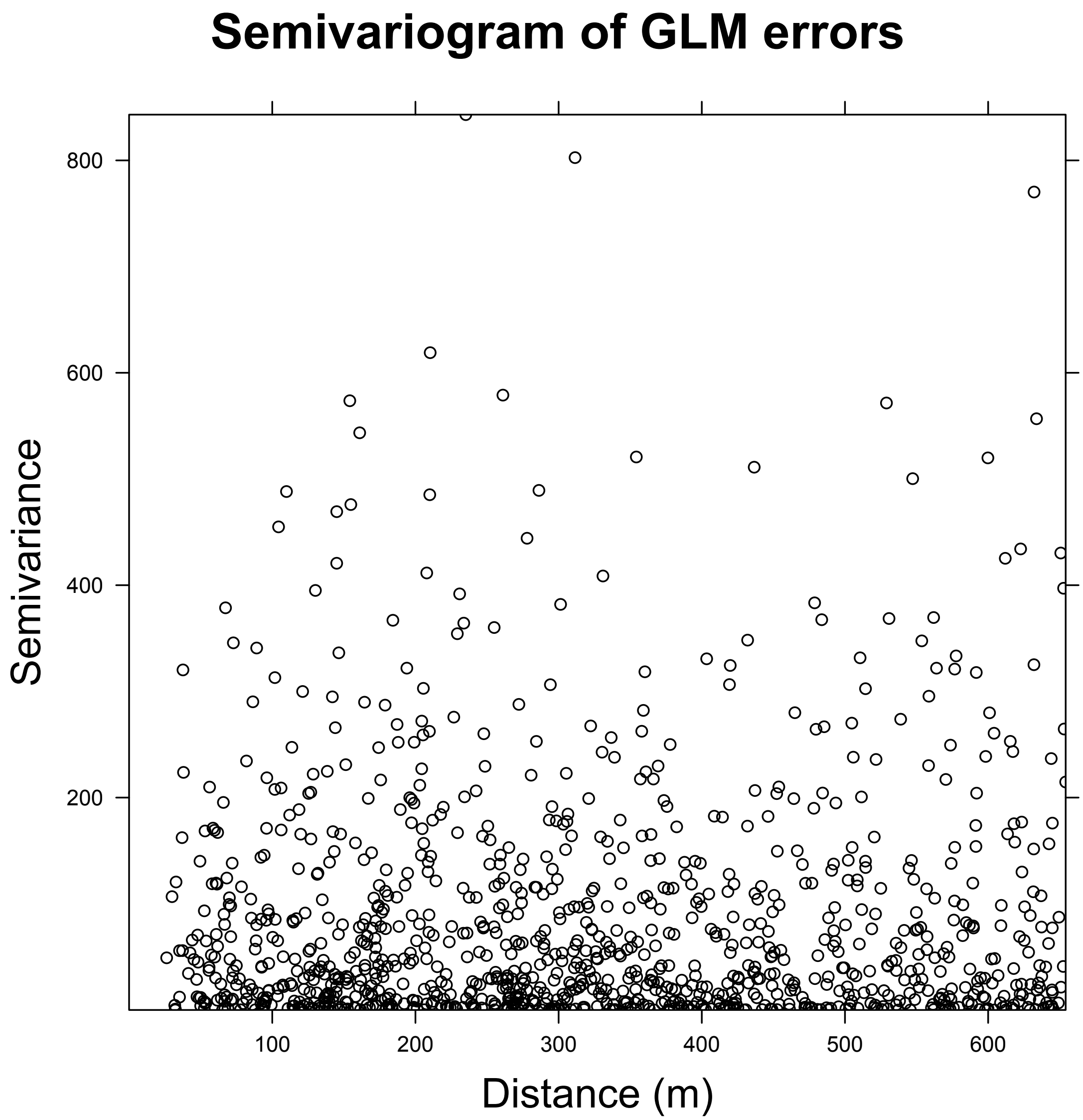


Figure 5: Burn Severity by pre-fire stand loss risk – High loss-risk stands tended to burn at higher severity and low loss-risk stands tended to burn at lower severity, with moderate loss-risk stands burning at moderate severity. Horizontal lines in the boxes indicate the median, whiskers indicate the first and third quartiles, and open circles indicate outliers.

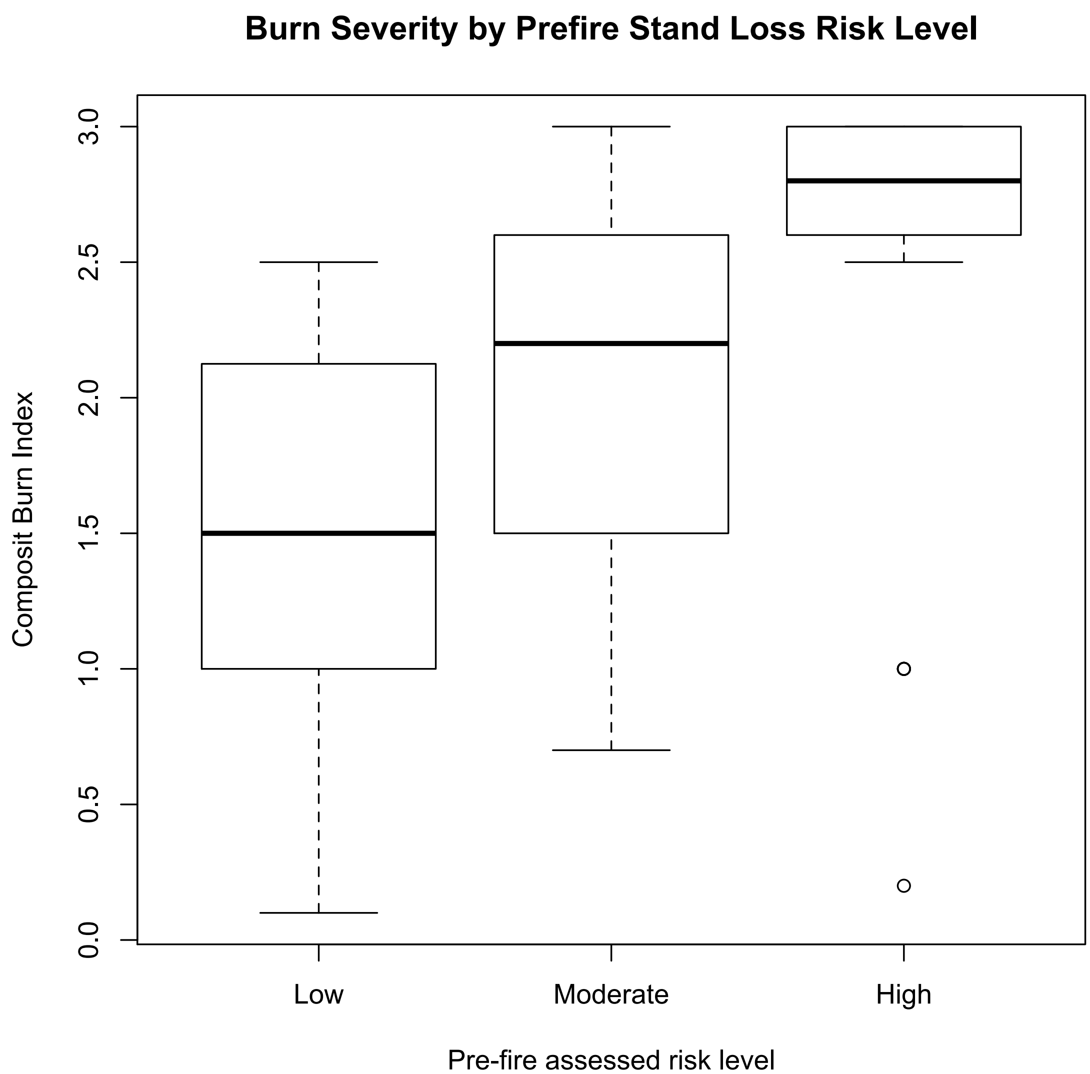


Figure 6: Post-fire ramet density by pre-fire stand loss risk – Aspen stands in all three stand loss-risk categories showed similar post-fire sprout densities. Horizontal lines in the boxes indicate the median, whiskers indicate the first and third quartiles, and open circles indicate outliers.

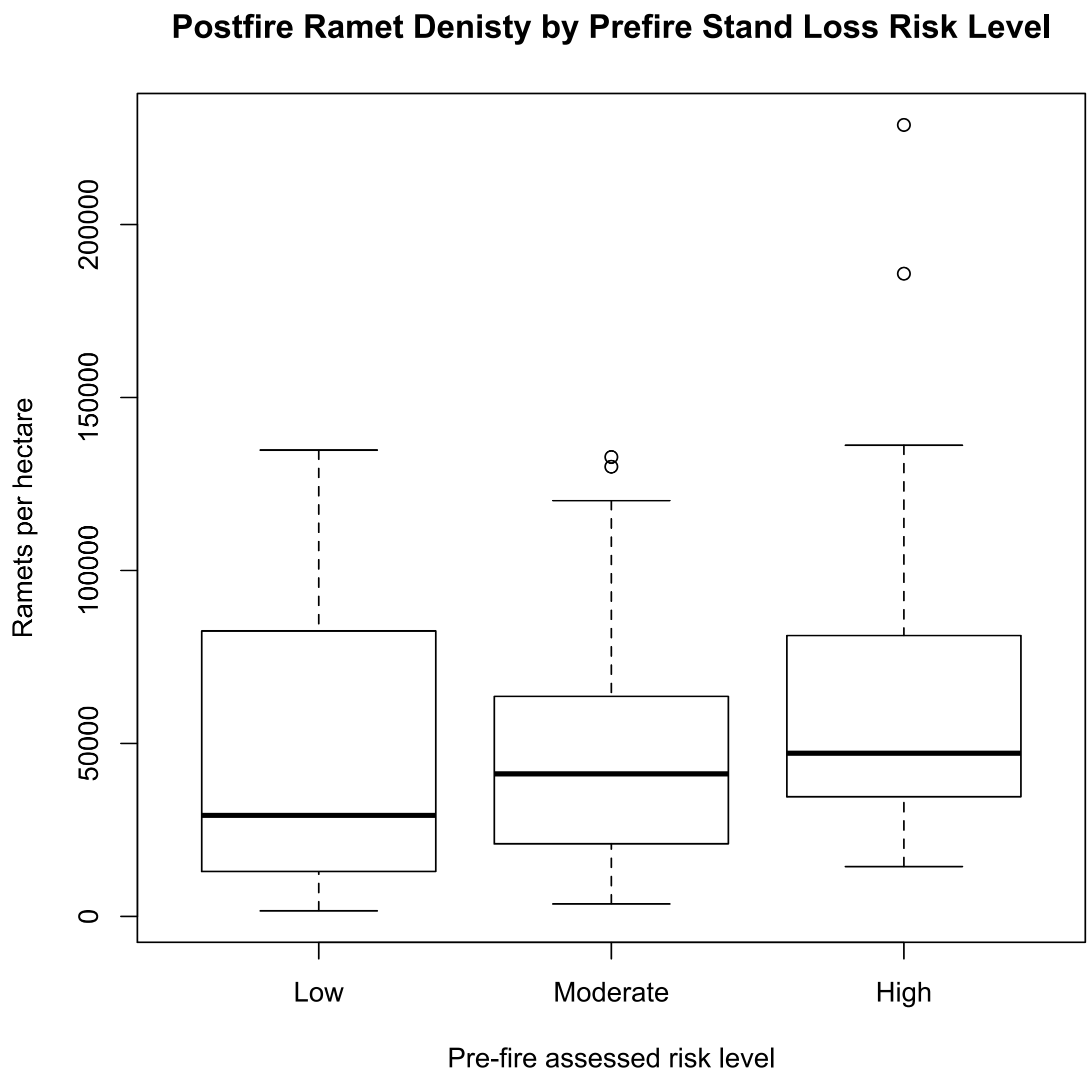


Figure 7: Fine root to shoot ratio by harvest source – Destructively sampled ramets from a post fire environment ("burned") had significantly higher fine root to shoot radios. Horizontal lines in the boxes indicate the median, whiskers indicate the first and third quartiles, and open circles indicate outliers.

