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Evolving paradigms of aspen ecology and management: impacts of stand condition and fire severity on vegetation dynamics

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Abstract. Quaking aspen (*Populus tremuloides* Michx.) comprises only a small fraction of western USA forests, yet contributes significant biological diversity and is considered by many to be the most important deciduous forest type in western North America. There is currently a high level of concern in the western United States as many seral aspen populations are declining in vigor due to drought, ungulate browsing, and lack of disturbance. It is also highly uncertain if aspen will successfully accommodate future climate warming via migration through seedling establishment, which has been assumed to be extremely rare. In recent years, fundamental assumptions concerning aspen clonal age, regeneration, and genetic diversity have been challenged, and these findings have important implications for management and persistence of aspen in western USA forests. In this study, we compared regeneration dynamics of aspen revitalization strategies (conifer removal and prescribed fire) to unplanned wildfires of low, moderate, and high severity in the Sierra Nevada, and related multiple components of pre-fire stand composition to post-fire aspen regeneration. To better understand the viability of aspen migration to accommodate future climate warming, we examined recent events of aspen seedling establishment. We found substantial evidence that greater disturbance severity yields increased aspen sprout density and growth rates, and that live conifer and/or dead aspen basal area in a stand before a fire reduces post fire sprout density. Additionally, we found evidence that aspen seedling establishment is more common than has been assumed, and represents a viable means for aspen migration. Future climate changes will present both challenges and opportunities for aspen. Increased temperatures and drought will stress existing populations, but increased high severity fire in forested areas, may provide opportunity for successful aspen migration and genet establishment. In addition to revitalizing existing aspen stands, future management goals should include the establishment of new stands in more suitable habitat.

Key words: climate adaptation; conifer removal; *Populus tremuloides*; prescribed fire; quaking aspen; regeneration; resilience; restoration; Sierra Nevada; wildfire.

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INTRODUCTION

Quaking aspen (*Populus tremuloides*) is the most widely distributed tree in North America,

yet comprises only a small fraction of the forested landscape in the western USA (Little 1971). As one of the few broadleaf deciduous trees in a conifer dominated landscape, western North

American aspen is considered a foundation species and contributes significant biological diversity in otherwise low diversity landscapes (Kay 1997). Aspen also has the broadest ecological amplitude of any western USA tree species, growing from the sagebrush (*Artemisia tridentata* ssp. *Vaseyana* (Rydb.) Beetle) steppe well into the subalpine forests and is occasionally found at tree line (Mitton and Grant 1996). Compared to conifer forests, aspen stands provide increased water yield and ecosystem resiliency to fire (Shepperd et al. 2006). For these reasons and others, many consider aspen the most important deciduous forest type in western North America (Long and Mock 2012).

Despite aspen's wide distribution and broad amplitude, currently, many aspen populations in the American West are declining in vigor due to drought, ungulate browsing, and lack of disturbance, particularly fire (Di Orio et al. 2005, Worrall et al. 2008, Rogers and Mittanck 2014). In the central Rocky Mountains, rapid and widespread mortality, referred to as "Sudden Aspen Decline" (SAD), is occurring as a result of moisture stress and hydraulic impairment (Worrall et al. 2010, Anderegg et al. 2012). Mortality such as this is projected to continue as the climate envelope for aspen diminishes in the next century (Rehfeldt et al. 2009).

In recent years, fundamental assumptions concerning aspen clonal age, regeneration, genetic diversity, and stand dynamics have been challenged (Mock et al. 2008, Long and Mock 2012, Rogers et al. 2014). Historically, it had been assumed that aspen sexual reproduction was exceedingly rare (Ellison 1943, Mueggler 1988, Romme et al. 2005), clones were thousands of years old (Einspahr and Winton 1976, McDonough 1985), stands were always successional to conifers (Baker 1925), and that genetic diversity was low. However, numerous aspen seedlings have been found after disturbance in recent years (Turner et al. 2003, Landhäusser et al. 2010, Krasnow et al. 2012, Fairweather et al. 2014) and a growing number of studies have shown that aspen stands contain much more genetic diversity than once assumed (Jelinski and Cheliak 1992, Hipkins and Kitzmiller 2004, Mock et al. 2008, De Woody et al. 2009), indicating that seedling establishment is likely more common than once thought, and that many stands are not

as ancient as once assumed. Measured by its range alone, aspen could be considered the most successful disperser in North America. There is also growing recognition that some aspen stands are successional stable and remain aspen dominated for extended periods of time (predominantly in the Colorado Plateau and western Canadian parklands, Rogers et al. 2014).

