CLIMATE EFFECTS ON FIRE AND COMPETITIVE DYNAMICS IN MIXED-CONIFER FORESTS OF THE SIERRA NEVADA

By

Christal Johnson

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ABSTRACT

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After decades of fire suppression, California's forests face increased fire risk from the buildup of fuels. Measurements of fuel loads suggested that stands dominated by a sugar pine (Pinus lambertiana) had significantly higher loads of fine fuels than ponderosa pine (Pinus *ponderosa*). Based on fire modeling, sugar pine may also show more severe fire behavior than ponderosa. Standard fuel models did not closely correspond to the custom fuel models in either fuel loads or predicted fire behavior, suggesting a need for further development of new fuel models. Climate can impact both fire behavior and species dominance, as well as overall forest health. Dendroclimatology suggested that warmer winters, cooler summers, and cooler springs in the past year were the best growing conditions, although effects varied by species. Greater precipitation and climate moisture index tended to be beneficial to all species almost year-round. Results on climate and competition indicated that climate could affect which species had a competitive advantage - e.g. conditions that were negative for pines but neutral for other species tended to produce greater growth from interspecific competitors than from dominant pines. However, conditions that were negative for both the dominant pine and the competitor showed some tendency to favor the dominant tree, while conditions that were beneficial to both tended to favor the competitor. Future climate change may have negative impacts on growth and alter competitive dynamics. Dominant trees may show greater resilience to negative conditions, and thinning treatments to reduce competition may also reduce climate stress in all trees.

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CHAPTER 1

INTRODUCTION AND BACKGROUND

The research presented in this thesis deals with an old-growth mixed-conifer forest in the northern Sierra Nevada of California. This forest, like the rest of California's forests, has shown a shift in species composition, age structure, stand density, and fire regime following a century of fire suppression. Concerns also abound about future climate change, both in how forests will respond to changing climates, and in how they may have value as a carbon sink to mitigate climate change. This introduction presents background on some topics that are relevant to this study and this forest: old growth pines and forest restoration, climate change and forest carbon, ecological resilience, fire ecology, and fire management. At the end of the chapter, an introduction is given to the study area and the objectives of this thesis. Chapter two will focus on fire behavior and fuels, including how stand structure relates to measured fuel loads, and how custom fuel models compare to standard models. In chapter three, a dendroclimatological approach will be used to examine the effects of climate for each tree species in the area. Interactions between climate and competition will be discussed, including how differing climate conditions may alter competitive dynamics and give advantages to certain species or dominance classes.

1.1 Old growth pines and forest restoration

Old growth forests form a unique habitat in the northwestern United States. They have been shown to provide preferred nesting places for birds and squirrels, increase bat activity, boost vertebrate diversity, and support epiphytes (Kelly et al. 1993; Humes et al. 1999; Mazurek and Zielinski 2004; Meyer et al. 2005; Sillett and Pelt 2007). As far as the human dimension, old growth trees have long been a source of awe and inspiration to visitors of our national parks and

forests, adding beauty to the landscape and generating interest in ecology and conservation (Hall et al. 2011). With mounting concern about the effects of greenhouse gas emissions, old trees are also an important sink for carbon, storing more of it as they grow and helping to mitigate climate change (Harmon et al. 1990; Bowman et al. 2013). Their rings hold information about past climate and disturbances, which provides scientists with a valuable record stretching back for centuries. When they are lost, they can take hundreds of years to replace, and their rarity and ecological importance should make them a priority for thinning treatments that reduce their fire risk and competitive stress (Fiedler et al. 2007). In spite of their importance, though, the rarity of old trees makes them difficult to study, and past silviculture has generally been more focused on regeneration of young trees (Kolb et al. 2007).

In northern California and other parts of the American west, many of these trees are at risk due to an increase in high-intensity fire, and more intense competition from shade-tolerant trees (Kolb et al. 2007). In most cases, this shift is not believed to be natural; instead, it is the result of past fire exclusion and human-driven climate change (Fry and Stephens 2006; Barth et al. 2015). Climate change is causing decreased humidity, increased temperature, and more erratic precipitation, all of which contribute to increase fire severity. Models have predicted that the effects of climate change will continue to increase the seasonal severity of fires (Miller and Urban 1999; Flannigan et al. 2000; Brown et al. 2004). A history of fire exclusion has also contributed greatly to a shift in forest composition, because for much of the past century, foresters believed that stopping fires was the best way to protect forests. In many places this has led to a much denser, younger forest as shade tolerant trees grow unchecked by fire (Taylor 2000; North et al. 2007; Knapp et al. 2013). This poses a variety of problems. The denser understory provides increased competition, making it more difficult for old trees to survive

droughts, disease, and other disturbances (Fiedler et al. 2007). The buildup of fuels also makes forests more fire prone (Van de Water and North 2011). Not only is this destructive to forests, it also causes a problem when fires reach the wildland-urban interface and pose a risk to homes, infrastructure, and people. Furthermore, smoke from fires impacts air quality and poses a health risk to communities (Moeltner et al. 2013). High-intensity fires also reverse the positive impact that forests have as a carbon sink. A well-managed forest can help mitigate climate change by removing carbon from the atmosphere and storing it in the trees; a forest ravaged by fire releases all of this carbon back into the atmosphere.

