Dendrochronological Methods to Examine Plant Competition with Changing Fire Regimes in Desert and Forest Ecosystems

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Dendrochronological Methods to Examine Plant Competition with Changing Fire Regimes in Desert and Forest Ecosystems

Rebecca Irene Lee

A thesis submitted to the faculty of Brigham Young University in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT

Dendrochronological Methods to Examine Plant Competition with Changing Fire Regimes in Desert and Forest Ecosystems

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Master of Science

Human activities are changing wildfire regimes globally through ignition, spread of invasive species, fire suppression, and climate change. Because of this, ecosystems are experiencing novel fire regimes that may alter plant growth and patterns of succession. Annual growth rings are one metric that can track changes in tree and shrub growth patterns over time in response to changing fire frequency. In Chapter 1 we explored the effects of fire on resprouting native shrubs in the Mojave Desert. Fires are becoming increasingly frequent due to the spread of highly flammable invasive grasses in the region. We monitored growth and fruit production of *Larrea tridentata* D.C. (creosote bush) on burned and unburned transects from three independent 2005 wildfires. Even though creosote has a high fire mortality rate, we found that resprouting creosote produced 4.7 times the amount of fruit and had stems that grew nearly twice as fast compared to creosote in unburned areas. Our data suggest that creosote can resprout after fire and thrives in its growth rates and reproduction in post-fire environments. In Chapter 2 we used annual Basal Area Increment to investigate how fire suppression has altered facilitation and competition interactions through stages of succession in mixed aspen-conifer forests. We found that aspen had lower growth rates in mixed aspen-conifer stands compared to aspen dominant stands. We also found that aspen growing with an associated fir tree due to facilitation had increasingly lower growth rates over time than those growing independently. Fir trees in mixed stands were facilitated over time by associated aspen trees while fir trees growing in association and independently in aspen stands showed no statistical difference from each other but grew better than independent fir trees in mixed stands. Our data suggest that restoring a more frequent fire regime will balance competitive interactions between aspen and conifer in subalpine forests.

Keywords: creosote bush, dendrochronology, fire ecology, *Larrea tridentata*, Mojave Desert, fire suppression, basal area increment, *Populus tremuloides*, *Abies lasiocarpa*
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CHAPTER 1

Creosote Growth Rate and Reproduction Increase in Postfire Environments

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ABSTRACT

Human activities are changing patterns of ecological disturbance globally. In North American deserts, wildfire is increasing in size and frequency due to fuel characteristics of invasive annual grasses. Fire reduces the abundance and cover of native vegetation in desert ecosystems. In this study, we sought to characterize stem growth and reproductive output of a dominant native shrub in the Mojave Desert, creosote bush (Larrea tridentata (DC.) Coville) following wildfires that occurred in 2005. We sampled 55 shrubs along burned and unburned transects 12 years after the fires (2017) and quantified age, stem diameter, stem number, radial and vertical growth rates, and fruit production for each shrub. The shrubs on the burn transects were most likely postfire resprouts based on stem age while stems from unburn transects dated from before the fire. Stem and vertical growth rates for shrubs on burned transects were 2.6 and 1.7 times higher than that observed for shrubs on unburned transects. Fruit production of shrubs along burned transects was 4.7-fold more than shrubs along paired unburned transects. Growth rates and fruit production of shrubs in burned areas did not differ with increasing distance from the burn perimeter. Positive growth and reproduction responses of creosote following wildfires could be critical for soil stabilization and re-establishment of native plant communities in this
desert system. Additional research is needed to assess if repeat fires that are characteristic of invasive grass-fire cycles may limit these benefits.

INTRODUCTION

Wildfires strongly influence plant community composition, biodiversity, and function across the Earth’s ecosystems (Moritz et al. 2014). Human activities are changing fire regimes globally (Bowman et al. 2011) through land use change, fire suppression, fire ignition, and climate change (Flannigan et al. 2009). North American deserts, which historically experienced fire return intervals on the century time scale, are now experiencing larger fires on shorter time intervals due to the introduction and spread of invasive annual grasses (Brooks et al. 2004). A critical question in the field of ecology is how human-altered fire regimes are changing the composition and function of native plant communities.

Native shrubs in desert ecosystems tend to be poorly adapted to fire (Brown and Minnich 1986, Abella 2009, Horn et al. 2015) and take long fire-free periods to recover. Some shrubs are able to survive and resprout after fire (Abella et al. 2009), though less is known about the growth and reproductive responses of these resprouting shrubs. Studies have examined the effects of reduced competition on growth rates of desert shrubs through mechanically thinning neighboring shrubs and annuals or the effects of fire on regenerating shrubs in other ecosystem types (Radosevich and Conard 1980, Holzapfel and Mahall 1999, McCarron and Knapp 2003, Lamont et al. 2011, Mahall et al. 2018). However, the growth rates of resprouting native desert shrubs in burned areas compared to shrubs in unburned areas are not well characterized. Concerning reproductive responses of native desert shrubs to fires, Lybbert et al. (2017) found that flower
and fruit production in regenerating generalist pollinated species tended to increase in burned areas.

Native plant response varies with burn severity and can be influenced by fuels, topoedaphic context, and weather (Whitman et al. 2018). Depending on burn severity, fire in deserts can lead to a short term increase in soil nutrients but can also lead to lower soil moisture and higher soil temperatures due to hydrophobicity and loss of vegetation and litter cover (Snyman 2003, Esque et al. 2010b, Allen et al. 2011). However, more water may become available for regenerating plants after fire due to reduced competition (Brisson and Reynolds 1994, Horn et al. 2015). Differences in burn severity at fire perimeters may result in edge effects that affect shrub growth responses. For example, shrub density on burn edges was found to be higher than shrub densities in the burn interior after fire in the Mojave Desert (Lybbert et al. 2017). The density of colonizing and resprouting shrubs in postfire arid environments has been shown to be influenced by topographic position of the burn edge, distance from the burn edge, and proximity to seed sources (Condon and Weisberg 2016). This led us to question if shrub growth and reproduction varies spatially from the edges to the interior of burned landscapes.