These evolving paradigms have important implications for management of western aspen. Today, aspen management focuses almost exclusively on attempting to rejuvenate existing stands, primarily through conifer removal, prescribed fire, and protection from herbivory (Shepperd 2001, Jones et al. 2005, Bates et al. 2006). Though, as our understanding of aspen ecology evolves and a warming climate threatens disturbance regimes and existing aspen populations, we need to better understand the impact and interaction of disturbance, management, and stand conditions on aspen vegetation dynamics. This information will enable more effective management and climate adaptation planning for this foundation species. In this study, conducted in the Sierra Nevada, California, we compare the impact of human management, wildfire severity, and pre-fire stand conditions on regeneration and growth of aspen populations as well as document and examine aspen seedling establishment in post-fire environments. Specifically, we address the following questions:

1. Management: How do vegetation dynamics following revitalization treatments compare to those observed following unplanned wildfires of varying severity?
2. Wildfire: How are post-wildfire aspen regeneration dynamics mediated by burn severity and pre-fire stand conditions?
3. Sexual regeneration: Under what conditions is successful aspen sexual reproduction occurring?

Aspen in the Sierra Nevada

Though the historic extent of aspen in the Sierra Nevada is unknown, it presently comprises less than 1% of the forest cover (Shepperd et al. 2006). Rogers and others (2007) hypothesize that there was a large pulse of aspen regeneration in the late 1800s due to widespread fires, dam building, mining, and logging. This may have

been the last major window of regeneration for Sierran aspen, as the 20th century marked the onset of extensive areas of fire suppression (Stephens et al. 2007) and reduced human disturbance. As a result, the predominantly seral aspen stands in the Sierra Nevada (Rogers et al. 2014) are often of advanced age and well along in the process of succession to conifers (Potter 1998). 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, indicated by a high level of conifer encroachment, major component of sagebrush understory, inadequate regeneration, and/or high levels of disease (Burton 2004). In the past decade, over 70% of assessed stands in the Sierra Nevada have been classified as moderate to highest risk of being lost (Shepperd et al. 2006, De Woody et al. 2009).

Despite our best efforts to document the conditions of current stands, we still have an incomplete understanding of how current stand conditions will impact the future trajectories of these forests (Frey et al. 2003, Rogers et al. 2010). Similarly, a better understanding of how disturbance severity and various management techniques impact aspen vegetation dynamics will be important to maintain aspen cover in the Sierra Nevada and other western USA forests (Sharik et al. 2010).

Burn severity

Recent decades have exhibited a trend in increasing fire severity in some forest types in the Sierra Nevada (Miller et al. 2009, Mallek et al. 2013) and this is likely to have important implications for post-fire vegetation dynamics. Many have advocated for the importance of severe disturbances for adequate aspen regeneration (DeByle and Winokur 1985), yet empirical studies are split on the question of fire severity on aspen regeneration, and there is no clear consensus among their findings. Bailey and Whitham (2002), Keyser et al. (2005), Fraser et al. (2004), and Wan et al. (2014) 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 and growth. In the present study, we present data from four

wildfires in California that burned aspen stands to examine sprout density and growth rates after low, moderate, and high severity wildfire.

Sexual reproduction

Even less well understood is the frequency and ecological importance of aspen seedling establishment (Romme et al. 2005, Long and Mock 2012). Given the paucity of knowledge concerning aspen seedling establishment, and the 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). A better understanding of aspen sexual reproduction dynamics and management techniques aimed at facilitating aspen migration are therefore urgently needed.

In the study that follows, we document successful aspen seedling establishment and discuss the importance and likely impact of sexual regeneration on the ability of western aspen to adapt to a rapidly changing climate

Study sites

Study sites were located in the Lake Tahoe Basin and the eastern Sierra Nevada (Fig. 1). Sample plots and transects were located in nine 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 the elevation of the current study sites (2,150–2,740 m), most precipitation occurs as snow, and averages 35–45 cm/year 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. Soils are weakly developed and well-drained decomposed

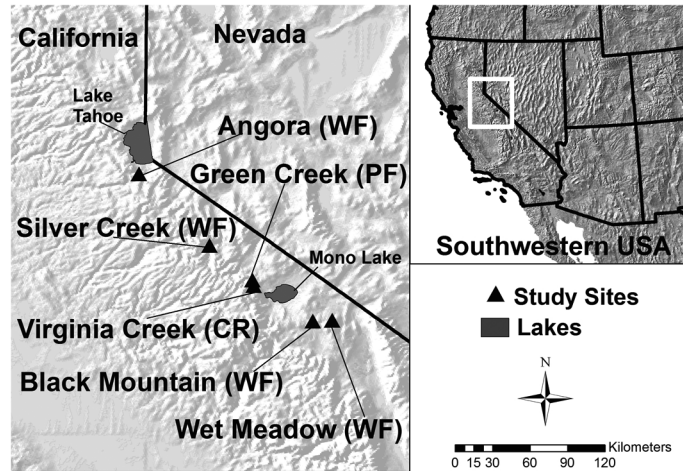


Fig. 1. Study site map: “WF” indicates wildfire, “PF” indicates prescribed fire, and “CR” indicates conifer removal treatment.