There is some debate about current vs. historical fire regimes, with some claiming that there has been an increase in fire intensity and area burned (Graham et al. 2004; Miller and Safford 2008, 2012), while others claim that no such increase has occurred and current fire regimes are within the historical range of variability (Odion and Hanson 2006; Hanson and Odion 2014; Odion et al. 2014), and still others say that the answer depends on forest type and elevation (Mallek et al. 2013). The question of fire regimes and appropriate restoration treatments currently has no easy answer. My research in Chapter 2 helps to provide models of current fuel loads in the area, and possible fire behavior under various weather conditions. Of course, weather conditions may continue to shift towards increasingly severe fire weather (Miller and Urban 1999).

Restoring the climate to its historical condition may be an unrealistic goal – countries are currently struggling (and largely failing) to meet objectives just to limit warming to only 2°C, a goal set by the United Nations Framework Convention on Climate Change in the 2010 Cancún agreements (UNFCCC 2011). However, it is possible to restore forests to their historical structure and to manage them in order to promote resilience to climate change (Millar et al.

2007). How can forest managers preserve old trees, limit the number and scope of high-intensity fires, and lower stand density to restore forests to their historical structure and balance? Can our forests stay healthy in the face of a shifting climate – and how can we manage them in ways that maximize their capacity to store carbon? In order to answer these questions, extensive data is needed on how the forest responds to disturbances. We need to know how to increase forest resiliency by managing forest structure – including age, species composition, and spatial distribution. But with the looming threat of catastrophic fires, droughts, and ever increasing emissions, we do not have time to experiment. Instead, the key lies in historical data. Old trees already contain a record of centuries past, including the conditions to which species are adapted, and how those conditions may be changing (Swetnam et al. 1999). From them we can learn about historical stand structures, climate, fire regimes, competition, and responses to disturbances. My research in Chapter 3 suggests both the climate conditions that have been most favorable for tree growth in the past, and they ways that greater competition can impact climate responses.

1.2 Climate change and forest carbon

Climate change provokes growing concern among scientists, and has many implications for the future of our forests. Species ranges are shifting farther north and to higher altitudes as temperatures warm (Walther et al. 2002; Parmesan and Yohe 2003), and many fear that climate change is increasing the success of invasive species (Walther et al. 2002). There has been an increase in average lows and a decrease in the number of extremely cold days, and precipitation is becoming more erratic, with more rain falling on fewer days for a dangerous combination of droughts and flooding (Easterling et al. 2000). Droughts have already been increasingly frequent

and severe in California, and are expected to increase as low precipitation coincides with warmer conditions (Diffenbaugh et al. 2015). Fires are most likely during extremely dry summers, or in dry summers that have been preceded by wet conditions that increase productivity and fuel loads (Swetnam and Betancourt 1997), so increases in drought and increasingly erratic precipitation may contribute to fire severity. With increases in temperature and dryness, California forests are projected to lose 76-129 teragrams of carbon due to decreases in productivity and increases in fire; with an intermediate temperature increase and no change in moisture, productivity may increase at the cost of a greater increase in fires (Lenihan et al. 2007). Climate change poses a severe and immediate problem for California's forests, with the potential for positive feedback loops in which more climate change leads to more fire leads to more climate change.

Fortunately, forests have the potential to be very valuable in mitigating climate change. Climate change is driven by the emission of greenhouse gases such as carbon dioxide and methane, which are released from burning fossil fuels, converting forests to pastures, and other human activities (e.g. tropical deforestation). Trees remove carbon dioxide from the atmosphere and store the carbon. Forests store 45% of terrestrial carbon, and in 2007, North America's forests were estimated to offset 13% of the continent's emissions (Loehman et al. 2014). The issue that concerns many scientists, however, is permanence (e.g. Daniels 2010). Carbon that is stored in forests now is not stored there forever; it can easily be released through burning, and forest fires can easily cause land to emit more carbon than it stores. Hence the issue of fire management is also one of climate change mitigation.

Fire extent tends to be worst in years with more productive growing seasons (Loehman et al. 2014); fortunately, thinning treatments have been shown to be effective at reducing fire intensity and helping to maximize forest carbon stocks (Stephens et al. 2009, 2012; Hurteau et al.

2014). Lower fire intensity means that less carbon is lost, and also that the ecosystem can recover its carbon losses more quickly. However, it is important to know the fire regime of the area; thinning more than necessary, or thinning in an area with low fire risk, is likely to be neither cost-effective nor effective at reducing carbon loss. Fuel models like the one measured and tested in Chapter 2 may be useful in determining whether thinning treatments are necessary, and what the effects of thinning treatments are on fuel loads, stand structure, and carbon balance.