The Mojave Desert is located the southwestern United States and is the smallest desert in North America. The Mojave has experienced an increase in the number and size of fires in recent decades (Brooks and Matchett 2006) causing changes in plant community structure and soil resource availability (Horn et al. 2015). These adjacent burned and unburned areas provide an opportunity to study native plant regeneration and resource competition. *Larrea tridentata* (DC.) Coville, or creosote bush (hereafter just creosote), is a multi-stemmed, evergreen species that is well adapted to desert environments and consequently is one of the dominant shrubs in the Mojave and other North American desert shrublands. Creosote can establish through both sexual
and asexual reproduction (Chew and Chew 1965, McAuliffe et al. 2007). This clonal shrub is long-lived although individual shoots are replaced as aging or drought occurs (Vasek 1980). Fire results in high mortality rates but if the root system or crown survives, resprouting is known to occur (Abella 2009). Creosote provides habitat and food for desert fauna and can increase soil nutrient and water supply through fertile islands, thus playing a key role in the ecosystem (Bainbridge and Virginia 1990). Understanding the growth and reproduction patterns of this shrub in burned and unburned areas is critical to understanding postfire desert ecosystem assembly and function.

The objectives of this study were to examine and assess differences in growth and sexual reproductive effort (fecundity) of regenerating creosote in burned and unburned landscapes. We asked the following questions: 1) How does growth rate for regenerating creosote stems in burned areas differ from that of stems from unburned areas? 2) How does sexual reproductive response (fecundity) differ for postfire regenerating and unburned creosote and how does that difference change over time? and 3) Does proximity to the fire perimeter (edges vs interiors of large fires) affect growth rates of burned/regenerating creosote?

MATERIALS AND METHODS

Study Location

This study was conducted in the Beaver Dam Wash in the northeastern Mojave Desert (Latitude 37.0837 N, Longitude 114.0119 W, elevation 1216 m). The 30-year mean annual precipitation from the nearest Lytle Ranch Climate Station is 26.5 cm (Western Regional Climate Center). Dominant vegetation includes Larrea tridentata, Yucca brevifolia Engelm., Ambrosia dumosa (A. Gray) Payne, and Coleogyne ramosissima Torr.. The landscape has low
sloping ridges with young alluvial soil with a sandy loam texture. The study area experienced three separate lightning caused wildfires in the summer of 2005: Westside Complex (June, 23782 ha), Burgess 1 (July, 60 ha), and Burgess 2 (July, 543 ha). The fire boundaries were identified using the Monitoring Trends in Burn Severity project (MTBS) and corroborated in the field (Horn et al. 2015, Monitoring Trends in Burn Severity Program 2017) (Figure 1-1). Transect analysis at our study area found that creosote density was reduced more than 4-fold in burned areas compared to unburned locations (0.8 shrubs per 100 m² vs 3.5 shrubs per 100 m²), but creosote densities did not differ between burned edge or burned interior locations (Lybbert et al. 2017).

Study Design

Creosote stem growth and sexual fecundity were characterized along four pairs of transects, each 1 km in length, and positioned on the burned and unburned side of fire boundaries of each of the three wildfires (Figure 1-2). Transects were located within 200 m of the fire boundary to ensure similar physiographic conditions. Four additional transects were located in the interior of the largest fire (Westside complex, >1.5 km from burn perimeter). Pared transects were located along the tops of ridges to help standardize topographic conditions between transects and fires. Burn interiors had less topographical variation. We sampled a single creosote shrub nearest to each 200-m interval point along each transect line. Study shrubs were tagged for measurement of annual fruit number and plant growth measurements (described below). There were three to five shrubs per transect with 17 total shrubs on the unburned transects, 19 on the burn edge transects, and 19 on the burn interior transects.
Growth Measurements and Dendrochronology

To assess age and annual radial growth, one stem sample was collected from each of the 55 study shrubs 12 years after the burn (2017). To standardize collection, the longest stem from each shrub was selected. The stem was cut as close to the base of the stem as possible. In the lab, stems were trimmed to 5 cm cross-sections, keeping the segment proximal to the root collar. Samples were then surfaced with increasingly finer sandpaper (150 grit-9 micron) until individual cells could be distinguished using a stereomicroscope to facilitate the determination of ring boundaries. These samples were used for ring count analysis.

Creosote is a diffuse porous species which makes annual growth rings difficult to identify. To account for this, three analysts independently aged each cross section. The ring for the collection year (2017) was counted as a full year. An age estimate was assigned for each stem by averaging the three independent estimates. Observer age estimates differed by four or fewer years for all of the samples from burned areas with over 80% of the samples differing by two or fewer years. Creosote have been observed to resprout in the same year as the fire (Dalton 1961), hence cross sections with 13 rings were classified as postfire. Stem age estimates from unburned areas had greater count disparities because the stems were older and outer rings were much narrower and less distinct. Therefore, ages for the cross sections from unburned areas may have been underestimated. However, if this is the case, difference in growth rates between the burned and unburned areas would be even more pronounced.

We calculated stem radial growth rate by dividing the average stem diameter by the assigned stem age for each cross section (Kitchen et al. 2015). Average diameter was calculated by averaging the longest diameter and the diameter perpendicular to it dissecting at pith. Stem number was counted in 2019 to further investigate growth rate and was the number of shoots of a
shrub that connected at or belowground. Vertical growth rates were calculated by dividing the height of each shrub (measured from the ground to the tallest point) by the age of the sampled stem. All growth measurements for each shrub were averaged across individual transects.