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 descriptions for Virginia Creek and Green Creek sites, see Krasnow et al. 2012). The Silver Creek, Wet Meadow, and Black Mountain study areas are mixed aspen-conifer forest, comprised primarily (90% of stems) of two species: aspen and Jeffery pine (*Pinus jefferyi* Balf.).

Table 1. Data acquisition summary: Treatment type (“Type”), transect/plot totals, aspen stand extent, and measurement year by study site.

| Site name | Type | Treatment transects | Control transects/ plots | Plot severity | | | Post treatment/ disturbance years measured | Extent of aspen stand(s) (ha) | Calendar years measured |
|------------------|-----------------|---------------------|--------------------------|---------------|----------|------|--|-------------------------------|------------------------------|
| | | | | Low | Moderate | High | | | |
| 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 Mt. | 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 | Rx fire | 3 | 3 | ... | ... | ... | 0, 1, 2, 3 | 1 | 2007, 2008, 2009, 2010 |
| Green Creek 2 | Rx fire | 5 | 2 | ... | ... | ... | 0, 1, 2, 3 | 8 | 2007, 2008, 2009, 2010 |

Notes: Low severity plots had a composite burn index (CBI) below 1.5, moderate severity plots had a CBI between 1.5 and 2.5, and high severity plots had a CBI over 2.5. Ellipses indicate no data for that cell. “Rx” stands for “Prescribed.”

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°C 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 native people, who migrated from the Great Basin during the summer (Beatty 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 that was sampled in this study is situated on the edge of Angora Creek on level ground.

METHODS

Aspen management

In 2003 the United States Bureau of Land Management 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 high lodgepole pine (*Pinus contorta* Douglas) 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 and 2, referred to hereafter as GC1 and GC2). Conifer treatments removed lodgepole pines within and surrounding each aspen stand by hand felling. This was followed by removal of tops and limbs and mechanical hauling to a landing outside of the aspen stand. Removed timber larger than 10 cm in diameter was sold as fire-wood and residual materials were chipped and scattered on site (chip depth limited to less than 5 cm). The wood volume removed from VC1, VC2, and VC3 was

85, 59, 156 m^3/ha , respectively. Prescribed fire was applied to GC1 and GC2 in the fall of 2007 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. Average flame lengths were 0.5–1 m, producing a low intensity fire with patches of moderate intensity fire (S. Volkland, *personal communication*).

Three to five permanent 30.5×1.8 m belt transects were established in treatment areas and two to three transects in untreated controls in each study site. In each transect, live aspen stems were measured in the following four size classes (SC) before treatment and up to five years after treatment: SC1 = height less than 0.45 m, SC2 = height 0.45 m to 1.5 m, SC3 = height above 1.5 m and diameter at breast height (dbh) less than 2.5 cm, and SC4 = height above 1.5 m and dbh greater than 2.5 cm (Jones et al. 2005). 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 thereafter for three years (Table 1; for more details on the treatments, see Krasnow et al. 2012).

Wildfire sampling

Areas in four recent wildfires that burned aspen stands in the Sierra Nevada were identified by personal communication with forest managers and the director of the Aspen Delineation Project (D. Burton and A. Escheveria, *personal communication*). Stands were sampled 1–6 years after burning with 50- m^2 circular plots. This plot design was preferred over transects for ease of installation and relocation of one central point, and more accurate delineation of the plot boundaries for longitudinal measures taken from a fixed central point, rather than a transect tape that can easily get blown, bent, or otherwise moved. 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 in a GIS at least 40 m apart in areas that contained aspen cover prior to the wildfire. 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 m of the fire perimeter (Silver Creek and Wet Meadow), control plots were randomly located at least 40 m apart using a GIS. In each circular 50-m² 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 dbh or basal diameter if it did not extend to breast height. Dead trees in the burned plots were determined to be alive or dead before the fire by a combination of indicators which included: presence and condition of foliage and bark, presence of basal sprouts (aspen only), and level of decay. Composite burn index (CBI; 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 (hereafter, “low severity” plots had a CBI below 1.5, “moderate severity” plots had a CBI between 1.5 and 2.5, and “high severity” plots had a CBI over 2.5). Additionally, canopy cover by species was measured with a sight tube (desitometer) on a square grid of 25 points separated by 2 m, aspect was measured with a compass, slope was measured with a clinometer, and the cover of bare rock and ground scorch were visually estimated. We defined ground scorch as areas of bare mineral soil where there was clear evidence of the combustion of coarse woody debris, which included an obvious linear shape formed by fallen limbs or tree boles that had combusted on the ground, remnant pieces of un-combusted coarse woody debris, and/or residue of light-colored ash on the soil surface. To estimate the average ramet (aspen sprout) basal diameter and height in each plot, the first 15 ramets intersected in each direction of a random azimuth from the plot center were measured ($n = 30$ in each plot). 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 (five plots in the Silver Creek Fire and four plots in the Wet Meadow

area).

Aspen sexual regeneration

One result of working in recently burned aspen forests was 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 contained a tap root and were not connected to any pre-existing lateral roots. A total of 125 aspen seedlings in three of the five sites were identified and tagged to monitor survival and growth.