1.3 Ecological resilience

Forest management today must meet a growing list of objectives: reducing fuel loads and fire severity, optimizing timber harvests and sales, protecting and providing habitat for wildlife, restoring forests to historical conditions, limiting the spread of pests and pathogens, and increasing forest resilience. Resilience is the forest's ability to respond to disturbances. A forest with higher resilience shows less response to disturbances and more ability to quickly return to equilibrium after a disturbance (Millar et al. 2007; Churchill et al. 2013; Magruder et al. 2013). While past management strategies often looked to manage risks and prevent disturbances (e.g. by suppressing fires), present research recognizes that disturbances are a natural and healthy part of most systems, and avoiding disturbances only increases their impacts when they eventually become inevitable (Taylor 2010). Therefore, rather than looking to prevent fires, forest managers today instead seek to minimize the impact of fires and ensure that forests are able to maintain or quickly regain their structure and function after a fire.

Resilience is especially important in the face of climate change, because climate change may cause new disturbances and amplify the effects of current disturbances (Dale et al. 2000; Millar et al. 2007). Climate change is the ultimate disturbance, promising increases in almost

every sort of natural catastrophe imaginable. Droughts, floods, storms, fires, and increasing minimum temperatures may all be on the horizon for California's forests (Easterling et al. 2000). Currently the majority of the state is suffering from a long-term drought. In the face of such an uncertain future of potentially severe and unpredictable disturbances, managing for resiliency and climate change mitigation may be the best that California's foresters can do.

In terms of measuring resilience, tree ring data can be a valuable tool. Radial growth is a strong indicator of tree health and responses to conditions, and these responses are consistent enough between trees to allow for stand-level or forest-level inferences about relationships between growth and climate (Fritts 1976). Tree ring data can suggest responses to recent changes (both disturbances and thinning treatments) (Misson et al. 2003; Kerhoulas et al. 2013; Valor et al. 2013), as well as giving a much longer record of changing conditions and responses over time (Barth et al. 2015). The oldest tree cores date back centuries, and can provide reliable baseline information about the conditions that trees are adapted to, past disturbance regimes, and the factors that promote resilience. These historical data may be the best place to start in determining management goals (Swetnam et al. 1999). In Chapter 3, tree ring data is used to determine whether more dominant trees/trees that are less impacted by competition show greater resilience to poor climate conditions.

1.4 Fire ecology

Fire is a natural part of the western United States, and in any fire prone ecosystem, the trees show some adaptation and resistance to fire (Agee 1993). Many fire-adapted trees have thick bark that protects them from flames, but is a costly investment if fire does not strike. Some have serotinous cones that only open and disperse seeds in the presence of great heat. Others

cannot sprout unless the soil is cleared of litter and rich in minerals, as it is after a fire (Sugihara et al. 2006). Some species, such as lodgepole pine (*Pinus contorta*) are even adapted to periodic high-intensity stand replacing fires, which serve as a primary means for regeneration (Collins et al. 2007). Fire is an integral part of these ecosystems, and disrupting the natural fire regime can have profound effects on which species are able to thrive in the forest (Arno and Fiedler 2005). For example, if the natural fire regime has a fire every twenty years, but fire suppression leads to no fires for sixty years followed by three fires in one decade, this will mean the death of many stands that have become denser and shifted towards less fire-resistant species in the interval. It will also mean that even the fire-resistant species may not survive due to the increased frequency and intensity of the fires. Young trees are often less able to survive fires, so a higher frequency their resistance before the next fire strikes (Van Mantgem and Schwartz 2003). Hence it is important to know the frequency and intensity of the fire regime to which the forest is adapted.

The frequency and intensity of fires depends on a variety of factors, mainly including stand density, fuel loads, topography, and weather conditions such as temperature, humidity, and wind speed (Stephens 1998; Flannigan et al. 2000; Cansler and Mckenzie 2014). Obviously fires need fuels in order to burn, so an increased availability of fuels allows fires to grow larger, spread farther, and do more damage. In a forest, fuels are classified by their size and their height (Graham et al. 2004; Agee and Skinner 2005). Stands are at more of a fire risk if they are denser and have more surface-level fuels and lower, more accessible ladder fuels. Ladder fuels are mid-level fuels that provide fires with a "ladder" that can be used to climb from the ground up into the canopy. Once a fire has reached the canopy, it is known as a crown fire, which can spread rapidly and destroy even fire-resistant trees (Graham et al. 2004).

1.5 Fire management

Fire management requires some form of fuel reduction, which usually involves thinning treatments, sometimes followed by prescribed burning. Thinning lowers the fuel density, and burning after thinning removes downed branches and other surface fuels that might otherwise be increased by the thinning treatment (Kolb et al. 2007; Schmidt et al. 2008). Thinning around old-growth pines can decrease mortality from fires, and can improve growth, resource uptake, and drought tolerance (Kolb et al. 2007). Selecting the ideal thinning treatment can be complicated, though; even a simple decision like whether to thin around large pines, or simply thin around all large trees regardless of species, could have effects on soils and regeneration (Miesel et al. 2009). Ideally, the goal of fire management is to restore forests to a self-sustaining state where fires are within the historical range of frequency and intensity, and little human intervention is needed to maintain the process – although naturally, the historical range of frequency and intensity will vary greatly between locations (Noss et al. 2006).