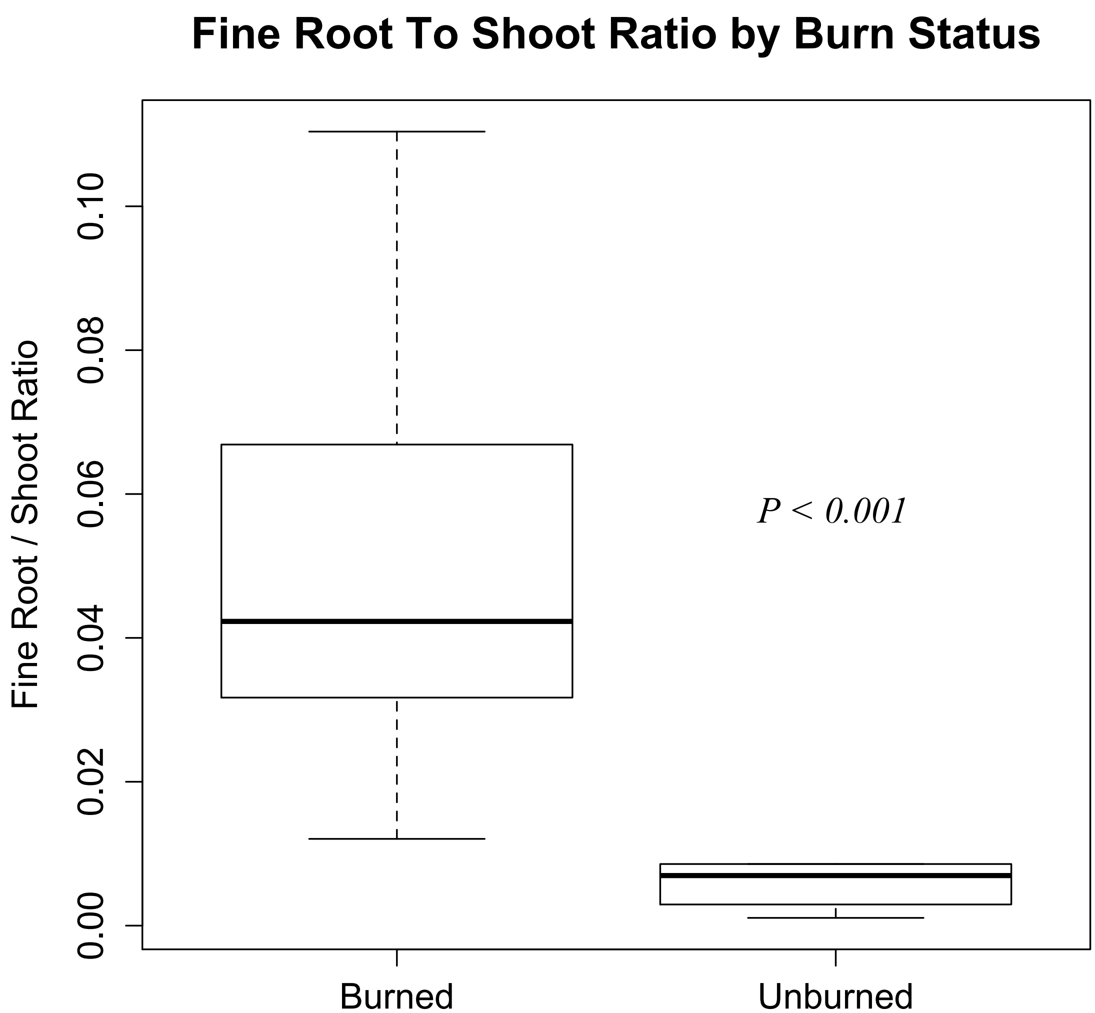
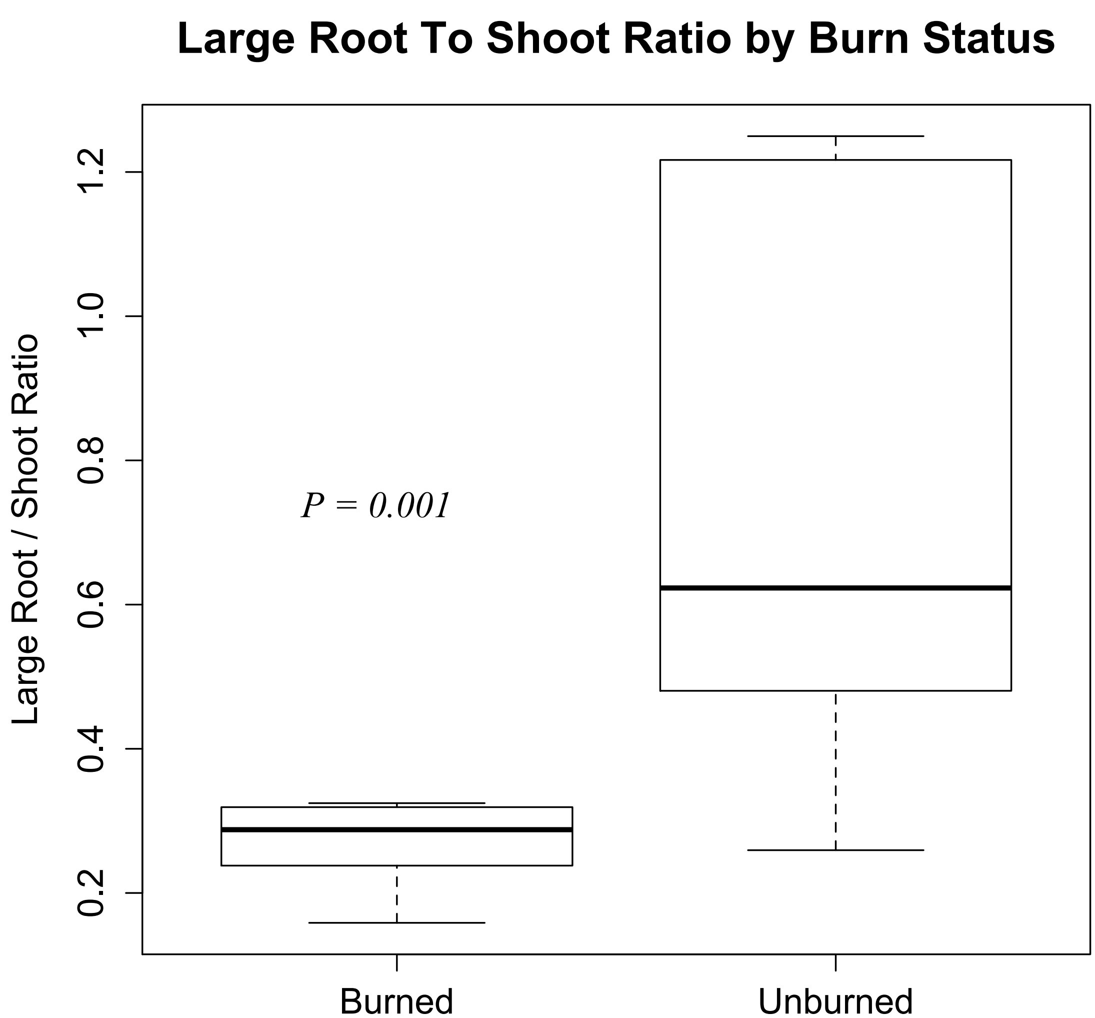


Figure 8: Large root to shoot ratio by harvest source - Destructively sampled ramets from a post fire environment ("burned") had significantly lower large root to shoot radios. Horizontal lines in the boxes indicate the median, whiskers indicate the first and third quartiles, and open circles indicate outliers.



References:

Anderegg, W.R.L., J.A. Berry, D.D. Smith, J.S. Sperry, L.D.L. Anderegg, and C.B. Field. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. Proceedings of the National Academy of Sciences 109: 233-237.

Aragon, T. 2010. Epidemiology Tools: EpiTools version 0.5-6. R Package for Epidemiologic Data and Graphics.

Bailey, J.K. and T.G. Whitham. 2002. Interactions among fire, aspen, and elk affect insect diversity: reversal of a community response. Ecology 83: 1701-1712.

Bartos, D.L., J.K. Brown, and G.D. Booth. 1994. Twelve years biomass response in aspen communities following fire. Journal of Range Management: 79-83.

Bates, J.D., R.F. Miller, and K.W. Davies. 2006. Restoration of quaking aspen woodlands invaded by western juniper. Rangeland Ecology & Management 59: 88-97.

Beaty, R.M. and A.H. Taylor. 2008. Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. Forest Ecology and Management 255: 707-719.

Brown, J.K. and N.V. Debyle. 1987. Fire damage, mortality, and suckering in aspen. Canadian Journal of Forest Research 17: 1100-1109.

Burton, D. 2004. An implementation monitoring protocol for aspen. Transactions of the Western Section of the Wildlife Society 40: 61-67.

Chesson, P. and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. Trends in Ecology & Evolution 4: 293-298.

Collins, B.M. and S.L. Stephens. 2010. Stand-replacing patches within a 'mixed severity' fire regime: quantitative characterization using recent fires in a long-established natural fire area. Landscape Ecology 25: 927-939.

Crawley, M.J. 2007. The R book. Wiley.

De Woody, J., T.H. Rickman, B.E. Jones, and V.D. Hipkins. 2009. Allozyme and microsatellite data reveal small clone size and high genetic diversity in aspen in the southern Cascade Mountains. Forest Ecology and Management 258: 687-696.

DeByle, N.V. and R.P. Winokur. 1985. Aspen: ecology and management in the western United States. USDA Forest Service General Technical Report RMRS-GTR-119, Fort Collins, Colorado, USA.

DesRochers, A. and V.J. Lieffers. 2001. Root biomass of regenerating aspen (*Populus tremuloides*) stands of different densities in Alberta. Canadian Journal of Forest Research 31: 1012-1018.

Di Orio, A.P., R. Callas, and R.J. Schaefer. 2005. Forty-eight year decline and fragmentation of aspen (Populus tremuloides) in the South Warner Mountains of California. Forest Ecology and Management 206: 307-313.