Statistical analysis

Comparing aspen sprout densities between treatments and wildfire.—Aspen sprout densities were compared between revitalization treatments (conifer removal and prescribed fire; see Krasnow et al. 2012) and wildfire of low, moderate, and high severity. Sprout densities in each transect or plot for each year of measurement were converted to stems per hectare and comparisons were made both before and up to five years post treatment or wildfire. Aspen sprout densities in revitalization treatment sites were the sum of all four sprout size classes measured. The wildfire data consists of wildfires surveyed one, two, and three years post fire (Angora Fire and Silver Creek Fire; Table 1). Year zero sprout densities for the wildfires were estimated from the mean sprout densities from the unburned control plots minus any one year old sprouts (as they were initially surveyed one year post fire). Mean sprout density and 95% Poisson confidence intervals were calculated using the *pois.exact* method in the R EpiTools statistical package (Aragon 2010). Means with non-overlapping confidence intervals differed significantly ($P < 0.05$) from each other (Cumming 2009).

Comparing aspen growth rates by burn severity.— Aspen sprout basal diameter measurements were compared between fire severity classes for one, two, three, four, and six years after wildfire. Measurements of the basal diameter of 30 randomly selected ramets from each plot in each wildfire study site were used to calculate the mean and 95% confidence intervals among plots in each fire severity class. Years one through three were comprised of combined measurements from the Silver Creek and Angora Fire plots; year 4 was comprised of measurements from the Black Mountain fire plots (aspen burned only at high severity in this fire); and year 6 measurements were from the Wet Meadow Fire plots. Means with non-overlapping confidence intervals differed significantly ($P < 0.05$) from each other (Cumming 2009).

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 composite burn index, aspen basal area killed in the fire, conifer basal area alive before the fire, dead aspen basal area before the fire, and the extent of ground scorch and bare rock in each plot. A generalized linear model (glm) 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). We built a full glm model that included all of our ecologically relevant predictor variables and interactions, and model selection followed Crawley (2007). Using the performance of this full model as a benchmark, we trimmed predictor variables that were insignificant in the model as well as tried different combinations of predictors for more parsimonious models that made ecological sense. We used both the Akaike information criterion (AIC; Pinheiro and Bates 2000) and the percent of deviance explained by each model as criteria to compare models. The possibility of collinearity of independent variables impacting the parameter estimates was examined by calculating variance inflation factors (VIF) to ensure that they did not exceed four (Rogerson 2001).

Having plots located in the same fire area, it was important to understand the possible impact of pseudoreplication (Hurlbert 1984) in our study design and results (Bailey and Whitham 2002). In

an effort to make the sample units as independent as possible, sample plots were set at a minimum distance of 40 m 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 with different levels of aspen cover, 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 our regression model results, we examined empirical semivariograms of the dependent variable (sprout density two years post-fire), each predictor variable, and the model residuals in each site. 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 scorched ground and bare rock cover. Though the dependent variable, aspen sprout density, showed no evidence of spatial structure nor did the other predictor variables in either site. Similarly, the residuals of the final model did not contain recognizable spatial autocorrelation, thus we 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).

RESULTS

Stand composition from unburned controls

According to measurements from the unburned control plots at the Silver Creek and Wet Meadow sites, there were 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, 30 trees of

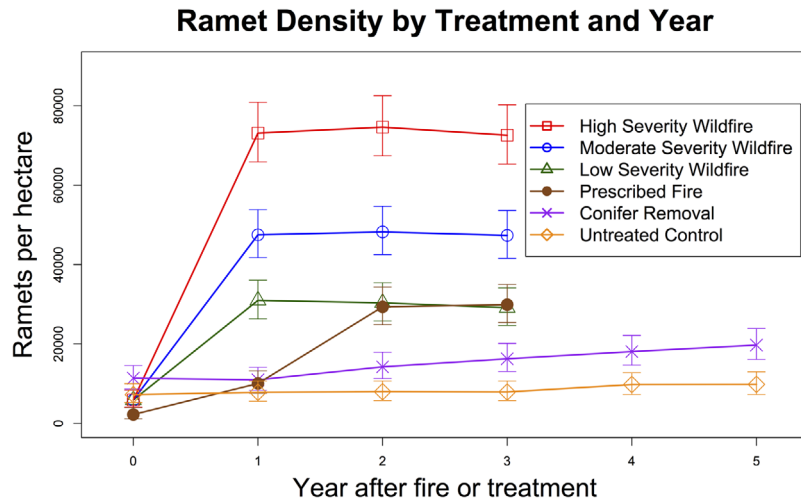


Fig. 2. Aspen ramet density is shown over time for prescribed fire, conifer removal, as well as from low, moderate, and high severity wildfire (Angora and Silver Creek Fires). Year zero sprout values for the wildfires were the mean new sprout totals from the unburned controls minus any one year old sprouts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