**Fruit Counts**

Fruit production was counted on each study shrub every June from 2015 to 2017. Where fruit numbers were high, the shrub was quartered with 1 m PVC pipes connected at right angles by a four-way cross connector. The fruits from a randomly selected quarter were counted and then multiplied by four (Lybbert et al. 2017). The fruit number for each shrub was averaged by transect.

To verify that observed trends in fruit number were not due to differences in shrub size, we calculated fruit density for the 2017 data. Volume was calculated for each shrub using the shape of an inverted cone (Chew 1965).

$$volume = \frac{1}{3} (\pi \times major\ radius \times minor\ radius \times height)$$

We divided the fruit number for each shrub by its volume and then averaged those values by transect.

**Statistical Analysis**

Linear mixed effects models were used to test the effects of burn condition (unburned vs burn edge) as well as burn location (burned edge vs burned interior) on stem age, stem diameter, stem number, stem radial growth rates, height, vertical growth rates, fruit number, and fruit density. Since fruit counts were collected for more than one year, year and the interaction were also included as fixed effects for the fruit number mixed effects models. Transect pair was used
as a random effect in all models. We used data exploration techniques to examine whether model assumptions for normality and equal variance of the residuals were met (Zuur et al. 2010). When the assumptions were not met, the data were square root transformed. All data exploration and statistical analysis was performed in the program R (R Core Team 2018) with additional car and nlme packages (Fox et al. 2012, Pinheiro et al. 2017).

RESULTS

Shrub Age

Creosote along burned transects were on average four years younger than those from unburned transects (Table 1). On average, shrub stems along unburn transects began growing in 2001 (pre-fire), while burn edge and burn interior shrub stems were dated to 2005 and 2006 just after the fires.

Growth Rate and Fruit Number of Adjacent Burn Edge and Unburned Transects

Creosote generally had positive growth responses along burned transects compared to adjacent unburned transects (Figure 1-3). Average sampled stem diameter in burned areas was 25.7 mm while average sampled stem diameter from unburned areas was 13.6 mm ($F = 12.0, P = 0.04$). The average number of stems from shrubs in burned areas was 9 while those in unburned areas was 20 ($F = 128.1, P = .002$). Average creosote stem radial growth rates along the burned edges were 2.6 times greater than in unburned transects (2.1 mm/year vs. 0.8 mm/year, $F = 31.7, P = 0.01$) (Figure 1-4a). Average vertical growth rates followed a similar pattern with shrubs in burned transects growing 1.7 times more per year than shrubs in unburned transects (13.9 cm/year vs. 8.2 cm/year, $F = 18.2, P = 0.02$) (Figure 1-4b). The mean heights of shrubs were
greater on burned edges compared to unburned edges, though not statistically significant at $P \leq 0.05$ (165.3 cm vs. 133.8 cm, $F = 6.1, P = 0.1$).

Mean fruit number differed between paired burn edge and unburned transects (Figure 1-5). Creosote on burn edge transects produced on average 4.7 times more fruit per shrub than shrubs on unburned transects (4281 fruit vs. 919 fruit, $F = 18, P = 0.0007$; Figure 1-5). Mean fruit density was 5.7 times greater for shrubs in burn edge transects versus shrubs in adjacent unburned transects (1297 fruit/m³ vs. 227 fruit/m³, $F = 15.9, P = 0.03$) (Figure 1-6). The effects of fire on fruit production were consistent (not statistically different) across the three years of data collection (Figure 1-5).

**Growth Rate and Fruit Number from Burn Edges and Burn Interior Transects**

Shrubs along burned edge transects and burned interior transects were not statistically different in stem diameter ($F = 0.4, P = 0.6$), number of stems ($F = 3.9, P = 0.1$), stem radial growth rates ($F = 1.5, P = 0.3$), height ($F = 0.3, P = 0.6$), vertical growth rates ($F = 0.9, P = 0.4$), fruit number ($F = 0.1, P = 0.7$), or fruit density ($F = 0.06, P = 0.8$).

**DISCUSSION**

Wildfires are increasing in size and frequency in North American deserts with varying effects on native plant density and composition (Brooks et al. 2004, Abella 2009), but growth responses of resprouting plants after fire in North American desert shrublands are largely unstudied. Our study documents the positive effects of postfire environments on individual creosote stem growth and sexual reproduction. Our data support the conclusion that postfire environments increase creosote growth rates (Figure 1-4) and increase fruit number (Figure 1-5). However, distance to
the fire perimeter did not affect growth rates or fruit number.

**Stem Age**

The majority of sampled stems along burned transects dated postfire, while unburned stems began growing before the fire (Table 1-1). There were only two sampled stems from burned transects that dated from before the fire (16 and 13.6 years old), indicating that only a small proportion of stems survived the fire. The majority of stems found in the burned areas of our study were determined to have begun growing after the fires and most likely as postfire resprouts (Bond and Midgley 2001). Resprouting has been documented in creosote after fire (Abella 2009), and varies depending on fire severity (White 1968, Brooks et al. 2018). A study done in our same study area found that after the 2005 fires, around 21 percent of shrubs survived or resprouted along the burn edges while around 3 percent survived or resprouted along burn interior transects (Lybbert et al. 2017). The fires in our study burned in June and July when mortality is highest and number of living sprouts has been shown to be the lowest (White 1968). Along burn edges, burn severity ranged from low to moderate while the burn interior transects had a higher proportion of moderate burn severity (Monitoring Trends in Burn Severity Program 2017).