Eidenshink, J., B. Schwind, K. Brewer, Z.L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology 3: 3-21.

Eliasson, L. 1971. Growth regulators in Populus tremula IV. Apical dominance and suckering in young plants. Physiologia Plantarum 25: 263-267.

Elliott-Fisk, D.L., T.C. Cahill, O.K. Davis, L. Duan, C.R. Goldman, G.E. Gruell, R. Harris, R. Kattelmann, R. Lacey, and D. Leisz. 1997. Lake Tahoe case study. Sierra Nevada Ecosystem Project. Addendum: 217-276.

Fechner, G.H. and J.S. Barrows. 1976. Aspen stands as wildfire fuel breaks. Department of Forestry and Wood Science, College of Forestry and Natural Resources, Colorado State University, Fort Collins, CO.

Fraser, E., S.M. Landhäusser, and V.J. Lieffers. 2004. The effect of fire severity and salvage logging traffic on regeneration and early growth of aspen suckers in north-central Alberta. The Forestry Chronicle 80: 251-256.

Frey, B.R., V.J. Lieffers, S.M. Landhausser, P.G. Comeau, and K.J. Greenway. 2003. An analysis of sucker regeneration of trembling aspen. Canadian Journal of Forest Research 33: 1169-1179.

Grubb, P. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological reviews 52: 107-145.

Hipkins, V.D. and J.H. Kitzmiller. 2004. Genetic Variation and Clonal Distribution of Quaking Aspen in the Central Sierra Nevada. Transactions of the Western Section of the Wildlife Society 40: 32-44.

Horton, K. and E. Hopkins. 1965. Influence of fire on Aspen [Populus tremuloides and P. grandidentata] suckering. Canada, Department of Forestry, Forest Research Branch. Ottawa.

Hurlbert, S.H. 1984. Psuedoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Jones, B.E., T.H. Rickman, A. Vazquez, Y. Sado, and K.W. Tate. 2005. Removal of encroaching conifers to regenerate degraded aspen stands in the Sierra Nevada. Restoration Ecology 13: 373-379.

Kay, C.E. 1997. Is Aspen doomed? Journal of Forestry 95: 4-11.

Key, C. and N. Benson. 2006. Landscape Assessment: Ground measure of severity, the Composite Burn Index, and remote sensing of severity, the Normalized Burn Ratio, RMRS-GTR-164.*in* Lutes, D., R. Keane, J. Caratti, C. Key, N. Benson, S. Sutherland, and L. Gangi, editors. FIREMON: Fire Effects Monitoring and Inventory System. USDA Forest Service Rocky Mountain Research Station, Ogden, UT.

Kurzel, B.P., T.T. Veblen, and D. Kulakowski. 2007. A typology of stand structure and dynamics of Quaking aspen in northwestern Colorado. Forest Ecology and Management 252: 176-190.

Landhäusser, S.M., D. Deshaies, and V.J. Lieffers. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. Journal of Biogeography 37: 68-76.

Landhäusser, S.M. and V.J. Lieffers. 2002. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. Journal of Ecology 90: 658-665.

Legendre, P., M.R.T. Dale, M.J. Fortin, J. Gurevitch, M. Hohn, and D. Myers. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25: 601-615.

Little, E.L. 1971. Atlas of United States trees: Vol. 1. Conifers and important hardwoods. Government Printing Office, Washington, D.C.

Millar, C., N. Stephenson, and S. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17: 2145-2151.

Miller, J., H. Safford, M. Crimmins, and A. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems 12: 16-32.

Mock, K.E., C. Rowe, M.B. Hooten, J. Dewoody, and V. Hipkins. 2008. Clonal dynamics in western North American aspen (Populus tremuloides).

Mueggler, W.F. 1988. Aspen community types of the Intermountain Region [USA]. General technical report INT (USA).

Pinheiro, J. and D. Bates. 2000. Mixed Effects Models in S and S-PLUS. New York: SpringerVerlag.

Potter, D.A. 1998. Forested communities of the upper montane in the central and southern Sierra Nevada. US Dept. of Agriculture, Forest Service, Pacific Southwest Research Station General Technical Report PSW-GTR-169.

Rehfeldt, G.E., D.E. Ferguson, and N.L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. Forest Ecology and Management 258: 2353-2364.

Rogers, P.C., W.D. Shepperd, and D.L. Bartos. 2007. Aspen in the Sierra Nevada: regional conservation of a continental species. Natural Areas Journal 27: 183-193.

Romme, W.H., M.G. Turner, G.A. Tuskan, and R.A. Reed. 2005. Establishment, persistence, and growth of aspen (Populus tremuloides) seedlings in Yellowstone National Park. Ecology 86: 404-418.

Schier, G.A. 1972. Notes: Apical Dominance in Multishoot Cultures From Aspen Roots. Forest Science 18: 147-149.

Schier, G.A. and R.B. Campbell. 1978. Aspen sucker regeneration following burning and clear-cutting on two sites in the Rocky Mountains. Forest Science 24: 303-312.

Schier, G.A., J.R. Jones, and R.P. Winokur. 1985. Vegetative regeneration. USDA Forest Service General Technical Report RM-GTR-119, Fort Collins, Colorado, USA.

Shepperd, W., P. Rogers, D. Burton, and D. Bartos. 2006a. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. USDA Forest Service General Technical Report RMRS-GTR-178, Fort Collins, Colorado, USA.

Shepperd, W.D., D.L. Bartos, and S.A. Mata. 2001. Above-and below-ground effects of aspen clonal regeneration and succession to conifers. Canadian Journal of Forest Research 31: 739-745.

Shepperd, W.D. and S.A. Mata. 2005. Planting Aspen to Rehabilitate Riparian Areas: A Pilot Study. USDA Forest Service Research Note RMRS-RN-26, Fort Collins, Colorado.

Shepperd, W.D., P. Rogers, D. Burton, and D.L. Bartos. 2006b. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-178.

Stephens, S.L., C.I. Millar, and B.M. Collins. 2010. Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. Environmental Research Letters 5: 9.

Topp, G., J. Davis, and A.P. Annan. 1980. Electromagnetic determination of soil water content: Measurements in coaxial transmission lines. Water Resour. Res 16: 574-582.

Turner, M.G., W.H. Romme, R.A. Reed, and G.A. Tuskan. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. Landscape Ecology 18: 127-140.

van Mantgem, P.J. and D.W. Schwilk. 2009. Negligible influence of spatial autocorrelation in the assessment of fire effects in a mixed conifer forest. Fire Ecology 5: 116-125.

Wan, X., S.M. Landh√ § usser, V.J. Lieffers, and J.J. Zwiazek. 2006. Signals controlling root suckering and adventitious shoot formation in aspen (Populus tremuloides). Tree Physiology 26: 681-687.
Wang, G.G. 2003. Early regeneration and growth dynamics of Populus tremuloides suckers in relation to fire severity. Canadian Journal of Forest Research 33: 1998-2006.
Worrall, J.J., L. Egeland, T. Eager, R.A. Mask, E.W. Johnson, P.A. Kemp, and W.D. Shepperd. 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. Forest Ecology and Management 255: 686-696.
Worrall, J.J., S.B. Marchetti, L. Egeland, R.A. Mask, T. Eager, and B. Howell. 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. Forest Ecology and Management 260: 638-648.
Zasada, J.C. and G.A. Schier. 1973. Aspen root suckering in Alaska: Effect of clone, collection date, and temperature. Northwest Science 47: 100-104.

Chapter 3: Spatial and Temporal components of Historical Fire Regimes in a Southern Sierran Mixed Conifer Forest, California

INTRODUCTION

Fire is a key ecological process in western forests that impacts nutrient cycling (Agee 1993), vegetative regeneration , species composition, stand structure (Stephens *et al.* 2009), air quality (Stephens *et al.* 2007), and ecosystem resilience (Holling and Meffe 1996). A century of fire suppression and logging practices of the early 20th century have greatly altered many American forests that once burned frequently, creating more dense (Covington and Moore 1994), homogenous forests that are less resilient to drought, insect attack and are more likely to burn at high severity (Miller *et al.* 2009). Understanding how to manage these forests to retain their invaluable ecosystem services (Hassan *et al.* 2005) and maintain resilience to climate change (Bonan 2008) and uncharacteristically large and severe fire will be one of the most important challenge for the US Forest Service and other forest managers in the next century.

Though the future promises to be different from the past and historical conditions may not be appropriate targets for future management (Millar *et al.* 2007b), understanding historical disturbance regimes, with which native plants and animals have evolved over thousands of years, is vital for those interested in building resilient ecosystems that can accommodate the uncertain future that lies ahead (Landres *et al.* 1999). There is growing evidence that the heterogeneity created by historical fires is vital for maintenance of species diversity and ecosystem resilience (North 2012). Understanding spatial and temporal components of these historical fire regimes can help us incorporate natural or planned disturbance in management plans aimed to promote ecosystem resilience.

Temporal components of historical fire regimes in the mixed conifer forests of the Sierra Nevada have been well studied (Kilgore and Taylor 1979, Swetnam 1993, Swetnam *et al.* 2000, Stephens and Collins 2004, Scholl and Taylor 2010), but there is still high uncertainty regarding spatial components of fire regimes in forests that historically experienced frequent, low to moderate severity fire. There has been much greater success reconstructing spatial patters in forests that historically experienced stand-replacing fires because ample evidence of these fires still exists.

Estimations of spatial components of high severity, stand replacing fires, have been conducted using tree stand age, tree height, density and composition (Heinselman 1973, Hemstrom and Franklin 1982, Agee *et al.* 1990, Sibold *et al.* 2006) yet this evidence depends on high mortality rates, which rarely occupy more than small patches in areas that historically burned frequently. Additionally, much evidence of historic stand structure and disturbance regimes have been lost to fires or logging in forests that once burned frequently (Fulé *et al.* 1997), such as the mixed conifer forests of the Sierra Nevada.

The most reliable evidence left in frequent, low severity fire regimes is the presence of fire-scarred trees and a mosaic of multi-aged stands. Unfortunately, neither of these data sources lends clear evidence of the spatial patterns of fire. Since trees often survive low severity fires and recruitment is typically chronic, tree ages tell us little about the spatial patterns of frequent low severity fires. Fire scars are a unique source of data in which a positive scar is evidence of the presence of fire, but the "absence of evidence is not evidence of absence" (T.T. Veblen, personal communication, February, 2007). In other words, trees that experience fire often do not scar. In fact, Stephens and others (2010a) have shown that when the fire interval is less than 10 years, the probability of a previously scarred tree to scar again is only 5% in the mixed conifer forests of the Sierra Nevada and Baja California, Mexico. These 'false negatives' create spatially noisy datasets that make reconstructing spatial patterns of fire difficult.