As a general strategy, it is recommended that managers attempt to retain more fireresistant species and reduce fuel loads on three levels: surface, ladder, and canopy (Agee and Skinner 2005). This is achieved through the application of thinning treatments, which seek to remove trees in order to decrease stand density and fuel loads. Past studies have suggested that thinning treatments can be effective at restoring natural fire behavior, reducing fire intensity, increasing ecological resilience, and promoting understory diversity (Stoddard et al. 2011; Fulé et al. 2012; Magruder et al. 2013; Stevens et al. 2014). However, in order to be most effective, thinning crews cannot simply come in and cut trees. They must also consider the historical structure of the forest – that is, the conditions that the forest is adapted to. Consensus must be achieved on the desired spatial arrangement, species composition, and age structure. Treatments

may wish to preserve older trees, increase the relative prevalence of fire-resistant species rather than shade-tolerant species, and restore a spatially diverse clumped mosaic distribution, all of which may contribute to fire resistance and resilience (where resistance is the ability to avoid negative effects from poor conditions, and resilience is the ability to recover from negative effects) (Millar et al. 2007). Some past thinning treatments have failed to properly account for all of these variables – e.g. North et al. (2007) found that thinning treatments in the Sierra Nevada had left too many small trees, removed too many medium trees, and failed to significantly reduce the percentage of shade-tolerant white fir in the stands, which was much higher than it had been historically.

After successful thinning, reintroduction of frequent fire can be very beneficial to an ecosystem. Webster and Halpern (2010) found that 10-20 years after burning, number of species and percent plant cover increase significantly in burned areas compared to controls. In a review, Abella and Springer (2015) similarly found that thinning and burning tended to increase the number of native species present and amount of plant cover in the understory. Furthermore, while first burns caused significant mortality for shade-tolerant *Abies concolor*, second burns caused little mortality of remaining trees (Webster and Halpern 2010). Fire can also help to restore spatial diversity and age diversity (Larson and Churchill 2012). Taylor (2010) found that an old-growth Ponderosa forest in Lassen National Forest had clumps of mixed ages, possibly due to partial mortality from fires followed by regeneration. The benefits of this diversity are many: the openings between clumps make it more difficult for fires, insect outbreaks, fungi, and pathogens to spread, and the diversity of species and ages may make it more difficult for pests to find hosts (Schmidt et al. 2008; Churchill et al. 2013). Openings also allow places for tree regeneration after disturbances, and provide variable environments for a greater variety of

understory plant species (Larson and Churchill 2012; Churchill et al. 2013). Restoring historical stand structures is particularly beneficial to native plants (Stoddard et al. 2011). The variation can provide more habitats for birds, squirrels, and other wildlife, as well as increasing general biocomplexity (Carey 2003). Thinning treatments show benefits for reducing both fire severity (the focus of Chapter 2) and competition (Chapter 3).

1.6 Study area

My thesis project is based in Lassen National Forest in northern California, a mixedconifer forest with four main tree species: ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*). The Mediterranean climate of California features hot, dry summers and mild, wet winters, which makes it ideal for fires. The ecosystem features high biomass and productivity (Kelly and Goulden 2016) (which makes for high fuel loads), as well as hot and dry summers which are ideal conditions for fires. Unfortunately, California's climate is expected to get even hotter and dryer in the summers, and even wetter in the winters.

The forest falls in the northern Sierra Nevada/southern Cascades region. The Sierra Nevada is one long, continuous mountain range stretching across eastern California. The mountains are estimated to be 1-3 million years old, but still continually (if slowly) evolving from continuing geologic and sometimes volcanic activity (Mount Lassen, near the study area, is still considered an active volcano, with its last major eruption in 1915) (Beesley 2004). Elevation at the sites is ~1500 m, which is within the elevation range occupied by ponderosa and mixed-conifer forests in the Sierra Nevada.

Many of the mixed-conifer/ponderosa pine forests of the west are believed to have had a very regular fire regime historically, ignited by lightning or by Native Americans (Sowards 2007). These frequent fires kept fuel loads low, allowed fire-resistant species such as *Pinus ponderosa* to thrive, reduced competition between and from young trees, maintained nutrient cycling, and created a more open environment for ungulates (Sowards 2007). This fire regime was altered by fire suppression, creating the much denser forests that exist there today.

1.7 Thesis objectives

The project is supported by the USDA Forest Service in order to further management goals in understanding appropriate fuel reduction and restoration objectives. My aim is to use both historical and current data to assist them in increasing the health and resilience of their forests, maintaining their oldest pines, and managing for and mitigating climate change. In Chapter 2, I will use fuel measurements to build custom fuel models for the two dominant pine species of the area, and compare these custom fuel models to standard fuel models. This will aid in predicting fire behavior and designing fuel treatments for the area. In Chapter 3, I will use dendroclimatology to explore how the forest historically responded to yearly variations in temperature, precipitation, and moisture availability, and how differences in competitive stress may have affected growth and climatic resilience.