**Growth Rates in Postfire Desert Communities**

We found that creosote stems in burned areas grew faster than shrubs in unburned areas (Figure 1-4). Postfire resprouting shrubs have been shown to have rapid growth rates (Radosevich and Conard 1980). Starch stored in the roots and root crowns of resprouting shrubs is vital for the production of new stem growth (Bowen and Pate 1993, Neke et al. 2006). The
creosote in burned areas had fewer stems, therefore, the increased growth rates we observed are likely in part due to the root system and nutrient reserves that previously provided for more stems (Bond and Midgley 2001). The number and diameter of stem resprouts per plant depend on species (Neke et al. 2006), though some studies have found that for certain species, stem number decreases with increasing fire intensity and diameter increases with higher levels of stored nitrogen and non-structural carbohydrates (Moreno and Oechel 1991, Kabeya and Sakai 2005, Neke et al. 2006). The fewer but larger stems we saw in burned areas could have been influenced by fire intensity and higher levels of postfire nutrients (Esque et al. 2010). Also, despite the creosote in our burned study areas having fewer stems at their base compared to unburned areas, Horn et al. (2015) found that creosote in the same burned areas as our study had a higher canopy density (Leaf Area Index) than those in unburned areas. This emphasizes that the diameter of stems may alter canopy morphology between burned and unburned areas.

Environmental conditions can also affect the growth and survival of resprouting shrubs (Oechel and Hastings 1983). Creosote has been documented to have higher growth rates with water addition treatments or combined water and nitrogen addition treatments in controlled studies (Sharifi et al. 1988). One possible effect of the fire is increased availability of water and nitrogen due to competitive release for soil resources since most of the neighboring shrubs were removed by fire (Horn et al. 2015, Valor et al. 2018). Our study sites had on average a 79 percent decrease of creosote on burned compared to unburned transect lines (Lybbert et al. 2017). This idea is further supported by studies that found that creosote shrubs grew larger after the neighboring shrubs were removed experimentally (Mahall et al. 2018), or increased growth rates for creosote with higher rainfall (Beatley 1974, Gibson et al. 2004). Fire also creates a pulse of nutrients, especially under shrubs (Abella et al. 2009, Esque et al. 2010b, Allen et al. 2011). This
postfire increase of nutrients could also explain more rapid growth rates observed in our study (Fisher et al. 1988). Additionally, with lower shrub density after fire (Horn et al. 2015), it is possible that there may be a greater proportion of rodent burrowing underneath the regenerating shrubs, which increases soil nutrient levels, soil permeability, shrub size, and seedling survival that can increase soil resource availability linked to faster growth rates (Titus et al. 2002, Walker et al. 2015).

Increases in creosote growth rates after fire could have multiple effects on both the shrub itself and the surrounding environment. Similar to our study, Parmenter (2008) found that resprouting creosote reached their pre-fire heights 12 years after fire. It is unknown how long the growth rates of the regenerating shrubs in our study will continue. Larger creosote have been shown to be more prone to drought stress, but larger shrubs may be able to access deeper water sources (Franco et al. 1994). Also, the regenerating shrubs may be able to prevent some of the homogenization of nutrients across the landscape that is associated with disturbance and deterioration of fertile islands through loss of mature shrubs (Klemmedson and Tiedemann 1986, Fuentes-Ramirez et al. 2015). Fertile islands exist under desert shrubs and increase plant community diversity (Garcia-Moya and McKell 1970, Yeaton 1978, Rostagno et al. 1991, Schafer et al. 2012) although invasive Bromus grasses can also be facilitated by shrubs (Holzapfel and Mahall 1999). Creosote in particular have been seen to have higher abundance of the invasive annual Bromus rubens L. on the north side of the shrub (Brooks 2000), but creosote can also have negative impacts on other annual plants depending on precipitation and distance to canopy (Schafer et al. 2012).
Postfire Reproductive Response

Over the three-year study period, fruit production was consistently higher along burned transects (Figure 1-5). Nitrogen additions have been shown to increase fruit production in creosote as well as other species (Willson and Price 1980, Fisher et al. 1988, Breen and Richards 2008). Conversely, water additions reduced the amount of fruit produced in creosote (Cunningham et al. 1979, Fisher et al. 1988). Increased fruit numbers could be also be driven by higher nitrogen availability following fire (Esque et al. 2010a), competitive release for soil resources (Ehleringer 1984, Horn et al. 2015), or higher levels of nutrients from root reserves or rodents (Kabeya and Sakai 2005, Walker et al. 2015). Differences in canopy density and morphology could also contribute to the higher fruit numbers in burned areas (Figure 1-5) (Horn et al. 2015).

An increase in fruit production per plant could partially compensate for fruit loss due to reduction of shrub density after the fire. However, total fruit per unit ground area is still lower in burned areas because of loss of shrub density (Lybbert et al. 2017), which may mean that fruits and seeds are not as evenly distributed across the landscape. Creosote seeds experience rodent predation (Boyd and Brum 1983) and more seeds in a concentrated area could have impacts on seed predation and dispersal (Vander Wall 2002, Li and Zhang 2007). A more concentrated distribution of fruits and postfire plant community characteristics could also increase the dispersal of creosote seeds by wind (Maddox and Carlquist 1985, Monty et al. 2013). However, studies showing that creosote takes many years to return to pre-fire densities, could indicate that creosote establishment from seed is not always very effective after fire depending on environmental conditions or rodent predation (Abella 2009, Engel and Abella 2011, Steers and Allen 2011).
Location Within Fire Effect on Growth Rates (Edges vs Interiors of Large Fires)

We found no statistical difference in growth rates on burned edges versus burned interior locations (Figure 1-4). In this region invasive ephemeral fuels, especially after high amounts of rainfall, provide enough fuel for fire to spread between shrubs as evidenced by the high rainfall preceding the 2005 fires (Brooks and Matchett 2006). Fire severity and continuity, however, depend on the distribution and physical attributes of different invasive annual grasses present in the area (Brooks 1999, Brooks and Matchett 2006). It is possible that differences in fuel loads affected burn severity between the burn edge and interior, but there was not enough of a difference in burn severity to significantly change resprouting morphology or the growth rates (if burn severity affects growth rates). Since creosote growth is often water and nitrogen limited (Sharifi et al. 1988), the similar increased growth rates indicate that burn edges and the burn interior possibly had similar increases in water and or nutrient additions to the shrubs whether through root reserves, total amount available, or through reduced competition.