These problems have been partially overcome by using area-based rules to infer approximate fire sizes from the proportion of samples or geographic plots that record scars each year (Taylor and Skinner 1998) or by using expert opinion to construct fire polygons (Everett *et al.* 2000, Heyerdahl *et al.* 2001). These methods have been effective, but are difficult to reproduce, and require some subjective decision-making. More recently, researchers have used automated methods in a GIS to produce objective fire areas across space and time. Hessl and others (2007) evaluated Thiessen polygons, kriging, and inverse distance weighted interpolation methods to reconstruct burned areas from binary fire scar data. Similarly, Collins and Stephens (2007) and Ferris and others (2010) used Thiessen polygons to reconstruct known fire areas from fire scar samples. Kernan and Hessl (2010) used an automated, spatially explicit inverse distance weighted interpolation method to create spatial mean fire interval maps of their study areas. This method has tremendous promise for understanding historical spatial fire dynamics via fire scar data, but the interpolation method can be problematic for data that contains many false negatives, such as fire scar data from frequently burned forests. As a result, the maps produced from this method can display inaccuracies around sample points due to the exact nature of the inverse distance weighting procedure.

In this manuscript, I will explore the application of thin plate splines as a fire-mapping tool with the ability to overcome problems introduced by false negatives that are often present in fire scar data from forests that once burned frequently. I will also examine the potential bias in fire scar synchrony introduced by preferentially sampling trees with the most visible fire scars, as is often done in fire history studies.

METHODS

Study Area

A mixed conifer forest watershed of approximately 3,000 ha (hereafter referred to as Sugar Pine) was studied in the Sierra National Forest on the western slope of the southern Sierra Nevada Mountains of California just south of Yosemite National Park (Figure 1). The climate is of a Mediterranean type, characterized by warm, dry summers, and cool, wet winters. Annual mean precipitation in this area is 109.1 cm, most of which (86%) falls as snow between November and April (data from 1,560 m from 1941-2002 in Yosemite National Park). Mean monthly temperatures range from 2°C in January to 18°C in July. Soils are shallow (<1 m), well-drained, and developed in Mesozoic aged granite (Hill 1975). Several small streams run through the study area and elevations range from 1,200 – 2,000 meters above sea level. The terrain is moderately complex, though there are few areas of extreme slope nor are there major dissecting features such as large rivers or steep ridges. Mt. Speckerman rises on the east side of the study area; so much of the watershed has a general western slope aspect.

Forests in this area are comprised of ponderosa pine (*Pinus ponderosa*) (nomenclature follows Hickman 1993), sugar pine (*Pinus lambertiana*), Jeffrey pine (*Pinus jeffreyi*), incense-cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*), with a small component of Douglas-fir (*Psuedotsuga menziesii*), and black oak (*Quercus kelloggii*). Species composition varies across the study area by site conditions and stand history (Scholl and Taylor 2010).

Native American activity in the study area was likely high before European settlement. Up until 1901 the area that is now Bass Lake (approximately 9 km from the study site) was a large, lush meadow inhabited by Chuckchansi and Mono tribes, who used fire extensively to keep the forest open, encourage herbaceous growth for game animals, and produce vegetative growth conducive to basket weaving and arrow construction (Anderson 2005). This area was called Crane Valley by a detachment of the Mariposa Battalion in 1851, shortly after their "discovery" of Yosemite Valley (http://basslakeca.com/history.html). In 1901, Willow creek, which ran through Crane Valley, was dammed for the production of hydroelectric power, thus producing Bass Lake, which is still dammed today.

From 1899 to 1931, the Sugar Pine Lumber Company operated kilometers of narrow gauge railroad in and around the Sugar Pine study site. During that time, five wood burning locomotives hauled nearly 1.5 billion board feet (3.5 million cubic meters) of lumber from the forest (Johnston 1997). At the time there was not a market for incense-cedar wood, so the harvest was almost exclusively ponderosa and sugar pine. Two wood burning locomotives still run a section of these tracks today as a museum and tourist attraction outside of Yosemite National Park.

Sample collection and processing

In order to attain a geographically distributed collection of fire scars across the study area, fire scars were sampled at grid points (n=75) established at 500 m intervals, starting from a randomly chosen point (sensu Scholl and Taylor 2010). Each grid point was visited and 0-5 scars were sampled with a chainsaw within a 100 m radius of each point (approx. 3 ha search area). Emphasis was placed on objectively collecting as much fire-scarred material as possible in the search radius of each grid point. Unlike many fire history studies, trees with more scars were not preferentially selected over those with fewer. In addition to samples from the grid points, 29 samples were collected when travelling from one grid point to the next, and were included in the present analysis at their sampled location. At the time of collection, sample tree species, diameter at breast/stump height, decay class (Waddell 2002), presence of bark, and geographic coordinates were recorded. A total of 148 samples were collected from live (n=61) and dead (n=87) fire scarred material.

Fire dates were determined by sanding each sample to a high polish and cross-dating each sample (Stokes and Smiley 1968, McBride 1983) against independent master tree ring chronologies developed from increment cores from 30-50 trees without fires cars within the study area and/or nearby chronologies from Blodgett Research Forest (Stephens and Collins 2004) and the international tree ring database (www.ncdc.noaa.gov/paleo/treering.html). If possible, scar position within the annual ring was used to assign one of five seasonality categories to the fire event: 1) early earlywood (first third of the earlywood), 2) middle earlywood (second third of the earlywood), 3) late earlywood (last third of the earlywood), 4) latewood (within the latewood), or 5) dormant (on the ring boundary). Dormant scar position was interpreted as a fire after the growing season of the ring prior to the scar (late fall), rather than the early spring of the next growing season (prior to growth initiation of the next ring) (Caprio and Swetnam 1995, Scholl and Taylor 2010). Fire dates were checked by at least two technicians before being entered and summarized in FHX2 (Grissino-Mayer 2001). If samples contained too few rings to cross-date, were not able to be cross-dated, or were too decayed to sand or visualize, they were not included in the present analysis (n=30).

Spatially Explicit Fire Area Reconstructions

The time period from 1750 – 1900 was selected as a window in which to construct spatially explicit fire frequency maps for the study area. This time frame was chosen because the fire scar sample depth drops considerably prior to 1750 and fire suppression practices in this area were initiated shortly after the formation of the US Forest Service in 1905 (Scholl and Taylor 2010). There have been reports of the fire interval increasing in the second half of the 1800's due to Euro-American settlement in the Cascade Range (Everett *et al.* 2000), but Scholl and Taylor (2010) did not detect a significant difference in fire interval statistics before 1850 (pre-settlement) and 1850 – 1904 (settlement) in a similar forest type in Yosemite National Park, nor do we detect a difference in fire frequency during the second half of the 1800's. Thus, our window of time between 1750 and 1900 should adequately represent the fire regime in the study area before modern day fire suppression.

Fire scar data from 116 samples (containing 675 individual fire scars) was used to construct Spatial Mean Fire Interval (SMFI) maps for the study area for the study period. After a fire initially scars a tree, it is more sensitive to be scared by subsequent fires due to the wound left from the first scar (Kilgore and Taylor 1979). As a result, it is common to not consider a tree a potential fire "recorder" before it has been scarred for the first time. In the current study, two samples that had not scarred before 1900 were excluded from the analysis because they were not recorder samples during our study period. Of the 116 samples, 61 (52%) were extracted from live trees, and 57 (48%) were from dead snags, stumps, or remnant material (Table 1). Most of the samples (86%) were from incense-cedar and the others (14%) were from ponderosa pine. Resulting fire scar density was 0.04 samples per hectare, which is comparable to sample densities in the fire history literature which range from 0.01 – 0.08 samples per hectare (Hessl *et al.* 2007).

For each fire scar sample, its fire years and geographic coordinates were input into a spatial points data frame in the R statistical package (R Development Core Team 2010). Individual samples were treated as binary point data across the study area (Figure 1). Fire perimeter maps were constructed for each year in which four or more samples recorded a fire (n=75), to eliminate small spot fires or possible non-fire injuries (Kernan and Hessl 2010). To do this, new spatial point data frames were constructed from only the recording samples for each fire year. Samples were codes as one (recording a fire) or zero (not recording a fire). For each year, the binary point data was then interpolated to construct a grid with an estimated value between zero and one in every pixel. Two interpolation methods were used and will be compared in the following analysis:

<u>1) Inverse Distance Weighting (IDW)</u> – a deterministic, exact interpolation method that predicts a value for any unmeasured location by using the known values surrounding the prediction location. IDW is an exact interpolator, meaning the prediction surface passes exactly through the known sample locations, causing the maximum and minimum values of the interpolated surface to occur at sampled points. Measured values that are nearest to the prediction location will have greater influence on the predicted value at that unknown point than those that are farther away (Cressie 1993). Users can specify a power for IDW interpolation, which controls how quickly local influence diminishes with distance—lower power values give more influence to distant points and create smoother surfaces (Hessl *et al.* 2007). In addition to the power, users control

the number of neighbors included in the local calculations. Hessl and others (2007) and Kernan and Hessl (2010) both use IDW interpolation to create SMFI maps using a power of two and 12 nearest neighbors. These same parameters were used in the current study and the gstat package (Pebesma 2004) for the R statistical package was employed for IDW interpolations.

IDW interpolations result in a surface ranging in values from sample point minimum to sample point maximum (from zero to one in this case). In order to classify pixels as burned or unburned a threshold must be chosen as a cutoff. The proportion of scarred recorder samples relative to the total number of recording samples has been used as a threshold for fire perimeter mapping (Hessl *et al.* 2007, Kernan and Hessl 2010) as well as predictive vegetation mapping (Franklin 1998), and was employed here.

<u>2) Thin Plate Spline (TPS)</u> – a deterministic, inexact interpolation method, which is a smoothed version of a spline (an exact interpolation method). I used the TPS algorithm from the Fields package in the R statistical package (Furrer et al. 2009). This algorithm fits a thin plate spline surface to irregularly spaced data with a smoothing parameter that is chosen by generalized cross-validation method, which minimizes the sum of squared errors of the fitted surface (Burrough and McDonnell 1998). The resulting surface does not necessarily pass through the values of the sample points and generally gives a smoother fit (Craven and Wahba 1978) than exact interpolators which force the interpolated surface through the sample points.

Unlike IDW interpolations, TPS interpolated surfaces typically do not have minimums or maximums as low or high as the sample data points because the surface generally passes smoothly between data points. Even though the range of interpolated values is typically not as large as with exact interpolators, it was still necessary to choose a threshold value to determine if a pixel burned or not. We implemented two threshold rules. First we used the proportion of scarred samples relative to the total number of recording samples (the same rule used for IDW interpolations). As a more conservative threshold for fire area estimations, we also used half of the maximum value of the interpolated surface. This midpoint of interpolation values represents an objective threshold that will predict more conservative fire sizes for out dataset than the proportion of recording samples scarred value because this proportion was always less than the midpoint in interpolation values.

Each of these interpolation methods produced a map of interpolated values for each fire year between 1750-1900 that scarred at least 4 samples (n = 75 years in which 4 or more samples scarred). In each of these maps, the pixels greater than or equal to the threshold for that method were reclassified to a value of one and were inferred to burn in that fire year. Those below the threshold were reclassified to a value of zero and were inferred to have not burned. The number of recorded fires classified as outside the fire area was counted and the fire size was calculated in each map for each fire year for each interpolation method. A map representing the number of times each pixel burned was then created from the sum of these resulting fire area maps for each interpolation method (hereafter called the ‘burn number’ map). Next, a map representing the number of fire intervals was made by subtracting one from each pixel on the burn number map (hereafter called the ‘interval number”’ map).