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CHAPTER 2

FUELS AND FIRE BEHAVIOR IN A SIERRA NEVADA MIXED-CONIFER FORESTS

2.1 Introduction

The ability to predict fire risk is important for both ecological and economic reasons. Thinning to remove small trees and reduce fire risk is often not profitable from the standpoint of cost of thinning vs. profit from timber sales (Ince et al. 2008). However, thinning also reduces the risk of large fires, thereby reducing fire suppression costs and introducing the possibility of payment for ecosystem services (e.g. increased carbon storage, prevented habitat destruction) (Rideout et al. 2014). The expected number and size of fires should be taken into account when planning for fire suppression costs and weighing the benefits of fuel management (Thompson et al. 2015). Many areas currently rely on standard fuel models to predict fire severity and make decisions about appropriate fuel treatments and responses to fires. More accurate modeling of fire behavior and current fuel loads may allow for more accurate prediction of fire-related costs, more fine-tuned fire response, and better informed fuel management.

Standard fuel models are popular for a number of reasons: they allow fire modeling without the need for intensive data collection, and they have already been validated by observations and experiments. In many cases, however, these fuel models may fail to accurately represent an area. Custom fuel models often are made to better represent areas with complex fuel structures (Parresol et al. 2012), areas that have not previously been modeled (Wu et al. 2011; Kucuk et al. 2015), areas where the dominant species has not previously been modeled (e.g. because it is invasive and the landscape has changed over time) (Pierce et al. 2014), and/or to

provide a more site-specific model than the standard models can offer (Elia et al. 2015). Fuel models for the wildland-urban interface are also increasingly needed (Cheyette et al. 2008; Elia et al. 2015). While 40 standard fuel models are enough to cover many places and situations (Scott and Burgan 2005), they are not nearly enough to cover every geographic region and species composition, which may significantly impact fuel loads and fire behavior.

Various studies have been conducted on modeled fire behavior in the Sierra Nevada. One popular subject area has been modeling effects of fuel treatments on fire behavior. Hurteau and North (2009) modeled the impacts of different fuel treatments on forest carbon storage and found that with an active fire regime, the best strategy for preserving carbon was to maintain lowdensity stands dominated by large pines. Other studies similarly found that thinning treatments significantly reduced vulnerability to carbon loss from wildfires in their models (Stephens et al. 2009), and that retaining large trees was particularly beneficial (Stephens and Moghaddas 2005; Stephens et al. 2012a). Simulations have also shown that fuel treatments can help to create less extreme fire behavior, reducing fire intensity, rate of spread, flame length, reaction intensity, and heat per unit area (Noonan and Tueller 2002), although some fuel treatments may be more effective than others (Stephens 1998). In evaluating the effectiveness of different spatial arrangements for fuel treatments, simulations found that a regular geometric arrangement was best, rather than a random arrangement or defensible fuel profile zones (Schmidt et al. 2008). Fuel treatments have been shown to have good longevity, with similar or even increased effectiveness measured 7 years after treatment for all fuel treatment types, compared to controls which show increased fire hazard over time (Stephens et al. 2012b). Models of fire potential over time with and without fuel treatments also show that the treatments reduce fire hazard even 40 years out (Collins et al. 2013).

Other studies have focused on relating stand structure to modeled fire behavior.

Compared to reconstructed historical forests, modern forests are significantly denser and more fire-prone, especially riparian forests which generally are not thinned due to the sensitive aquatic habitat (Van de Water and North 2011). Compared to reconstructed historical stands, current stands had significantly higher basal area, stand density, snag volume, fuel loads, and canopy bulk density (Van de Water and North 2011). These differences between current and historical stand structure and fuel loads meant that current forests showed higher flame length, probability of torching, and predicted mortality, especially for riparian forests. Before 1905, fire had a significant impact on stand structures, with frequent fires serving to thin out snags and small-diameter trees and allow regeneration (Taylor 2010).

When possible, of course, observations of actual fires may yield more reliable results than simulations. One study of prescribed fire in the Sierra Nevada showed that fuel consumption varies greatly based on site and on season, from 15% consumption at a moist site in early spring to 92% at a dry site in early fall (Kauffman and Martin 1989). Fuel treatments and species composition also make a difference in observed fire behavior. Fuel treatments significantly reduce fire severity during wildfires (Pollet and Omi 2002), and fire-tolerant species like ponderosa pine show less post-fire mortality than less tolerant species like white fir (Safford et al. 2012). While untreated areas may have very low post-fire survivorship, areas that have had both thinning and prescribed burning have the highest survivorship, with the greatest risk to trees that are near the edges of the treatment (Ritchie et al. 2007). Observations of post-wildfire conditions in thinned vs. unthinned areas also support the idea that thinned areas are less impacted by wildfire and show greater resilience after wildfire (Stevens et al. 2014). Fuel loads vary depending on the history and composition of a stand, and fuel loads have a significant impact on fire behavior. While past studies have modeled impacts of thinning and stand structure, this study aims to build a custom fuel model for sites in Lassen National Forest in the Sierra Nevada region of northern California. These data also provide a useful estimate of pre-thinning fuel loads, which may be compared in the future to post-thinning loads. Sierra Nevada forests are very fire prone, with increasing fire risk due to increasing temperature, drought, and fuel loads. The two dominant pine species considered are *Pinus ponderosa* (a generally well-studied species, perhaps due to its wide range across most of the western United States) and *Pinus lambertiana* (which appears in far fewer studies, perhaps due to its range being restricted mainly to mountainous areas of California and Oregon). Custom fuel models for the area may prove useful in determining whether fuel loads differ significantly by dominant species, and whether measured fuel loads differ from the closest standard fuel models. A custom fuel model could also be useful in allowing more accurate, site-specific fire predictions, and in highlighting an area where further research and validation may be needed.