CONCLUSION

In our study system, shrubs that resprouted after fire were able to do so vigorously. Fires have been shown to dramatically decrease the abundances of certain desert shrub species (Abella 2009). This has led to concerns about increasing fire size and frequency in deserts due to shifts in invasive plant dominance. These fires could potentially lead to invasive grass-fire cycles that result in a loss of ecosystem services and loss of biodiversity (Dantonio and Vitousek 1992). However, our study indicates that fire can also provide opportunities for more rapid shrub growth and reproduction. The surviving shrubs, although fewer than pre-fire, could facilitate the re-establishment of native plants after fire, stabilize the soil, and provide wildlife habitat (Esque
et al. 2003, Bradley et al. 2006, Horn et al. 2012, Schafer et al. 2012, Soulard et al. 2013). While these increases in growth rates and reproduction occur after one fire, Brooks (2012) has shown that repeat fires further decrease abundance and diversity of native plants. The shrubs we studied were able to survive and resprout after one fire, but consecutive fires may limit re-establishment success. If this happens any of the discussed benefits of these shrubs could be lost. More research is needed to know what the effect of repeat fires are on growth rates and reproduction of these shrubs.

ACKNOWLEDGEMENTS

We would like to thank Andrew Lybbert and Kevin Horn for their help with study design and Joshua Day for his help with data collection. We are grateful for Randy Larsen and his advice with the statistical analysis and Scott Abella and an anonymous reviewer for feedback that improved the writing of the manuscript.
LITERATURE CITED


Figure 1-1 The burned and unburned side of a fire boundary in the northeastern Mojave Desert 14 years postfire.
Figure 1-2 Map of the fire extents and transect locations in the northeastern Mojave Desert study site near the Beaver Dam Wash (Latitude 37.0837 N, Longitude 114.0119 W, elevation 1216 m).
Figure 1-3 Cross sections from creosote stem samples collected from unburned (top), burn edge (bottom left), and burn interior transects (bottom right).
Figure 1-4 A Mean stem radial growth and B vertical growth rates ± SE of creosote by burn condition and burn location. Significant differences (P < 0.05) are denoted by different letters.
Figure 1-5 Average fruit number per creosote by burn condition and location for each observed year ± SE. Unburned transects compared to burn edge transects (burn condition) had $F = 18$ and $P = 0.0007$, Year had an $F = 2.0$ and $P = 0.2$, and Burn condition*Year effect $F = 0.3$ and $P = 0.7$. Burn edge compared to burn interior (burn location) had $F = 0.1$ and $P = 0.7$, Year had $F = 2.1$ and $P = 0.2$ and Burn location*Year had $F = 0.09$ and $P = 0.9$. 
Figure 1-6 Average number of fruits per unit creosote shrub volume by burn condition and location ± SE. Significant differences (P < 0.05) are indicated with differences in letter.
Table 1-1 The average creosote stem age for each transect type from the study site is shown with ± SE. The lower portion of the table shows the F-values from the mixed models. U = unburned, E= burn edge, I= burn interior. Significance is denoted with asterisks: ** $P < 0.01$.

<table>
<thead>
<tr>
<th>Fire</th>
<th>Average stem age (yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unburned (U)</td>
<td>16.6 ± 0.5</td>
</tr>
<tr>
<td>Burn edge (E)</td>
<td>12.1 ± 0.6</td>
</tr>
<tr>
<td>Burn interior (I)</td>
<td>11.1 ± 0.3</td>
</tr>
<tr>
<td>U × E</td>
<td>32.1**</td>
</tr>
<tr>
<td>E × I</td>
<td>2.9</td>
</tr>
</tbody>
</table>
CHAPTER 2

Fire Suppression Alters Competitive Balance and Forest Succession in Mixed Aspen-Conifer Forests

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Master of Science

ABSTRACT

Facilitation and competition interact over time resulting in patterns of plant community succession. Human activities are changing historical fire regimes that alter these successional cycles. We investigated the long term facilitative and competitive relationships of quaking aspen and subalpine fir growing in association across two successional aspen stages. In aspen dominant and mixed aspen-conifer forests, we sampled trees growing independently and in association. We aged trees and compared annual Basal Area Increment from both species in both stand and proximity types across time. Aspen growth rates decreased by more than half for trees in mixed stands compared to aspen dominant stands. Aspen growth rates decreased over time for trees growing in association with fir trees. Growth rates for fir trees in aspen stands were similar for both associated and independent trees and increased over time in relation to those growing independently in mixed stands. Fir trees in mixed stands associated with aspen trees had higher growth rates over time than fir trees growing independently. Our data underscores the importance of restoring natural fire regimes in mixed aspen conifer forests in order to prevent competitive imbalance that favors fir dominance and reduced aspen vigor.
INTRODUCTION

Facilitation and competition between plants influence plant community structure and succession (Callaway 1995, Brooker et al. 2008). The stress gradient hypothesis posits that facilitation tends to strengthen with greater abiotic stress and consumer pressure while competition often strengthens with greater resource availability (Bertness and Callaway 1994, Gomez-Aparicio et al. 2004). Plants can experience both competition and facilitation with environmental conditions influencing patterns of plant community succession (Callaway and Walker 1997, Maestre et al. 2009, Holmgren and Scheffer 2010). Furthermore, the influence of facilitation and competition on plant community assembly varies across time through successional stages (Cavard et al. 2011).

Established plants often facilitate younger plants in early stages of plant establishment when they are vulnerable to stress (Gomez-Aparicio et al. 2004). This usually occurs through amelioration of abiotic stresses (e.g. soil moisture deficit, high light, temperature extremes) but can also be the result of modifying biotic interactions (i.e. herbivory, seed dispersal) (Rousset and Lepart 2000, Flores and Jurado 2003, Garcia and Obeso 2003). The majority of studies documenting facilitation have focused on these early stages of plant development or spatial associations of older trees (Callaway 1992, Calder and St Clair 2012, Wright et al. 2014). Much less is known about facilitative relationships of long-lived plant species across stages of plant community succession (Cavard et al. 2011, Lebourgeois et al. 2013, Pretzsch et al. 2013, del Rio et al. 2014).