Additionally, a ‘recording ring depth’ map was made for each interpolation method. To do this, the number of recording rings between 1750 and 1900 were calculated for each sample and the resulting values were interpolated with the same IDW and TPS methods described above (though no cutoff value was necessary). Finally, to compute a Spatial Mean Fire Interval (SMFI) map, we divided the recorder ring depth map by the interval number map (Kernan and Hessl 2010).

Spatial Mean Fire Interval map analysis

To examine the relationship of slope aspect and SMFI values from each of the SMFI maps were extracted to the 75 sample grid points. Each point was classified with a predominant aspect of north (316° - 45°), east (46° - 135°), south (136° - 225°), or west (226° - 315°). Grid points in the various aspect categories were examined for variation in SMFI using a distribution-free Kruskal-Wallis *H* test (Scholl and Taylor 2010). Histograms of the pixel values for each SMFI map were also created.

Non-spatial fire interval calculations

In addition to temporal estimates of fire occurrence derived from the above spatially explicit method, point (PFI) and composite (CFI) fire return intervals were also calculated in FHX2 (Grissino-Mayer 2001). PFI are calculated from the intervals in each sample tree separately, and represent the mean fire return interval to a single point and are a more conservative estimate of fire frequency (Kitzberger and Veblen 1997). CFI are calculated using all the samples in the study and may be filtered by counting only years that scar a certain percent of the samples (typically 10-25%). CFI are more sensitive than point records to changes in burning conditions (Dieterich 1980), but are also highly scale and sample number dependent (increasing the scale or sample number typically decreases the CFI).

To examine the presence of a potential bias in fire scar synchrony introduced by the common practice of preferentially sampling trees with the most visible scars we also calculated PFI and CFI statistics with only the samples that contained more than the mean (7) number of scars (n=38).

RESULTS

Overall, in the analysis period from 1750-1900, there were 75 years in which four or more samples scarred. During those fire years there were a mean of 89.4 recorder samples, a minimum of 26, and a maximum of 116 (Table 2). On average seven samples (8%) were scared during each fire year.

Interpolation methods had similar trends in fire shapes for fire years, but varied in the resultant fire sizes and continuity (Figure 2). Both the interpolation method as well as the threshold chosen had a large influence on the resulting predicted fire area and shape. As an exact interpolation method, inverse distance weighting (IDW) forces the prediction surface to pass through the sample points, and as a result, the predicted fire perimeters often had unburned pockets around samples that did not record a fire that were close to samples that did (Figure 2). When the same threshold was used (the proportion of recorder samples that recorded a fire relative to all recording samples, hereafter called "proportion scarred"), IDW interpolation had a lower mean fire size (884 ha) than did the thin plate spline (TPS) interpolation method (1,210 ha) (Table 3). When the same interpolation method (TPS) was used, but the threshold was changed from proportion scarred to half of the maximum value of the interpolated surface (hereafter called "half max."), the resulting fire areas were, on average, smaller (mean = 565 ha). Percent of the study area burned and fire rotation period are both a function of the area burned and followed similar trends (though a smaller average fire size yields a larger fire rotation period – the time required to burn an area equal to the study area) (Table 3).

The Spatial Mean Fire Interval (SMFI) maps from the various interpolations showed similar general trends in the sections of the study area that had the highest and lowest fire intervals, but varied in the predicted values (Figure 3). The IDW interpolation had an intermediate SMFI of 5.81 years (mean of all pixels), and showed the greatest discontinuities in the predicted values. The resulting IDW SMFI map shows clearly the "bulls eye" pattern of higher fire intervals (lower fire frequency) around most of the sample points. The TPS interpolation with a proportion scarred threshold showed the lowest mean fire interval of all the compared methods with an average of 3.12 years. Using the half max threshold, the TPS interpolation method resulted in the highest average burn interval of 7.27 years (Figure 3).

Slope aspect and fire frequency

No significant differences were detected in SMFI between plots in the four classes of slope aspect in any of the three interpolation methods ($P > 0.05$ for all tests: Kruskal-Wallis *H* test) (Figure 4). Figure 5 shows the TPS half max. burn interval map with the topography of the study area.

Seasonality

Using the position of the fire scar within the annual growth ring, we were able to infer the seasonality of 86.6% of the fire scars dated. In this area, most of the fires occurred after the growing season had ended (dormant = 51.1 %), or late in the growing season (latewood = 44.7 %). Fires occurring during the growing season were less common with 3.3% of scars occurring in the late earlywood, and 0.9 % of the scars occurring in the middle earlywood. None of the dated scars occurred in the early earlywood.

Non-spatial fire interval calculations

The point mean fire interval (PFI) was 14.3 years, which represents the average time required for fire to re-scar the same sample within the study area. The composite fire interval (CFI) for all fires (even those scarring fewer than 4 samples) was 1.1 years, and increased to 3 years when only fires that scarred 10% of the recording trees were considered. There were not enough fire events that scarred 20% of the recording samples to calculate a statistic for the 20% composited fire interval.

When we computed the same fire frequency statistics on only the samples with eight or more scars (n=38) (Figure 6), the PFI was approximately 3 years shorter (11.7) than when all the samples were used (Table 4). There was a similar reduction in the 10 % composite mean fire interval (3.3 years). With this reduced dataset, there was also an increased synchrony in fire events, leading to a 20% composite mean fire interval of 14.2 years.

DISCUSSION

Comparison of interpolation methods

As a result of the exact nature of IDW interpolations, the prediction surface must pass through the sample points. As a consequence, the resulting fire area maps for each fire year from the IDW interpolation method usually contained unburned pockets within burned areas surrounding recording samples that did not scar in that year (Figure 2). Similarly, the IDW fire number map and recording ring depth map both contained "bulls eye" discontinuities surrounding most of the sample points. An exact interpolation method will yield more accurate values at sample points, but given the nature of this dataset (with many "false negatives"), the

IDW interpolation does not appear to be the best choice for reconstructing spatial fire dynamics due to the resulting discontinuities at sample locations (Figure 3). There is similar evidence of these artifacts around sample points in the IDW fire area maps published by Hessl and others (2007) and the IDW fire interval maps published by Kernan and Hessl (2010), but these maps do not show the extreme discontinuities that resulted in the current IDW fire interval map. This is likely due to the longer fire intervals in the higher latitude forests of Washington that were analyzed in these studies. With longer fire intervals, the scarring probability for recording trees is increased (Stephens *et al.* 2010a), thus reducing the likelihood of false negatives which are the source of these discontinuities.

Thin plate splines are a good tool for smoothing noisy data (Craven and Wahba 1978), and effectively eliminated the interpolation artifacts around sample points for our dataset. Though, accuracy at sample points is sacrificed for this smoothness, and the TPS methods had greater misclassification rates of recorded fires than did the IDW interpolation method (Table 3). Comparing the two TPS interpolation methods indicates that a balance can be achieved between excessively large fire areas and recorded fire misclassification rate through the threshold chosen for pixel reclassification.

Without a known history of spatial fire dynamics during the study period, it is hard to quantitatively evaluate the accuracy of the results from this study. But we can compare the predicted fire sizes to other studies in nearby areas and with the well-accepted non-spatially explicit fire statistics calculated with the same samples. In a recent study in a nearby forest in Yosemite National Park, Scholl and Taylor estimated the mean fire size for a comparable study period to be between 203-266 ha, but also made the qualification that many of these fires burned up to the edge of their study area, so were probably larger. In this study, the TPS interpolation method using a threshold of half of the maximum predicted pixel value predicted closest to Scholl and Taylor's estimate with a mean fire size of 565 ha (Table 3). The IDW method and the TPS method with a proportion scarred threshold predicted mean fire sizes of 884 and 1,210 ha, respectively.

Overall, I was most satisfied with the TPS with the half max threshold. The IDW interpolation method was inadequate because of the artifacts of lower fire frequency created around most of the sample points due to the presence of false negatives in our dataset. The TPS method with the proportion scarred threshold predicted fire sizes that were too large in relation to the distribution of recorded fires, and I believe consistently overestimates fire size. Even though the TPS half max. method had the highest misclassification rate (16.5%), most of the samples that were misclassified were within 300 meters of the fire perimeter, which is an acceptable margin of error at the scale of this study.

Thin plate splines have promise for estimating spatial patterns of fire for areas that historically burned frequently and will likely have the presence of large numbers of false negatives in the fire scar record (Stephens *et al.* 2010a). We prefer the objectivity of using a threshold of half the maximum interpolation value, but recognize that adjustment of this threshold may be necessary to balance predictions of fire size with misclassification rates for particular study sites.

I found, as did Kernan and Hessl (2007), that the SMFI was an intermediate value between the PFI, which is a conservative estimate of fire frequency, and the CFI, which tends to estimate artificially low fire intervals (especially for large sample sizes). The SMFI of the TPS half max method (7.27 years) was only slightly higher than the 10% CFI (5.0 years), which has often been used as an accurate statistic to describe fire frequency (Stephens and Collins 2004).

Another advantage to the SMFI is that with adequate sampling density, it should be scale independent, which composited fire intervals are not.

Sampling bias and fire synchrony

My sampling strategy differed from most fire scar history studies in that I did not preferentially sample fire scared trees with the most visible scars. As objectively as possible, I sampled all viable fire scarred material within the search radius from each grid point in order to assess if sampling bias might be introduced from "cherry picking" the fire scar samples with the most visible scars. Curiously, when I analyzed the full dataset, there were not enough years in which 20% of the samples scarred to calculate this composite statistic, which is not common for fire history studies. But when I analyzed only the samples that had more than the mean number (7) of scars, there was more synchrony in fires and I was able to calculate a 20% composite statistic. This seems to be evidence that choosing the trees with the most scars a priori may create a sampling bias for fire synchrony because these particular trees may be more physiologically sensitive to scarring or possibly have a higher likelihood of scarring via their topographic position or microsite. This topic warrants further investigation, which could likely be done with existing datasets.

Other possible causes of the lower level of fire synchrony in this study include the occurrence of many small and patchy fires due to high Native American use and burning in this area, which could have been frequent enough to create very low intensity fires that did not scar most trees. Another possibility is that the probability of scarring is different in incense-cedars and pines, which most other fire history studies have typically used (Stephens and Collins 2004). Cedars lack the flammable resin often found in and around pine scars, which could reduce the likelihood of cambial damage to an incense-cedar during a fire. Additionally, ponderosa pine litter depth is on average 5 times greater than incense-cedar litter depth (van Wagtendonk *et al.* 1998) , which could reduce the intensity of surface fires under cedars and reduce the likelihood of scarring, which across many samples would reduce the synchrony of scarring in cedars.