each species cored for age estimates at each site). The average dbh (\pm standard deviation) for live aspen and Jeffrey pine at the Silver Creek site was 20.1 (\pm 9.2) and 26.9 (\pm 14.8) cm, respectively, and at the Wet Meadow site, 19 (\pm 8.7) and 30 (\pm 12.4) cm, respectively. In addition to being larger, the cored pines were also younger than the aspen (56–86 years, mean = 73 vs. 98–140 years, mean = 113, respectively). Thirty-one percent of the aspen stems were dead, whereas for Jeffrey pine only one percent were dead. In these stands, the dead aspen basal areas makes up over 32% of the total basal area of live and dead aspen trees, whereas the dead Jeffrey pine only comprises 1.5% of the total basal area for that tree species. Mean conifer canopy cover in these unburned areas was 50% whereas mean aspen canopy cover was 31%. The mean aspen sprout density was 1,338 stems per hectare (median of 900 stems per hectare), which is close to the lower end of what would be considered adequate regeneration to restock a well-functioning aspen stand. Campbell and Bartos (2001) delineated four risk factors for the loss of aspen cover: (1) dominant aspen greater than 100 years old, (2) >25% conifer canopy cover, (3) <40% aspen canopy cover, and (4) fewer than 1,235 stems per hectare that are 1.5–4.6 m tall. Given

their advanced age, level of conifer encroachment, and the density of regeneration, these aspen stands appear to be well along on the process of succession to conifer dominated forests.

Management, wildfire, and aspen regeneration

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

Similarly, greater fire severity yielded increased aspen sprout growth rate (Fig. 3). Sprouts had the largest basal diameter after high severity wildfire, followed by moderate severity, and then low severity. These differences were

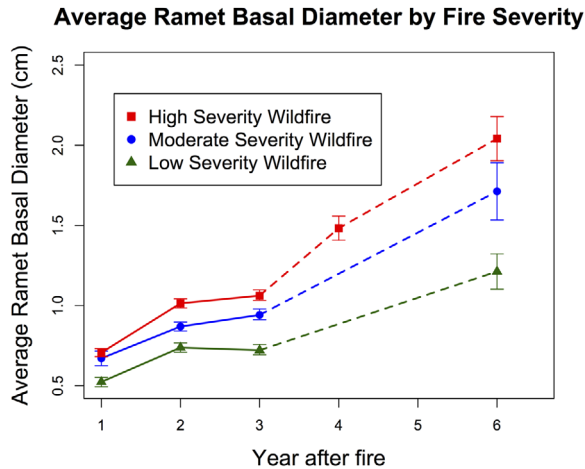


Fig. 3. Average aspen ramet basal diameter is shown over time by fire severity class. Years one to three are comprised of measurements from the Silver Creek and Angora Fire plots. Year four is comprised of measurements from the Black Mountain fire plots; and year six measurements are from the Wet Meadow Fire plots (dashed line used to indicate different sites). 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.

significant two and three years following wildfire in the Angora and Silver Creek sites and persisted for at least six years after wildfire in the Wet Meadow site (Fig. 3).

The impact of pre-fire stand composition on aspen sprout density

The generalized linear model explained 52% of the deviance in the data and supports the finding

that fire severity was the most significant predictor of aspen sprout density two years post-fire (Table 2). However, various components of the pre-fire stand condition also impact post-fire sprout density. The basal area of aspen killed by the fire had a significant positive relationship to post-fire sprout density, whereas the basal area of live conifers and basal area of dead aspen prior to the fire were both negatively correlated with post-fire sprout density. Additionally, the percentage of the plot occupied by bare rock and ground scorch was negatively associated with post-fire aspen sprout densities (all terms were significant at $P < 0.001$). Variance inflation factors for the generalized linear model did not exceed 1.1 for any independent variable, indicating that multicollinearity did not heavily impact regression coefficients (Rogerson 2001).

Sexual regeneration

Three years after the Silver Creek fire, seedling sites 1, 2, and 3 exhibited cumulative mortality rates of 100%, 12%, and 10%, respectively (Table 3). 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

Management, wildfire, and aspen regeneration

As an early seral species, aspen are poor competitors but have the ability to capitalize quickly on available resources (DeByle and Winokur 1985). These life history traits of aspen are clearly shown through the strong positive relationship between burn severity and post fire

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. An ellipsis indicates no data for that cell.

| Model term | Coefficient estimate | Standardized estimate | Z value |
|--------------------------------------|----------------------|-----------------------|---------|
| Intercept | 4.529 | ... | 142.71 |
| Composite Burn Index | 0.523 | 0.0019 | 43.12 |
| Aspen basal area killed by fire | 4.537 | 0.0010 | 31.12 |
| Rock cover | -0.020 | -0.0006 | -15.32 |
| Thousand-hour fuel combustion | -0.011 | -0.0006 | -15.93 |
| Aspen basal area dead before fire | -73.540 | -0.0014 | -7.05 |
| Conifer basal area alive before fire | -2.153 | -0.0015 | -37.73 |

Notes: All model terms were highly significant ($P < 0.001$) and the model explained 52% of the deviance in the data. The standardized estimates are calculated as: (model estimate/that variable's standard deviation)/(response variable standard deviation), and allow direct comparisons of the relative contribution of each independent variable.