Facilitation in early stages of development can develop into competitive interactions over time because of the close proximity of associated plants (McAuliffe 1984, Calder and St Clair 2012). Even though not all facilitative relationships demonstrate this response (Butterfield 2009,
Pretzsch et al. 2013), research has shown competitive interactions emerging from facilitation in many plant species (Archer 1995, Miriti 2006, Armas and Pugnaire 2009, Calder and St Clair 2012). Plant community characteristics also affect the strength of competitive interactions between plants in close proximity due to facilitation (Cavard et al. 2011). However, more poorly documented are the facilitative to competitive transitions across the stages of plant community development and succession (Burns 1993, Landesmann et al. 2016).

Disturbance characteristics strongly impact patterns of forest succession and the role of facilitation and competition in structuring forest communities (Loucks 1970, Attiwill 1994, Schoennagel et al. 2004). Human activities are changing the frequency and size of wildfires across Earth’s ecosystems (Bowman et al. 2011). Fire suppression is lengthening forest succession cycles and increasing conifer abundance in mixed forests which may alter facilitative and competitive interactions in these forest systems (Gallant et al. 2003). Additionally, increases in competition due to lengthened disturbance return intervals can inhibit the regeneration success of early successional species that often facilitate the establishment of other species (Parsons and DeBenedetti 1979, Smith et al. 2011).

The effects of facilitation and competition responding to the effects of fire suppression on forest succession can be explored with dendrochronological methods. Conifer encroachment in oak woodlands has been studied by assessing species composition and age structure (Schriver et al. 2018). Other studies have analyzed the complex interactions of facilitation and competition among different species in different forest types by quantifying changes in growth rates over time (Callaway 1998, Cavard et al. 2011, Landesmann et al. 2016). However, lacking are studies that directly compare differences in tree growth responses of associated trees due to facilitation and how they change over stages of forest succession.
Mixed-aspen conifer forests are widespread in the northern hemisphere and demonstrate strong facilitative and competitive interactions in their successional development (Calder and St Clair 2012, St Clair et al. 2013) and have experienced fire suppression over the last 100 years (Gallant et al. 2003, Strand et al. 2009). Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) seedling establishment is facilitated at the base of quaking aspen (*Populus tremuloides* Michx.) trees, which over time creates a strong spatial association that increases aspen mortality in later stages of stand succession (Calder and St Clair 2012, Buck and St Clair 2014). The objective of this study was to examine patterns of facilitation and competition across the successional stages of mixed aspen-conifer forests using dendrochronological techniques. The following questions were explored: 1) Does increasing conifer abundance (change from aspen dominant to mixed stands) related to fire suppression reduce aspen growth rates over time? 2) Do conifer trees facilitated by aspen trees reduce aspen growth rates through competitive effects as they grow larger? 3) Does the early benefit of facilitated conifer trees growing next to aspen persist across the stages of forest succession?

**MATERIALS AND METHODS**

*Study Location*

This study was conducted at seven different sites spanning the Fishlake National Forest, Utah, USA (Figure 2-1). Elevation ranged from 2700 m to 3000 m and slope ranged from 6 to 23 degrees across the study sites. The two dominant tree species at our sites were aspen and subalpine fir. Douglas-fir (*Pseudotsuga menziesii* Carriere) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) were also present. Each site had three adjacent stand types: 1) aspen dominant stands (>80% aspen), 2) mixed aspen and conifer stands (approximately 50% of
each species), and 3) conifer dominant stands (>80% conifer). Annual average precipitation across the sites has ranged from 430 to 1014 mm and mean annual temperature has ranged from 2.6 to 5.8°C. Thirty-year normal mean annual precipitation is 64 cm with a mean annual temperature of 3.8°C (PRISM, Oregon State University, http://prism.oregonstate.edu, data created 12 Feb 2019). Fire histories for aspen and mixed conifer forests near our sites at similar elevation from 1500 CE to 2000 CE show fire-return intervals averaging between 18 and 34 years though individual intervals range from 4 years to 100 years (Heyerdahl et al. 2011). These fire histories also show a clear loss of fire post Euro-American settlement resulting in fire intervals of 150 years or more in some areas (Heyerdahl et al. 2011, Kitchen 2016).

Dendrochronology: Collection and Analysis of Samples

In most cases, two core samples were taken from each study tree. Trees were cored with an increment borer as close to the ground as possible while allowing for the turning radius of the borer handle. This height was adjusted in cases of rot, buttresses, or large branches. In the case of eight aspen, the heartwood had rotted to the point that a solid core could not be taken, so the trees were cut down and cross sections were taken instead. At each site within each stand type (aspen dominant, mixed, and conifer dominant), we classified trees into three diameter classes (approximately 14-19 cm, 20-25 cm, and 26-30 cm). For each diameter class and stand type, when present we sampled an aspen and fir pair that were in close proximity (<10 cm at soil level) and an aspen and fir that were distant from each other (more than 3 m) and thus growing independently (Figure 2-2). Adjustments were made for years to pith by using concentric ring transparencies (Applequist 1958) but adjustments were not made for coring height.
In the lab, samples were dried and glued to a slotted mount with care being taken to mount the core with a perpendicular transverse surface. Cores were sanded with increasingly finer grits to 1200-grit and 9-micron grit finishing film to create a surface where individual cells could be distinguished to facilitate crossdating. A Velmex digital sliding encoder was used with the program Measure J2X (Voortech 2005) to measure and record ring width to the nearest 0.001 mm. Samples were then crossdated visually and verified using the software COFECHA (Holmes 1983). Missing rings were rare and only occurred in the aspen and were corrected. We recorded the age of the trees as well as the age difference between the aspen and fir pairs.