2.2 Methods

2.2.1 Study site

Sample plots were located in Lassen National Forest (40.2° N, 121.3° W), in the northern Sierra Nevada Mountains of California. Weather data were obtained from the nearby weather station in Chester, CA using the Kansas City Fire Access Software (USDA 1996). These data indicate a fairly mild, dry climate for 1980-2010. The average daily temperature for December-February was 1.4°C; average daily temperature for June-August was 18.6°C. Average yearly precipitation for this period was 102 cm, with winter months averaging 17 cm each and the

summer months averaging only 1.25 cm each, based on data from the PRISM climate group (Daly et al. 2008). Soils in the area are primarily a mix of Holland, Skalan, Inville, and Wintoner (USDA 2016). Descriptors for these soil types include loam, gravelly, sandy, cobbly, and bouldery, sometimes with clay or bedrock deeper below ground. All soil types tend to be well-drained with medium to high run-off (depending on slope) and low to moderate water storage, with a low water table (USDA 2016).

2.2.2 Data collection and processing

Fuel measurements were taken from a total of 40 sites. Six different plot types were selected that differed in plot radius and in the number of large pines present within the plot (Table 2.1). All plots were centered on a dominant pine (either *Pinus ponderosa* or *Pinus lambertiana*) with a diameter at breast height (DBH) of at least 63.5 cm. Hereafter, "large pine" refers to a pine with a DBH of at least 63.5 cm, and "focal tree" refers to the largest pine in a plot, which is positioned at the center of the plot. Plot types included R30 (a plot with a 30 ft, or 9.1 m, radius and one large pine), R30C1 (a plot with a 30 ft radius and one large competitor pine, for a total of two large pines in the plot), R30C2 (a plot with a 30 ft radius and two large competitor pines, for a total of three large pine in the plot), RD (a plot with a radius equal to the DBH of the focal tree * 12, with one large pine in the plot), RD1.2 (a plot with a radius equal to the DBH of the focal tree * 15), and Control (a plot with a radius equal to the DBH of the focal tree * 15), located in an area not scheduled for thinning). Plot radii varied in order to study the effects of radial release on focal trees, with 30 ft (9.1 m) being the usual thinning radius used by the forest service. While effects of radial release are not included in this study, plots have been

thinned since the conclusion of this study and effects of release will be a direction for future research. This study serves to set a baseline for pre-thinning stand structure and fuel loads.

Fuel measurements were taken along the North-South diameter of all plots, using the planar intersect method (Brown 1974). In practice, with the varying plot diameters, this meant that transect lengths varied from two 8.8 m transects in a plot (one along the northern radius and one along the southern) to two 18.0 m transects in a plot. Litter, duff, and woody debris depths were measured at ½ plot radius and at approximately 1 m away from the North-South transect line, on both the north and south sides of each plot. Fuels were tallied based on size class or, more specifically, time-lag class: a 1-hr fuel is less than 0.64 cm in diameter, a 10-hr fuel is 0.64-2.54 cm, a 100-hr fuel is 2.54-7.62 cm, and a 1000-hr fuel is >7.62 cm (Fosberg 1970). One-hour fuels were tallied for the first 1/8 of the plot radius; 100-hr fuels were tallied for ¼ of the plot radius; 100-hr fuels were tallied for the full radius; 1000-hr fuels were counted, measured for diameter, and noted as sound or rotten along the full plot radius.

Fuel counts were converted to fuel loads (tonnes/hectare) using Brown's equation for calculating tons/acre, and then converting to metric (Brown 1974) (Equation 2.1). For maximum accuracy, this equation requires species-specific values for fuels' squared average diameter, specific gravity, and non-horizontal angle correction factor. Values for each of these factors were taken from van Wagtendonk et al. (1996). Because plots had a mix of different species, the values that were used were based on what percentage of the plot was composed of each species, as Brown (1974) suggested for estimating squared average diameter (d^2) (Equation 2.2). In this way, the species composition of each plot, and the possible influence of different species, was accounted for in calculating fuel loads. For 1000-hr fuels, d^2 was calculated from measured fuel diameters rather than taken from the literature. For rotten fuels >3 inches, a specific gravity of

0.3 was used rather than the literature value for sound fuels, after Brown (1974). Brown's methods for measuring fuels and calculating fuel loads are standard in the current literature (e.g. Pierce et al. 2014; Simard et al. 2011; Stottlemyer et al. 2015). Litter and duff fuel loads were calculated from measured depths using the equation described in van Wagtendonk et al. (1998) (Equation 2.3). Values used for the litter and duff coefficient were based on the species composition at each plot, as with squared average diameter, specific gravity, and non-horizontal angle correction factor. Total fuel loads were calculated as the sum of 1-hr, 10-hr, 100-hr, and 1000-hr fuels plus litter and duff loads.