Aspect and fire frequency

While studies of mixed conifer forests in the Blue Mountains (Heyerdahl *et al.* 2001) and the Klamath Mountains (Taylor and Skinner 2003) have found evidence that northern facing slopes burn less frequently than south facing slopes, this study, nor one conducted in a site very near (Scholl and Taylor 2010) did not find any differences in slope aspect and fire frequency. This is likely due to topography. Both studies that found differences in aspect were conducted more complex terrain than those that did not find differences. When there are discreet features that separate slope aspects (such as steep ridges or large rivers) that can effectively limit the spread of fire, then differences in fire frequency are more likely between varying aspects or topographic facets. The current study did not have extreme terrain features and the study site is dominated by Mount Speckerman rising to the east. In the absence of features that effectively stop fire spread, it is not surprising that differences in fire frequency between slope aspects was not detected.

Reconstruction of spatially explicit fire frequency maps holds great promise for informing landscape level disturbance-based adaptive management. Current forest management goals include the important idea that structural heterogeneity is key for ecosystem resilience and maintenance of species diversity (North 2012North 2012). Having a spatially explicit understanding of historical fire frequency will be valuable information as managers make pivotal decisions about how to intentionally create spatial heterogeneity that has been lost in many mixed conifer forests due to a century of homogenization from logging and fire suppression.

Table 1: Summary of fire scar samples included in this analysis

	Sugar Pine
Total samples cross dated	118
Live scars	61 (52%)
Dead scars	57 (48%)
Incense cedar scars	101 (86%)
Ponderosa pine scars	17 (14%)

Table 2: Fire scar sample summary during fire years analyzed in the 1750-1900 period (n = 75 years when 4 or more samples scarred):

	Minimum	Maximum	Mean ± SD
Number recording	26	116	89.4 ± 23.8
Numbered scarred in a single year	4	23	7.0 ± 3.6
Percent scarred in a single year	3	25	8.0 ± 4.0

Table 3: Comparison of fire size, percent of the study area predicted to burn, interpolation values, fire rotation period (Fire Rot.), spatial mean fire interval (SMFI) and misclassification percent (Miss-class %) for inverse distance weighting (IDW) and thin plate spline (TPS) interpolation methods with thresholds of the proportion of samples with a fire scar relative to the total number of recording samples in a particular year (Prop. scarred) and half of the maximum value in the interpolated grid for a particular year (Half max. value).

		Fire Size (ha)			Percent of study area burned			Maximum Interpolation value			Fire Rot. (yr)	SMFI (yr)	Miss-class %
Method	Threshold	Min.	Max.	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.	Mean ± SD			
IDW	Prop. scarred	439	1,376	884 ± 186	15	46	29 ± 6	1	1	1 ± 0	3.4	5.81	0
TPS	Prop. scarred	652	1,892	1,210 ± 271	22	63	40 ± 9	0.12	0.77	0.35 ± 0.15	2.5	3.12	3.6
TPS	Half max. value	211	1,542	565 ± 268	7	51	19 ± 9	0.12	0.77	0.35 ± 0.15	5.3	7.27	16.5

Table 4: Point and composite fire-return interval statistics for the Sugar Pine study area.

Samples included	Number of intervals	Mean FRI (yr)	Meadian FRI (yr)	SD (yr)	Min. (yr)	Max (yr)
All samples (n=116)						
Point (PFI)	500	14.3	11.0	11.3	2.0	76.0
Composite all	140	1.1	1.0	0.3	1.0	3.0
Composite 10%	27	5.0	3.0	4.5	1.0	18
Composite 20%	Not enough fire years to calculate statistics					

Samples with 8 or more scars (n=38)						
Point (PFI)	291	11.7	9	8.7	2.0	53
Composite all	121	1.2	1.0	0.7	1.0	5.0
Composite 10%	44	3.3	2.5	2.7	1.0	13
Composite 20%	5	14.2	12	9.5	1.0	24

Figure 1: Study area map

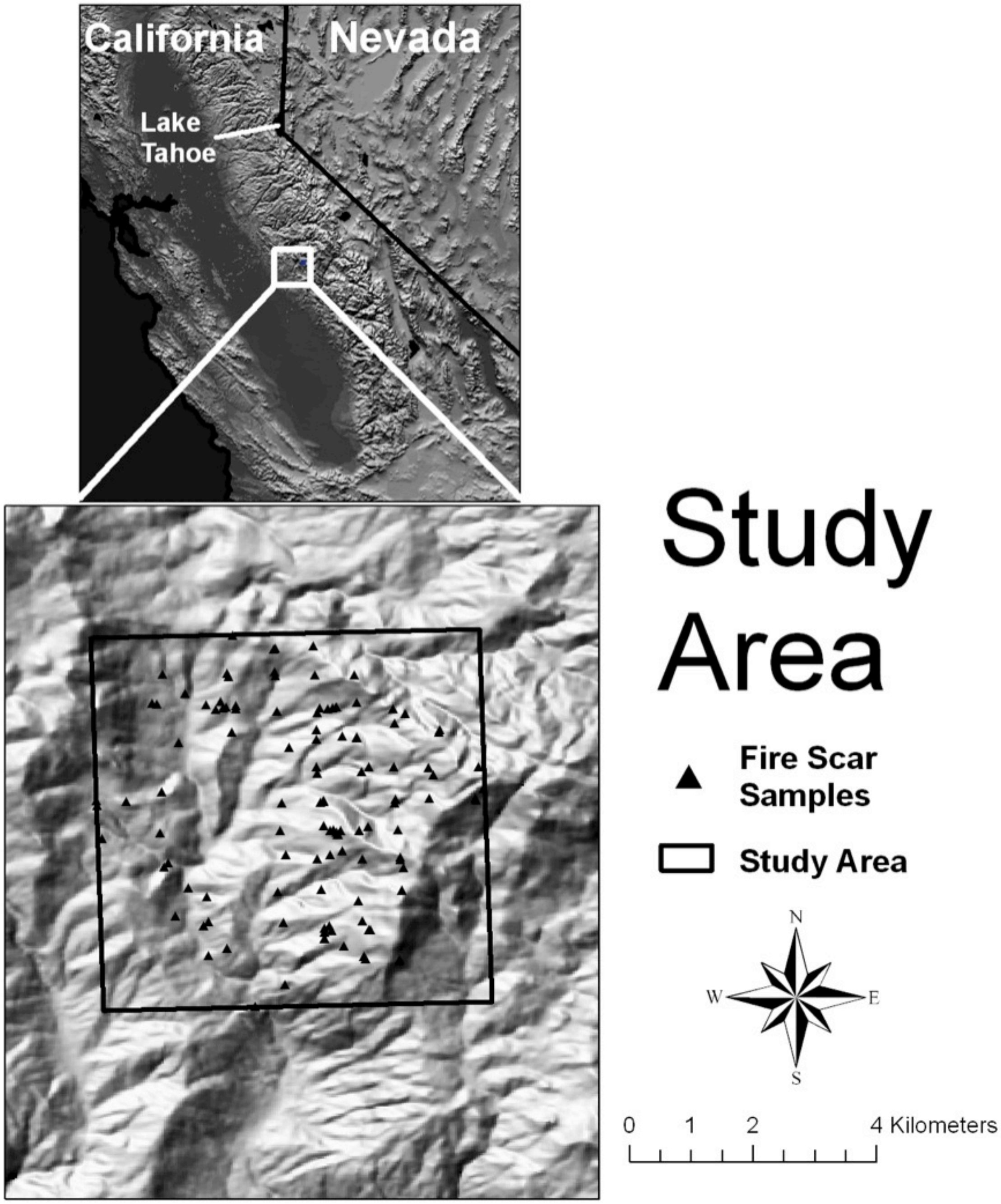


Figure 2: Fire area maps for 1844 and 1874 comparing Thin Plate Spline (TPS) with a threshold of the half the maximum value (top), TPS with the proportion of recording samples scarred threshold value (middle), and inverse distance weighting (IDW) with a proportion scarred threshold (bottom).

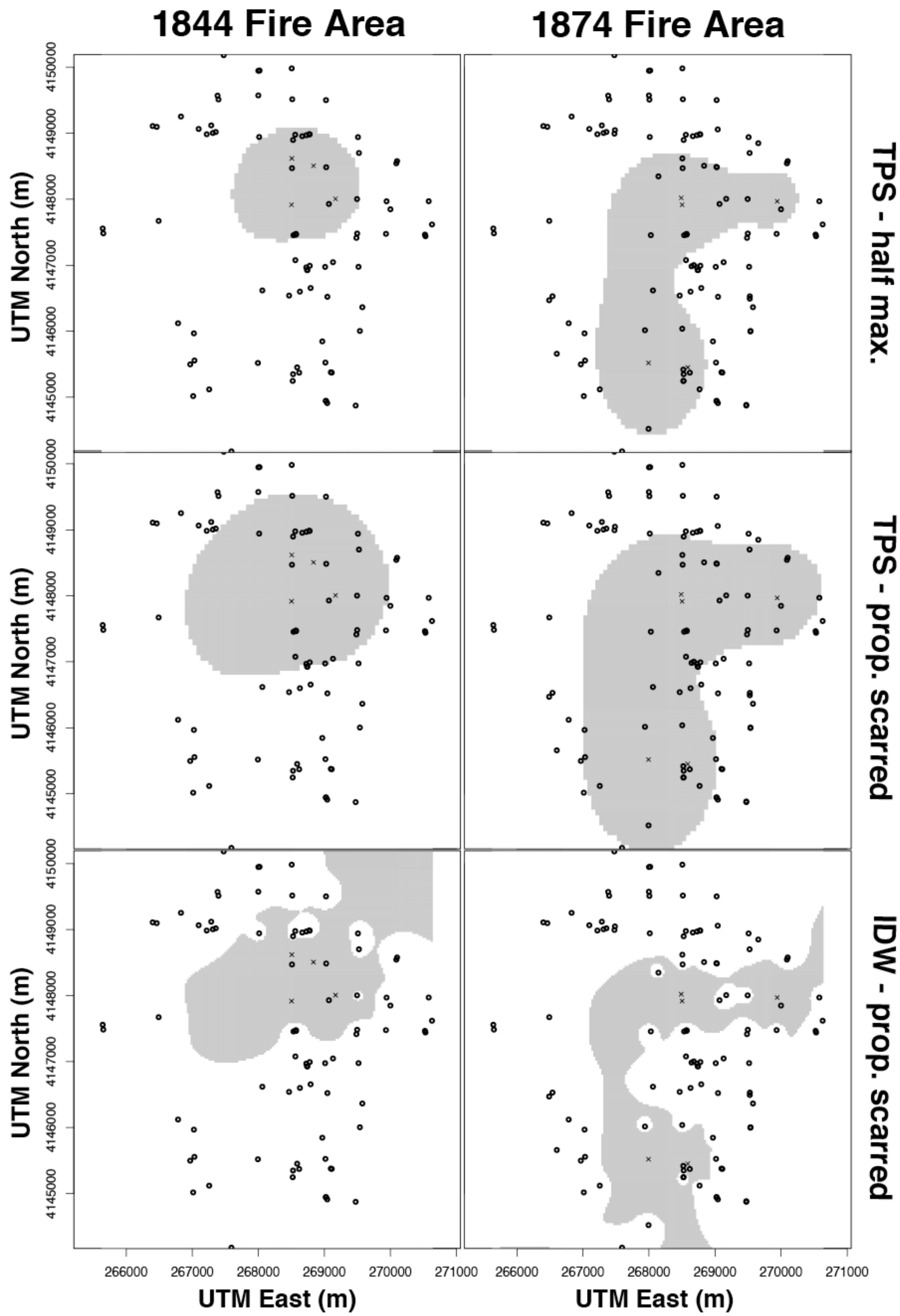


Figure 3: Comparison of burn interval maps, pixel distribution for each map, and annual area burned for IDW with a proportion scarred threshold (left), TPS with a proportion scarred threshold value (middle), and Thin Plate Spline (TPS) with a threshold of the half the maximum value (right).