Table 3. Aspen seedling data by site: Sample quantities, mortality rates, and mean height and basal diameter of seedlings. An ellipsis indicates no data for that cell.

| Metric | Seedling site | | |
|---|---------------|-------|-------|
| | 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 |

ramet density (Fig. 4). 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 (Kurzelt et al. 2007, Cocking et al. 2014). Though an interruption of the flow of auxin from shoots to roots is necessary for post-disturbance vegetative regeneration in aspen (Schier et al. 1985), it is not sufficient for sprout vigor and long-term survival, which also requires a resource rich growth environment (and protection from possible herbivores) (Shepperd et al. 2006).

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), Alberta (Fraser et al. 2004), and South Dakota (Keyser et al. 2005). There are two important caveats to this trend: (1) the presence of heavy coarse woody debris within an aspen stand and (2) heavy post-fire ungulate browsing pressure. We 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 the soil surface. Presence of this type of smoldering



Fig. 4. Photos of two-year post-fire high severity (left) and a low severity (right) fire patches from the Silver Creek Fire (2008), illustrating differences in the density and growth rate of aspen regeneration. The high severity patch (left) shows high-density regeneration, high solar radiation, death of competing conifers, and relatively tall sprouts. Conversely, the low severity patch (right) shows low-density regeneration, low solar radiation, live conifer competition, and relatively short aspen sprouts.

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.

Bailey and Whitham (2002) examined the interaction between fire severity and elk browsing after the Hochderfer wildfire in Arizona. They showed that the biomass of aspen asexual reproduction was ten times greater in areas of high burn severity compared to intermediate burn severity, but that elk selectively browsed aspen in these high severity areas, negating the enhanced regeneration. In our study there was little evidence of browse pressure after wildfires, as elk are absent and mule deer populations are low in both the Tahoe Basin and our study sites in the eastern Sierra Nevada. It should be noted that areas with high browsing pressure (from native or domestic ungulates) may be subject to similar interactions with burn severity and aspen regeneration discussed by Bailey and Whitham (2002).

In reference to fire severity, prescribed fires can be problematic for aspen revitalization because they are often burned under moderate environmental conditions resulting in reduced fire intensity and severity, compared to naturally occurring wildfires that often burn under more extreme conditions (lower fuel moistures and higher wind speeds). This is likely most problematic in aspen stands with competing vegetation that can survive low-intensity fires. If aspen regeneration is a management goal, it will likely be better met by using managed wildfires to burn rather than attempting to conduct a prescribed fire (unless high-intensity prescribed fire is possible). In areas where allowing managed wildfires may not be socially acceptable, revitalization treatments such as conifer removal may be a viable alternative (Shepperd 2001, Jones et al. 2005, Krasnow et al. 2012).

In this study of immediate trends in post-fire vegetation dynamics, we focus on sprout density and growth rates, as these metrics are likely to be valid indicators for future aspen site capture and

ability to recover from losses to browsing, pathogens, and insects (Peterson and Peterson 1992). Additionally, higher initial growth rate and leaf area has been shown to limit encroachment of competing vegetation (Landhäusser and Lieffers 1998) and maintain more of the clonal root system (DesRochers and Lieffers 2001, Landhäusser and Lieffers 2002). Though in some instances, post-disturbance stands of varying density can also converge to a common density over time (Peterson and Peterson 1992, Frey et al. 2003). Long term trends in stem density, growth rate, and competing vegetation certainly merit further investigation.

Pre-fire stand composition, disturbance severity, and aspen regeneration

We 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, soil moisture, and soil nutrients), which are reduced by competing vegetation.
2. The quantity of belowground resources stored and protected from lethal heating during the fire.

Post fire growing environment is of primary importance as our data clearly demonstrate that fire severity (measured via composite burn index; Key and Benson 2006), which directly reduces post fire biotic competition and indirectly increases soil moisture, soil temperature, and solar radiation (DeByle and Winokur 1985), is the most important predictor of post fire aspen sprout density and growth (Fig. 4, Cocking et al. 2014). Though we did not measure these resources directly, we concur that the link between fire severity and post-fire aspen density and growth is mediated through post-fire resource availability (DeByle and Winokur 1985, Bailey and Whitham 2002). 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.

Belowground resources, which are likely a combination of live root mass (DesRochers and

Lieffers 2001, Shepperd et al. 2001) and root non-structural carbohydrate reserves (Anderegg et al. 2012), have been shown to be 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, aspen 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 reduces competition and releases the stored reproductive capacity. Though this “storage” does appear to have an important temporal limit; our data show that as more aspen basal area dies before a disturbance, some resource storage is likely lost, as evidenced by lower post-fire sprout densities with higher pre-fire dead aspen basal area.