Other measurements taken at all plots include DBH and species for all trees greater than 20.3 cm in DBH, tree height and height to live crown for the focal tree and its 1-3 greatest competitors, and plot slope in the E-W and N-S directions. Selection of competitors was based on visual assessment of size and distance from the focal tree, and on meeting at least two out of three criteria: competitors were required to be at least 1/3 of the diameter of the focal tree, at least 1/3 of the height of the focal tree, and/or have a gap between the competitor's crown and the focal tree's crown that was less than the crown width of the focal tree. The Lorimer Competition Index used when needed to make the final selection of competitors (Lorimer 1983) (Equation 2.4). Plot measurements were used to calculate other stand variables such as basal area (BA), quadratic mean diameter (QMD), stand density index (SDI), trees/hectare (TPH), and live crown ratio (LCR). Only live trees were included in calculating these stand variables. Percentages of snags (standing dead trees) were also calculated for both sugar pine plots and ponderosa plots.

Statistics were run on transformed fuel load data and stand structure data to determine possible relationships between fuels and stand characteristics. Data transformations used

included log, inverse, square root, fourth root, and ³/₄ power. Normality was verified using the Shapiro-Wilk normality test (Shapiro and Wilk 1965), skewness, and kurtosis (Komsta and Novomestky 2015). Statistical tests included Pearson correlation tests (for comparing two continuous variables such as 1-hr fuels by basal area) and t-tests (for comparing fuel loads by focal tree species). It was found that the distributions for 1000-hr fuels at ponderosa sites, and numbers of snags at both ponderosa and sugar pine sites could not be transformed to a normal distribution. For distributions that could not be normalized, a non-parametric Spearman rank test was used in place of the Pearson correlation tests (for comparing PIPO 1000-hr fuels to stand structure characteristics), and the Wilcoxon rank sum test was used in place of the t-test (for comparing numbers of snags in ponderosa plots to numbers in sugar pine plots).

Fuel loads were also compared to the fuel loads predicted by standard fuel models TL3 (moderate load conifer litter) and TL8 (long needle litter) (Scott and Burgan 2005) using a one sample t-test. The TL3 model was chosen because it most closely matched the fuel loads found in the stands. It is a model for short-needle conifers with few coarse fuels, with a very low spread rate and a low flame length. Because the stands have high numbers of short-needled white fir, the TL3 model was considered appropriate to represent the effects of all the short-needle conifers in the area. The TL8 model was also chosen because it is for long-needle pines, like the ponderosa pine and sugar pine in these plots. It has a moderate fuel load and spread rate, with a low flame length. Because the stands have both long-needle pines and other short-needle conifers, fire models for the stands were compared to both standard models to see which matched best with the custom models. This allows insight into whether the stands should be considered more short-needled due to high numbers of white fir, or long-needled due to the dominance of large pines.

2.2.3 BehavePlus modeling

Standard fuel models exist in order to predict the fuel loads in a certain type of forest, and from there, predict how a fire might behave in that forest. Rothermel (1972) published 11 fuel models, which were later expanded to 13 by Albini (1976). These models represented different ecosystem types, including different types of grass, chaparral/shrub, timber litter, and slash environments. Scott and Burgan (2005) expanded on and added to these original 13 fuel models to create a total of 40 models, adding dynamic fuel models (i.e. the model decides what portion of the herbaceous fuels are alive or dead based on fuel moisture). They also added new fuel models in an attempt to provide better options for modeling humid areas, modeling forests with a mix of litter, grass, and/or shrub, and modeling forests that have had fuel treatments applied (Scott and Burgan 2005). The standard models used here are from Scott and Burgan (2005). Due to the large number of equations used in fire modeling, equations may be found in Appendix B. Appendix A contains tables and figures.

Once fuel loads had been calculated for each focal tree species (ponderosa pine and sugar pine), they were used to create a custom fuel model for each species in BehavePlus (Andrews 2009; Heinsch and Andrews 2010). Custom fuel models were created using the measured values for fuel bed depth, 1-hr fuel load, 10-hr fuel load, and 100-hr fuel load. One-hr surface area/volume (SAV) ratios were calculated as an unweighted average based on species-specific values reported by van Wagtendonk et al. (1996). For ponderosa sites, 1-hr SAV was set as the average of white fir, incense cedar, and ponderosa pine; for sugar pine sites, it was set as the average of white fir, incense cedar, and sugar pine. In this way again, a variety of species were incorporated into fuel models. Ponderosa pine has a low average 1-hr SAV, which resulted in a lower 1-hr SAV for ponderosa sites than for sugar pine sites. Dead fuel moisture of extinction
was set to 35%, the same as the TL8 model. Extinction moisture is the fuel moisture content needed to stop uniform fire spread; a higher difference between the fuel moisture and the moisture of extinction leads to a higher rate of spread and intensity (Burgan 1987). Compared to the TL3 model, the TL8 model had the higher dead fuel moisture of extinction; this higher value was selected for the custom fuel models in order to create a slightly higher rate of spread and intensity, better fitting to observed fires in the area. The value used for moisture of extinction; at the low fuel moistures used here, the difference is fairly small. All other values were the same between all fuel models. For non-fuel load input values for all fuel models, see Table 2.2. (Fuel load inputs are shown in Table 2.3). Surface fire modeling and scorch height modeling were then run under different weather scenarios.