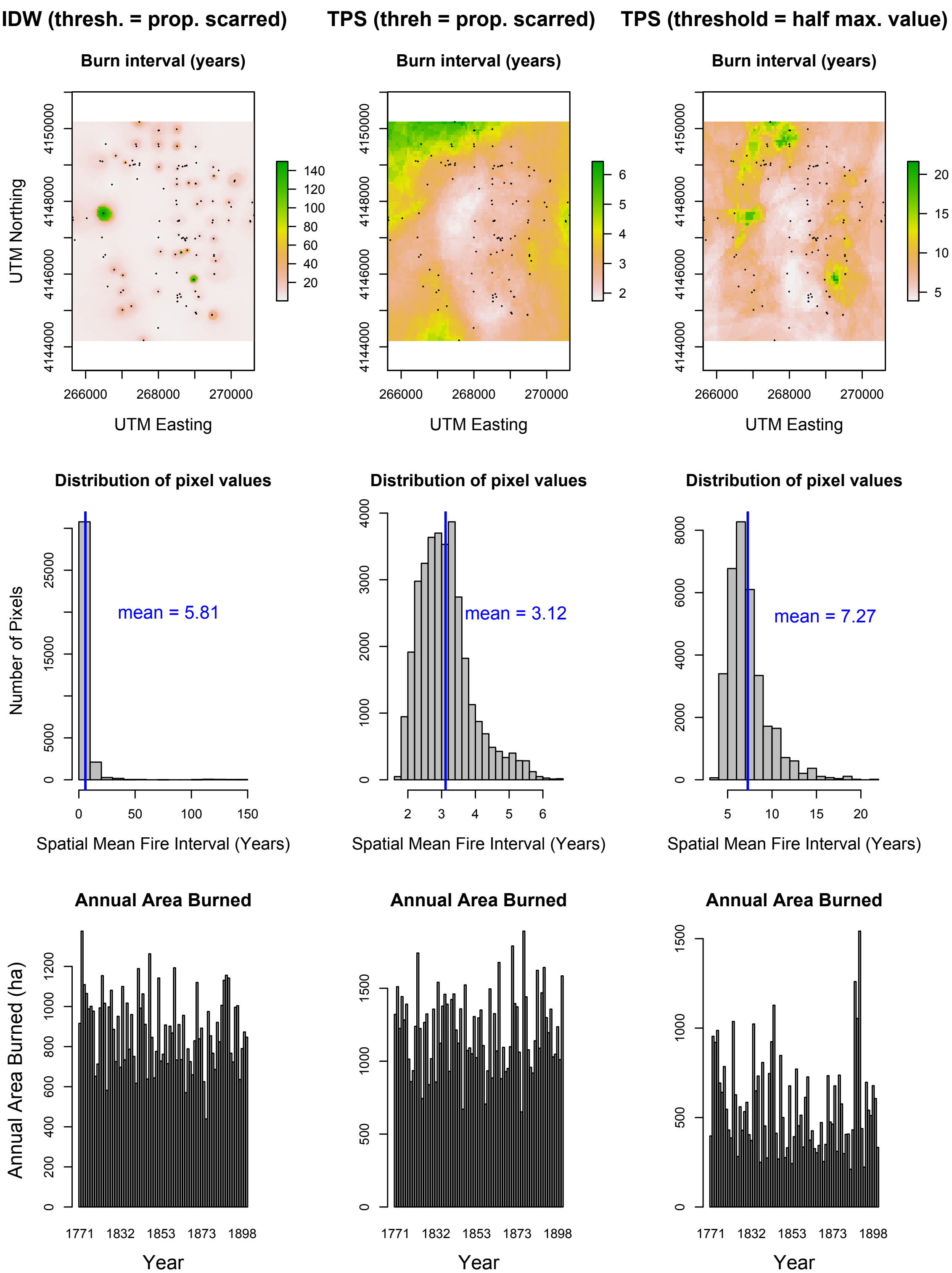


Figure 4: Spatial mean fire interval by slope aspect for each interpolation method. Horizontal lines in the boxes indicate the median, the ends of the boxes indicate the first and third quartiles, and the whiskers indicate minimum and maximum values.

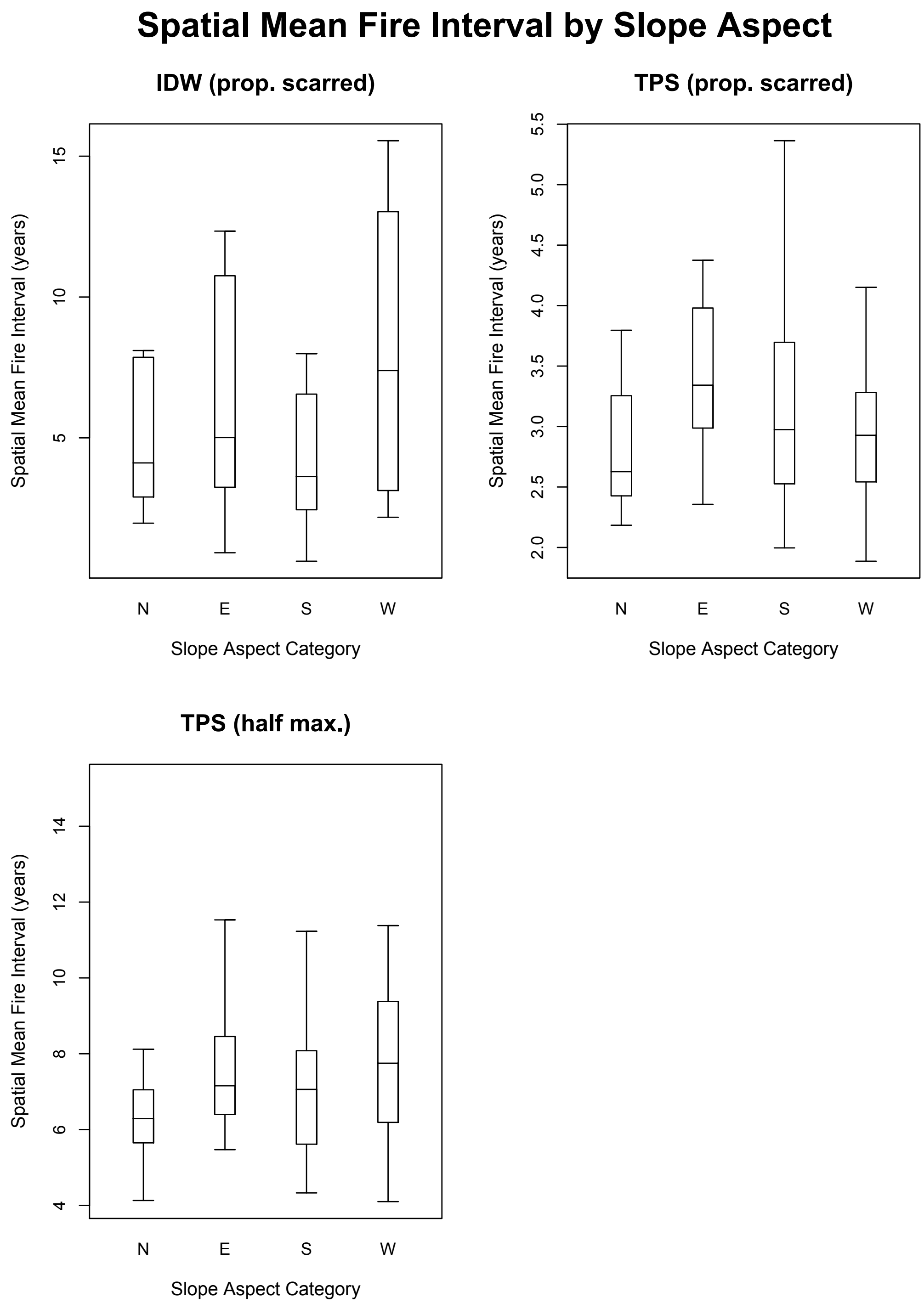
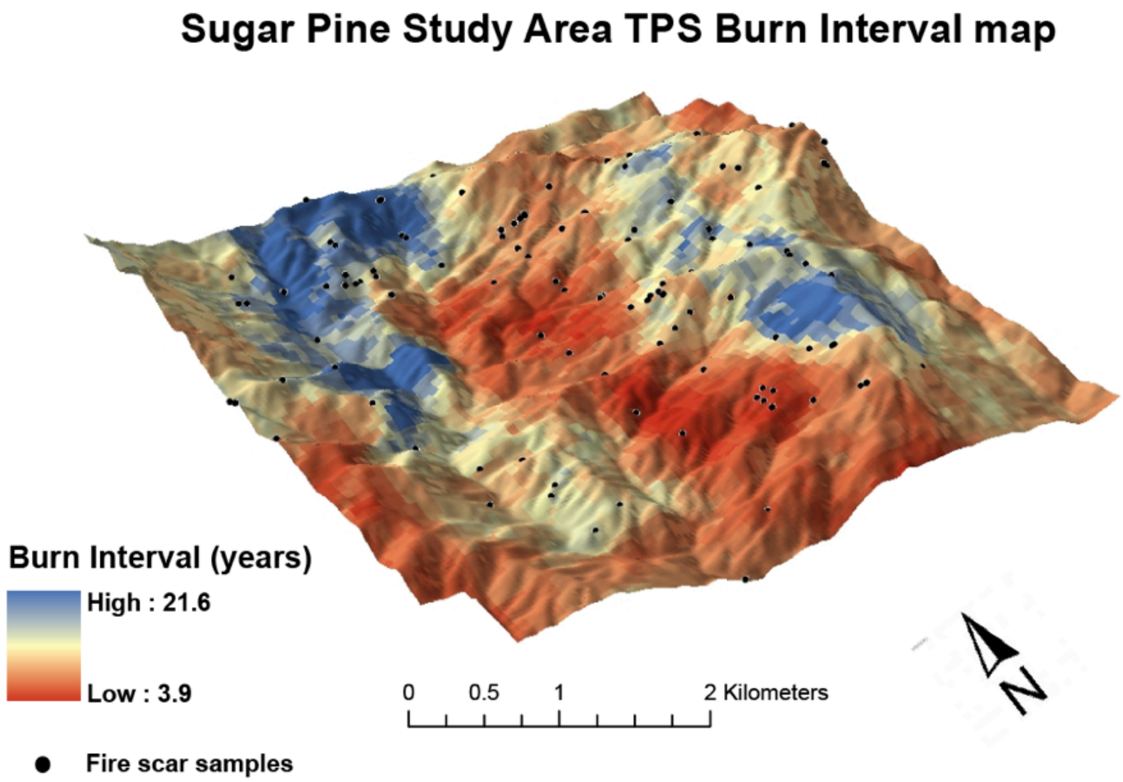
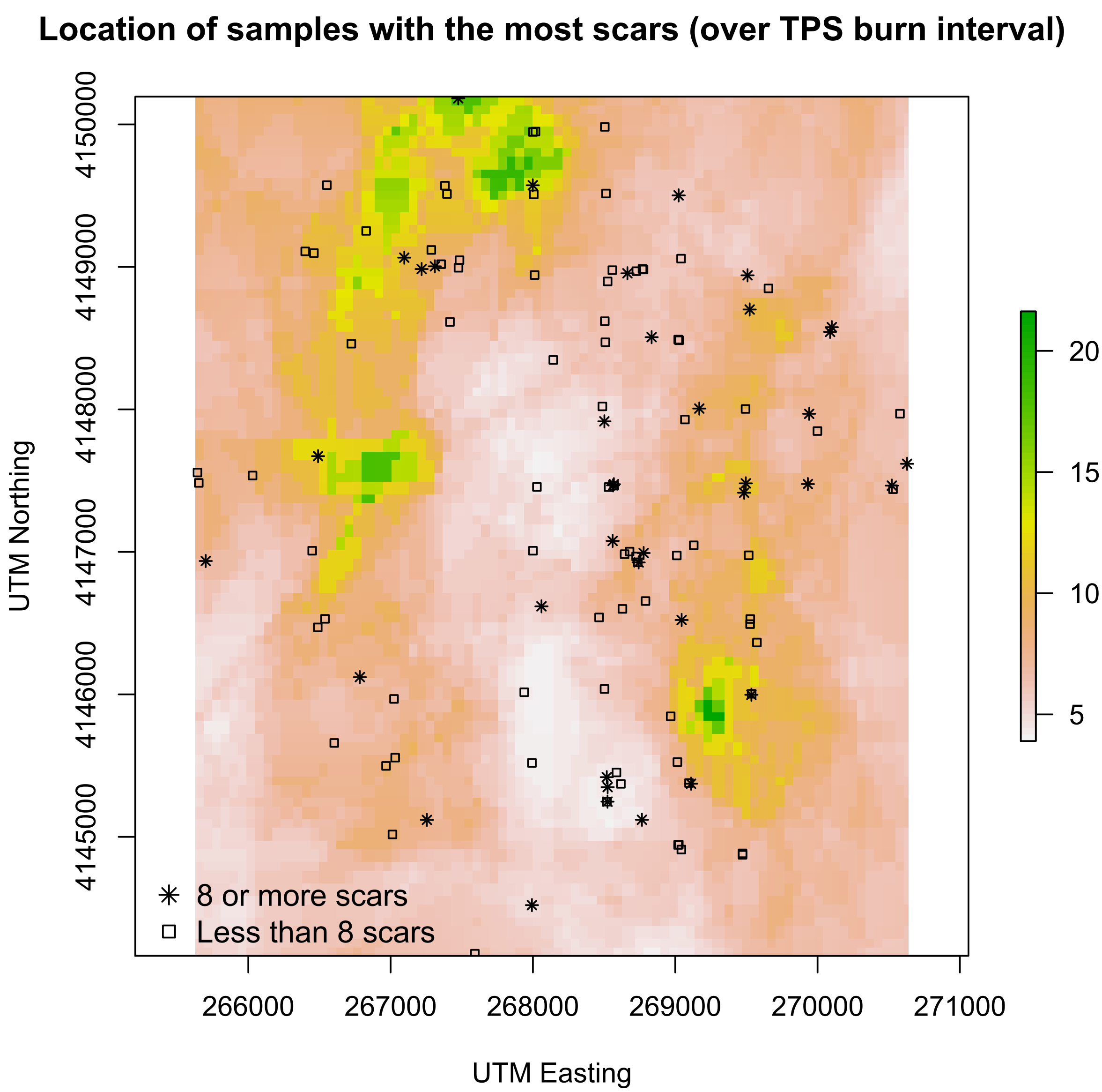