The covariates other than composite burn index in our statistical model likely impact post fire sprout density indirectly by modulating the amount of underground resources stored in each stand. Our results indicate that the basal area of live aspen killed by fire is positively related to post fire sprout density, which we attribute to increased underground resources. DesRochers and Lieffers (2001) found that the basal area of aboveground aspen is a good indication of the amount of live roots belowground, but Shepperd and others (2001) found no difference in root mass between stands that differed in aboveground biomass and growth rate. Much emphasis in aspen sprout initiation and growth has focused on the interruption of apical dominance and hormonal control under the direct control of auxin and cytokinin (Eliasson 1971, Schier 1972, Wan et al. 2006), though studies of other plant species indicate that these hormones may only be indirectly involved in sprout initiation (Ahmad et al. 1987). Though, hormonal control of sprouting is undoubtedly important, 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 into aspen stands has a negative influence on post-fire sprout density, as does the pre-fire basal area of dead aspen. Not surprisingly, we 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.

Sexual regeneration

Recent findings (Turner et al. 2003, Landhäusser et al. 2010, Fairweather et al. 2014) and our own discovery of numerous seedlings after the Silver Creek Fire indicate that aspen sexual reproduction does 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) that 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. De Woody 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. We 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, we 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 (Perry et al. 2011), and the low frequency of high soil moisture areas within these severely burned patches. 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, that were subjected to 40 years of managed wildfire. Regardless of the historic patterns of high severity fire, successful sexual regeneration and dispersal of aspen in the future will depend heavily on the occurrence of high severity fire, the availability of a seed source, proper microsite characteristics, and a future climate that will support aspen.

Aspen management in uncertain futures

Future climate changes will present both challenges and opportunities for aspen (Kula-

kowski et al. 2013). 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 genotypes to establish that may better tolerate future climates than current stands (Tuskan et al. 1996).

Forestalling the impacts of conifer encroachment to highly valued aspen stands is often the primary strategy resource agencies use to maintain the important biological diversity supported by this foundation species. This is a ‘resistance’ to change strategy (Millar et al. 2007, Stephens et al. 2010), that will likely require high resource costs, with uncertain outcomes as current environments warm. We suggest that “resilience” and “response” strategies (Millar et al. 2007) be used in tandem with resistance strategies, such as creating conditions for the establishment of new stands by allowing desirable wildfires to burn, or more directly through out-planting seedlings, transplanting ramets, or merely dispersing seed to viable microsites after disturbance.

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LITERATURE CITED

- Ahmad, A., A. S. Andersen, and K. Engvild. 1987. Rooting, growth and ethylene evolution of pea cuttings in response to choroidole auxins. *Physiologia Plantarum* 69:137–140.
- 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. <http://cran.r-project.org/web/packages/epitools/index.html>
- 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.
- Baker, F. S. 1925. Aspen in the central Rocky Mountain region. Bulletin 1291. USDA Forest Service, Washington, D.C., USA.
- 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.
- Beatty, 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.
- Campbell, R. B., and D. L. Bartos. 2001. Aspen ecosystems: objectives for sustaining biodiversity. Pages 299–307 *in* W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, compilers. *Sustaining aspen in western landscapes: symposium proceedings*. Proceedings RMRS-P-18. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Chesson, P., and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology & Evolution* 4:293–298.
- Cocking, M. I., J. M. Varner, and E. E. Knapp. 2014. Long-term effects of fire severity on oak-conifer dynamics in the southern Cascades. *Ecological Applications* 24:94–107.
- 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*. John Wiley & Sons, Chichester, UK.
- Cumming, G. 2009. *Inference by eye: reading the*