For each sample, Basal Area Increment (BAI) was calculated for each ring to determine how much wood the tree produced each year and account for age-related growth. BAI was calculated with the equation from Silva, Aand, and Leithead (2010):

$$BAI = \pi (R_n^2 - R_{n-1}^2)$$

where R is the radius and n is the year of the tree ring. Because of rot or difficulty finding paired trees of the same size class, we had complete replicates (both the independent and associated tree for both stand types) only for the middle size class of aspen and for the smaller and middle size classes of the fir for the BAI analysis (16 aspen from four total sites and 32 fir from six total sites). There were not enough samples for sufficient replication from the conifer dominant stand type, so this was excluded from the analysis.

Climate Data

We used the seascorr function in the treeclim package in R (Zang and Biondi 2015, R Core Team 2018) to examine growth-climate relationships and later account for it in our analysis. We assessed precipitation, temperature, maximum vapor pressure deficit (max VPD), and the
Standardized Precipitation-Evapotranspiration Index (SPEI) to see which metric best predicted annual ring growth for both species. We found that precipitation and max VPD best explained the climatic response. Climate data was obtained through the Parameter-elevation Regression on Independent Slopes (PRISM, Oregon State University, http://prism.oregonstate.edu, data created 12 Feb 2019). Monthly values were acquired for each site by using the 4-kilometer² pixel centered over the latitude and longitude coordinates to 4 decimal points for each site.

Statistical Analysis

Mixed effects models were run to determine if there were differences in tree age between facilitated trees and the independently growing comparison tree or other main effects. For aspen, Stand Type and Proximity Type were included as fixed effects with Site as a random effect. A similar model was run for the fir ages but with Size added as a fixed effect. Assumptions of normality and heterogeneity for all mixed models were checked using qqnorm plots, histograms, and scatterplots (Zuur et al. 2010).

Forward and backward stepwise regression were used for model selection for linear regressions for the climate for each site (Pettit et al. 2018). Our global model included monthly values for both precipitation and max VPD. We also combined June, July, and August for a growing season variable, previous May through October for a 6-month warm season variable, and previous August to current August for a water year variable. To avoid overfitting, we included dummy variables in our global model and restricted variables to those that lowered the AIC value by 2 or more into our final model. Collinearity was checked using a variance inflation factor of 4. We selected climate variables that were significant across the majority of sites to include as covariates in our mixed models in order to account for climate related growth. Mixed
effects models were run for each species individually to see the effects of Year, Stand Type, and Proximity Type and their interactions. Random effects were Site/Tree for both species. Size was included as a covariate for the fir. We accounted for temporal autocorrelation of the BAI measurements by including a correlation of AR1 in our models. Data was log transformed when it did not meet the assumptions.

RESULTS

Tree Age

Aspen trees in this study established between 1845 and 1945 with a median of 1886 and a mean of 1896 (114 years old). There was no statistical difference in the age of aspen trees growing independently or in associated pairs with subalpine fir ($t = -1.06, P = 0.31$), or aspen growing in aspen dominant versus mixed stands ($t = -1.43, P = 0.18$). Fir trees in mixed stands established 11 years earlier on average than fir in aspen dominant stands (63 versus 52 years old, $t = -3.22, P = 0.004$). Facilitated fir trees were similar in age to the independent fir trees growing at the same site ($t = 0.15, P = 0.88$). There was no statistical difference in age between the smaller and larger size classes of fir ($t = 0.67, P = 0.51$). Aspen growing in association with fir trees ranged from 15 to 120 years old (Figure 2-3).

Aspen Growth Responses to Stand Conditions and Fir Associations

Aspen growing in mixed stands had on average about half the BAI of aspen growing in aspen dominated stands (394 mm²/year compared to 208 mm²/year, $F = 3.98, P = 0.003$) (Figure 2-4 & Table 2-1) a trend that was consistent across time. Aspen growing independently had an annual BAI that increased over time (Figure 2-4), while aspen growing in a facilitated pair with fir
decreased in BAI over time (Figure 2-4). These trends were true for both aspen in aspen dominant and mixed stands (Figure 2-4 & Table 2-1).

*Fir Growth Responses to Stand Conditions and Aspen Associations*

The was no statistical difference in the growth rate of fir trees growing in aspen stands that grew independently or in association with aspen trees though both increased over time (Figure 2-5). Fir trees growing in mixed stands showed lower BAI over time in contrast to firs in aspen stands (Figure 2-5 & Table 2-2). However, facilitated fir trees in mixed stands had significantly higher BAI over time than independent fir trees growing that showed a strong decrease in BAI over time (Figure 2-5).

**DISCUSSION**

This study documents the overall trends of facilitation and competition on individual and stand level relationships of mixed aspen-conifer forests over time. We found that both aspen and fir experience reduction in growth in mixed stands compared to aspen dominant stands. Aspen that are associated with a conifer have declining growth rates over time. Also, we document that subalpine fir continue to be benefited by adjacency to aspen over time, long after they leave the seedling stage.

**Tree Age**

Our results indicate that aspen facilitate conifer seedling survival at a wide variety of ages (Figure 2-3). No aspen younger than 15 in our study were found to have an associated fir tree. This suggests that aspen are able to facilitate fir across different sizes as observed for other tree
species (Callaway and Walker 1997). Additionally, on average, the fir in mixed stands established earlier than the fir in aspen stands. This is likely evidence of the different successional stages of the stand types (Chen and Popadiouk 2002). Since we chose tree pairs by size class, it could also indicate that fir in aspen dominant stands took less time to grow to the same size as those in mixed stands potentially because of facilitation.