Figure 5: Spatial mean fire interval map for the TPS half maximum threshold interpolation method overlaid on topography. Fire scar sample locations are shown with black dots.



Figur 6: Location of samples containing 8 or more scars relative to those containing less than 8 scars, showing a similar distribution across the study area.



References:

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington D.C., USA.

Agee, J.K., M. Finney, and R. De Gouvenain. 1990. Forest fire history of Desolation Peak, Washington. Canadian Journal of Forest Research 20: 350-356.

Anderson, M.K. 2005. Tending the Wild: Native American Knowledge and the Management of California's Natural Resources. University of California Press, Berkeley, CA.

Bonan, G. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320: 1444.

Burrough, P.A. and R.A. McDonnell. 1998. Principles of GIS. Oxford University Press New York, NY, USA:.

Caprio, A.C. and T.W. Swetnam, editors. 1995. Proceedings: Symposium on Fire in Wilderness and Park Management. U.S. Department of Agriculture, Forest Service, 30 March - 1 April 1993, Missoula, MT.

Collins, B.M. and S.L. Stephens. 2007. Fire scarring patterns in Sierra Nevada wilderness areas burned by multiple wildland fire use fires. Fire Ecology 3: 53-67.

Covington, W.W. and M.M. Moore. 1994. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. Pages 153-181 *in* Sampson, R. N. and D. L. Adams, editors. Assessing forest ecosystem health in the Inland West. The Haworth Press, Inc.

Craven, P. and G. Wahba. 1978. Smoothing noisy data with spline functions. Numerische Mathematik 31: 377-403.

Cressie, N. 1993. Statistics for spatial data John Wiley and Sons. Inc., New York, USA.

Dieterich, J.H. 1980. The composite fire interval--a tool for more accurate interpretation of fire history. USDA, Forest Service General Technical Report RM-GTR-81, Tuscon, Arizona, USA.

Everett, R.L., R. Schellhaas, D. Keenum, D. Spurbeck, and P. Ohlson. 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. Forest Ecology and Management 129: 207-225.

Farris, C.A., C.H. Baisan, D.A. Falk, S.R. Yool, and T.W. Swetnam. 2010. Spatial and temporal corroboration of a fire-scar-based fire history in a frequently burned ponderosa pine forest. Ecological Applications 20: 1598-1614.

Franklin, J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. Journal of Vegetation Science 9: 733-748.

Fulé, P.Z., W.W. Covington, and M.M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications 7: 895-908.

Furrer, R., D. Nychka, and S. Sain. 2009. fields: Tools for spatial data. Rpackage version 6.

Grissino-Mayer, H.D. 2001. FHX2--Software for analyzing temporal and spatial patterns in fire regimes from tree rings. Tree-Ring Res. 57: 115-124.

Hassan, R., R. Scholes, and N. Ash. 2005. Ecosystems and Human Well-being: Current State and Trends, Volume 1. Island Press, Washington, DC.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary research 3: 329-382.

Hemstrom, M.A. and J.F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quaternary research 18: 32-51.
Hessl, A., J. Miller, J. Kernan, D. Keenum, and D. McKenzie. 2007. Mapping paleo-fire boundaries from binary point data: comparing interpolation methods. The Professional Geographer 59: 87-104.
Heyerdahl, E.K., L.B. Brubaker, and J.K. Agee. 2001. Spatial controls of historical fire regimes: a multiscale example from the interior west, USA. Ecology 82: 660-678.
Hickman, J.C. 1993. The Jepson Manual: higher plants of California. University of California Press, Berkeley, California.
Hill, M. 1975. Geology of the Sierra Nevada. University of California Press, Berkeley, California, USA.
Holling, C. and G. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation biology 10: 328-337.
Johnston, H. 1997. The Whistles Blow No More: Railraod Logging in the Sierra Nevada 1874-1942. Stauffer Publishing.
Kernan, J.T. and A.E. Hessl. 2010. Spatially heterogeneous estimates of fire frequency in ponderosa pine forests of Washington, USA. Fire Ecology 6: 117-135.
Kilgore, B.M. and D. Taylor. 1979. Fire history of a Sequoia mixed conifer forest. Ecology 60: 129-142.
Kitzberger, T. and T.T. Veblen. 1997. Influences of humans and ENSO on fire history of *Austrocedrus chilensis* woodlands in northern Patagonia, Argentina. Ecoscience 4: 508-520.
Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179-1188.
McBride, J.R. 1983. Analysis of tree rings and fire scars to establish fire history. Tree-Ring Bulletin 43: 51-67.
Millar, C.I., N.L. Stephenson, and S.L. Stephens. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications 17: 2145-2151.
Miller, J., H. Safford, M. Crimmins, and A. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems 12: 16-32.
North, M. 2012. Managing Sierra Nevada forests. USDA Forest Service General Technical Report PSW-GTR-237, Albany, California, USA.
Pebesma, E.J. 2004. Multivariable geostatistics in S: the gstat package. Computers & Geosciences 30: 683-691.
R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Scholl, A.E. and A.H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecological Applications 20: 362-380.
Sibold, J.S., T.T. Veblen, and M.E. Gonzalez. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. Journal of Biogeography 33: 631-647.
Stephens, S.L. and B.M. Collins. 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. Northwest Science 78: 12-23.

Stephens, S.L., D.L. Fry, B.M. Collins, C.N. Skinner, E. Franco-Vizcaíno, and T.J. Freed. 2010. Fire-scar formation in Jeffrey pine –mixed conifer forests in the Sierra San Pedro Mártir, Mexico. Canadian Journal of Forest Research 40: 1497-1505.
Stephens, S.L., R.E. Martin, and N.D. Clinton. 2007. Prehistoric fire area and emissions from California's forests, woodlands, shrublands and grasslands. Forest Ecology and Management 251: 205-216.
Stephens, S.L., J.J. Moghaddas, C. Ediminster, C.E. Fiedler, S. Hasse, M. Harrington, J.E. Keeley, E.E. Knapp, J.D. McIver, K. Metlen, C.N. Skinner, and A. Youngblood. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19: 305-320.
Stokes, M.A. and T.L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, IL, USA.
Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. Science 262: 885-888.
Swetnam, T.W., C.H. Baisan, K. Morino, and A.C. Caprio. 2000. Fire history along elevational transects in the Sierra Nevada, California. Final report to Sierra Nevada Global Change Research Program, United States Geological Survey, Biological Resources Division, Sequoia, Kings Canyon, and Yosemite National Parks, Tucson, AZ, USA.
Taylor, A.H. and C.N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management 111: 285-301.
Taylor, A.H. and C.N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications 13: 704-719.
van Wagtendonk, J.W., J.M. Benedict, and W.M. Sydoriak. 1998. Fuel bed characteristics of Sierra Nevada conifers. Western Journal of Applied Forestry 13: 73-84.
Waddell, K.L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecological Indicators 1: 139-153.