- overlap of independent confidence intervals. *Statistics in Medicine* 28:205–220.
- DeByle, N. V., and R. P. Winokur. 1985. *Aspen: ecology and management in the western United States*. General Technical Report RMRS-GTR-119. USDA Forest Service, 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.
- 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.
- 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.
- Einspahr, D. W., and L. L. Winton. 1976. *Genetics of quaking aspen*. Research Paper WO-25. USDA Forest Service, Washington, D.C., USA.
- Eliasson, L. 1971. Growth regulators in *Populus tremula* IV. Apical dominance and suckering in young plants. *Physiologia Plantarum* 25(2):263–267.
- Elliott-Fisk, D. L., T. C. Cahill, O. K. Davis, L. Duan, C. R. Goldman, G. E. Gruell, R. Harris, R. Kattelman, R. Lacey, and D. Leisz. 1997. Lake Tahoe case study. Sierra Nevada Ecosystem Project. Addendum: 217–276.
- Ellison, L. 1943. A natural seedling of western aspen. *Journal of Forestry* 41(9):767–768.
- Fairweather, M. L., E. A. Rokala, and K. E. Mock. 2014. Aspen seedling establishment and growth after wildfire in central Arizona: an instructive case history. *Forest Science* 60(4):703–712.
- 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. W., and E. J. Hopkins. 1965. *Influence of fire on aspen suckering*. Department of Forestry Publication Number 1095. Canadian Ministry of Forestry, Ottawa, Ontario, Canada.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Jelinski, D. E., and W. M. Cheliak. 1992. Genetic diversity and spatial subdivision of *Populus tremuloides* (Salicaceae) in a heterogeneous landscape. *American Journal of Botany* 79(7):728–736.
- 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. In D. Lutes, R. Keane, J. Caratti, C. Key, N. Benson, S. Sutherland, and L. Gangi, editors. FIREMON: fire effects monitoring and inventory system. General Technical Report RMRS-GTR-164. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.
- 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(11):2679–2684.
- Krasnow, K. D., A. S. Halford, and S. L. Stephens. 2012. Aspen restoration in the eastern Sierra Nevada: effectiveness of prescribed fire and conifer removal. *Fire Ecology* 8 (3):104–118.
- Kulakowski, D., M. W. Kaye, and D. M. Kashian. 2013. Long-term aspen cover change in the western US. *Forest Ecology and Management* 299:52–59.
- 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. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. *Canadian Journal of Forest Resources* 28:396–401.
- 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. Volume 1. Conifers and important hardwoods. Government Printing Office, Washington, D.C., USA.
- Long, J. N., and K. Mock. 2012. Changing perspectives on regeneration ecology and genetic diversity in western quaking aspen: implications for silviculture. *Canadian Journal of Forest Research* 42(12):2011–2021.
- Mallek, C., H. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere* 4(12):153.
- McDonough, W. T. 1985. Sexual reproduction, seeds and seedlings. Pages 25–28 in N. V. DeByle and R. P. Winokur, editors. *Aspen: ecology and management in the western United States*. General Technical Report RM-119. USDA Forest Service, Fort Collins, Colorado, USA.
- Millar, C., N. 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.
- Mitton, J. B., and M. C. Grant. 1996. Genetic variation and the natural history of quaking aspen. *BioScience* 46(1):25–31.
- 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(22):4827–4844.
- Mueggler, W. F. 1988. Aspen community types of the Intermountain Region. General Technical Report INT-250. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, A. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *Forest Ecology and Management* 262:703–717.
- Peterson, L. B., and N. M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. Special Report 1. Forestry Canada, Northern Forestry Centre, Edmonton, Alberta, Canada.
- Pinheiro, J., and D. Bates. 2000. *Mixed effects models in S and S-PLUS*. Springer, New York, New York, USA.
- Potter, D. A. 1998. Forested communities of the upper montane in the central and southern Sierra Nevada. General Technical Report PSW-GTR-169. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- 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., S. M. Landhäusser, B. D. Pinno, and R. J. Ryel. 2014. A functional framework for improved management of western North American Aspen (*Populus tremuloides* Michx.). *Forest Science* 60:345–359.
- Rogers, P. C., A. J. Leffler, and R. J. Ryel. 2010. Landscape assessment of a stable aspen community in southern Utah, USA. *Forest Ecology and Management* 259(3):487–495.
- Rogers, P. C., and C. M. Mittanck. 2014. Herbivory strains resilience in drought prone aspen landscapes of the western United States. *Journal of Vegetation Science* 25:457–469.
- 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.
- Rogerson, P. 2001. *Statistical methods for geography*. Sage, London, UK.
- 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 multi-shoot cultures from aspen roots. *Forest Science* 18:147–149.
- Schier, G. A., and R. B. Campbell. 1978. Aspen sucker regeneration following burning and clearcutting 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. General Technical Report RM-GTR-119. USDA Forest Service, Fort Collins, Colorado, USA.
- Sharik, T. L., et al. 2010. Emerging themes in the ecology and management of North American forests. *International Journal of Forestry Research* 2010:964260.
- Shepperd, W. D. 2001. Manipulations to regenerate aspen ecosystems. Pages 355–365. in W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, compilers. *Proceedings of the sustaining aspen in western landscapes symposium*, Grand Junction, Colorado, June 13–15, 2000. Proceedings RMRS-P-18. USDA Forest Service, Rocky Mountain Research Station, 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., P. Rogers, D. Burton, and D. L. Bartos. 2006. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. General Technical Report RMRS-GTR-178. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Stephens, S. L., R. E. Martin, and N. E. 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., 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.
- Tuskan, G. A., K. E. Francis, S. L. Russ, W. H. Romme, and M. G. Turner. 1996. RAPD markers reveal diversity within and among clonal and seedling stands of aspen in Yellowstone National Park, U.S.A. *Canadian Journal of Forest Research* 26:2088–2098.
- 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, H. Y., A. C. Olson, K. D. Muncey, and S. B. St Clair. 2014. Legacy effects of fire size and severity on forest regeneration, recruitment, and wildlife activity in aspen forests. *Forest Ecology and Management* 329:59–68.
- Wan, X., S. M. Landhäusser, 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.