Aspen Growth Rates over Time with Increasing Conifer Abundance

Aspen growth rates were lower in mixed stands than in aspen dominant stands (Figure 2-4). This is consistent with studies that found that aspen growth was impeded by conifers in mixed stands and actually increased when conifers in mixed stands were killed by an insect outbreak (Shepperd et al. 2001, Smith and Smith 2005, Cavard et al. 2011, Bretfeld et al. 2015, Jiang et al. 2018). Differences in environmental conditions between aspen and mixed stand types are likely one reason for this observed difference in growth rates. Studies have found that light, nutrients, mycorrhizal relations, and water relations are more optimal in aspen dominant overstory stands compared to mixed-conifer stands (Puettmann and Reich 1995, LaMalfa and Ryle 2008, Calder et al. 2011, Clark and St Clair 2011, Buck and St Clair 2012). Furthermore, Calder et al. (2012) found that the light and nutrient stress typical of conifer stands decreased aspen sapling growth. Additionally, Smith et al. (2011) documented that fire suppression increases conifer stand abundance over time and results in decreasing aspen regeneration response when stands eventually burn.

Aspen Growth Rates Related to Adjacency of Conifer Trees

Aspen with associated fir trees decreased in BAI over time while BAI increased over time in
aspen growing independently (Figure 2-4). This is consistent with another study that found that aspen growing in association with subalpine fir or with greater overstory conifer abundance were reported to have much higher mortality rates than those growing independently or in aspen dominant stands (Calder and St Clair 2012). Various benefactor species have been found to have higher mortality rates or decreases in growth as the associated plant grows older and larger (Archer 1995, Meyer et al. 2008). This is likely driven by the increasing size of the facilitated conifer trees resulting in competition for light, nutrients, and water resources (McAuliffe 1984, Calder et al. 2011).

**Fir Growth Rates Related to Stand Composition and Proximity of Aspen**

Our data show clear evidence of growth benefits by aspen to associated conifers over time in mixed stands (Figure 2-5). This is consistent with research showing that subalpine fir trees have higher survival rates when facilitated by aspen even in later stages of development (Calder and St Clair 2012). In fact, Callaway (1998) showed a decrease in growth rates of subalpine fir at high elevations when its associated benefactor tree died. These results in mixed stands support the stress gradient hypothesis that facilitation is stronger in higher stress environments (Maestre et al. 2009). Additionally, this proximity facilitation effect is observed more strongly in drier western US forests compared to wetter forests of eastern Canada (St Clair et al. 2013).

The increase in BAI of fir either associated with an aspen or growing in an aspen stand is likely due to improved resource availability. Aspen stands have been shown to have higher levels of light, and soil resources than conifer dominant stands (Price and Watters 1989, Cote et al. 2000, Buck and St Clair 2012). The soil directly at the base of aspen tend to have higher levels of soil moisture related to stem flow (Buck and St Clair 2014), which may explain some of the
positive growth benefits of firs next to aspen even in later stages of stand development (Figure 2-5). Higher light levels in relation to aspen stands have been shown to increase subalpine fir biomass (Calder et al. 2011). The growth benefit of associated fir trees from aspen in mixed stands could also be in part due to below ground processes. Commonly, plant species exude compounds from their roots that in turn are used by soil microbes and bacteria to increase nutrient availability (Bais et al. 2006). Aspen has been shown to increase the amount of mass specific carbon allocated to exudates when stressed (Karst et al. 2016). In theory, competitive stress of aspen by fir trees could increase aspen root exudation thereby benefiting associated fir trees (Teste et al. 2015).

CONCLUSION

The facilitation of aspen by conifers that develops into competition drives successional cycles in aspen-conifer forests (Calder and St Clair 2012). Historically, fire typically resets and balances the system (Shinneman et al. 2013). However, fire suppression lengthens cycles of aspen regeneration that leads to increasing conifer abundance (Bergeron and Dansereau 1993, Sampson et al. 1994, Peterson and Squiers 1995). Our data underscores the importance of restoring natural fire regimes in order to prevent further loss of aspen. Forest restoration failure or reduced vigor is possible if the aspen, because of conifer induced mortality, are not there to regenerate post-fire nor facilitate the establishment and growth of later successional species (Shepperd et al. 2001, Buck and St Clair 2014). Mitigation efforts such as prescribed fires or mechanical removal in tandem with ungulate regulation are needed to address these concerns (Di Orio et al. 2005, Maxwell et al. 2019).
ACKNOWLEDGEMENTS

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LITERATURE CITED


Kitchen, S. G. 2016. Climate and human influences on historical fire regimes (AD 1400–1900) in the eastern Great Basin (USA). The Holocene 26:397-407.


Figure 2-1 The six sites where samples were collected on the Fishlake National Forest:
Figure 2-2 Example of a subalpine fir growing at the base of quaking aspen.
Figure 2-3 Histogram of all sampled quaking aspen ages when the associated subalpine fir began growing next to them.
Figure 2-4 The annual Basal Area Increment (BAI) in mm²/year for quaking aspen of both proximity types growing in both stand types over time. Points are the raw BAI values and the lines are the best fit lines from the predicted values from the mixed model. Associated fir finished establishing next to these aspen trees in 1968.
Figure 2-5 The annual Basal Area Increment (BAI) in mm²/year for subalpine fir of both proximity types growing in both stand types over time. Points are the raw BAI values and the lines are the best fit lines from the predicted values from the mixed model.
TABLES

Table 2-1 Results from a mixed model comparing Stand type, Proximity type, and Year for quaking aspen trees. Climate variables are included as covariates. VPD measurements are the average max VPD for the variable listed. The 6-month VPD variable is the average of the previous May to previous October.

<table>
<thead>
<tr>
<th></th>
<th>Coefficient</th>
<th>SE</th>
<th>df</th>
<th>t-value</th>
<th>P-value</th>
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<td>Previous Oct vpd</td>
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Table 2-2 Results from a mixed model comparing Stand type, Proximity type, and Year for subalpine fir trees. Climate and Size variables are included as covariates. The VPD measurement is the average max VPD for the previous year’s September.

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