Weather scenarios used in these models were 50th percentile, for examining possible fire behavior in a deliberately set prescribed fire, and 97th percentile, for examining possible wildfire behavior under more extreme conditions, when wildfires are both more likely and more dangerous. Both percentiles were based on the summer fire season of May-August only, when there tend to be higher winds, higher temperatures, and lower humidity. 50th percentile wind speed was set at 11.3 km/h at 10 m high (the standard height used by weather stations for wind measurements), while 97th percentile wind speed was set at 20.9 km/h, based on data from the Chester Weather Station for 1980-2010. Due to the forested conditions, a wind adjustment factor of 0.3 was used in BehavePlus to determine mid-flame wind speeds and 20-ft wind speeds from these 10 m wind speeds. As in Van de Water and North (2011), weather data were obtained from the Kansas City Fire Access Software, and weather percentiles were calculated in FireFamily Plus software (Bradshaw and McCormick 2000). Dead fuel moisture percent was calculated for

both 50th percentile and 97th percentile conditions as well. To calculate dead fuel moisture, the Fine Dead Fuel Moisture Tool in BehavePlus 5.0.5 was used, with inputs from the Chester Weather Station for temperature and relative humidity (Andrews 2009). This resulted in a 50th percentile dead fuel moisture of 4%, and a 97th percentile dead fuel moisture of 2%. Slope steepness was entered based on the average of the maximum slopes measured at plots: 11.2% for PILA plots, 16.0% for PIPO plots, and 13.1% for the TL3 and TL8 fuel models based on the maximums for all plots. Maximum slope was used because fire will tend to spread in the direction of the steeper slope. Naturally slope is not constant between all sites and the maximum slope measured at plots varied from 2% to 28.5%. A steeper slope leads to greater pre-heating of up-slope fuels and a faster rate of spread. However, the effect of slope tends to be small (Burgan 1987).

BehavePlus uses Rothermel's equation for rate of spread (Rothermel 1972) (Equation 2.7). In order to explain the results, intermediates used in the fire behavior equations were also produced in BehavePlus. Intermediates are values such as the relative packing ratio, the surface area to volume ratio, and the wind factor, which are generally not desired as output values, but are values that BehavePlus must calculate before it can calculate the output values (Andrews 2009). Examining these values and the equations that use them gives insight into how the program arrived at the output values. These intermediate values are summarized in Table 2.7 and discussed further in section 2.4.2, the discussion section on the surface fire simulations.

Crown fire modeling was also attempted based on measurements of canopy base height (CBH) that had been taken for each focal tree and its 1-3 greatest competitors. For each focal tree species, 20th percentile canopy base heights were used after Hunter el al. (2011), which resulted in an estimate of 5.79 m for sugar pine and 5.77 m for ponderosa pine. The base of the crown

was considered to be the lowest live branch that had other live branches within approximately 1 m above it. An estimate for canopy bulk density was taken from Van de Water and North (2011). Van de Water and North measured canopy bulk density at 15 sites in Lassen National Forest, at sites with a similar elevation, species composition, and location to the ones used in this study. An estimate of 100% foliar moisture was used for both species, which is considered a safe estimate for foliar moisture under dry conditions when more specific data is lacking (Scott and Reinhardt 2001; Agee et al. 2002). For live woody moisture, an estimate of 100% was used after Simard et al.'s (2011) estimate for lodgepole pine (*Pinus contorta*) under "very dry" conditions.

2.3 Results

2.3.1 Fuel loads

Significantly different fuel loads were found between sugar pine sites, ponderosa pine sites, and the TL3 and TL8 fuel models (Table 2.3). The custom models had different loads of 1hr fuels compared to each other and compared to each of the standard models. The lowest loads of 1-hr fuels were found in ponderosa sites, with the highest loads predicted by the TL8 fuel model. For 10-hr fuels, sugar pine sites had similar fuel loads to those for TL3, but ponderosa sites once again had significantly lower fuel loads than any of the other models. TL8 was in between, with significantly higher 10-hr fuel loads than ponderosa and significantly lower loads than sugar pine. Sugar pine and ponderosa pine had similar 100-hr fuels to each other and to TL8, but both had lower fuel loads than TL3. TL3 and TL8 did not include estimates for 1000-hr fuels, total fuels, or litter-duff, but ponderosa and sugar pine both had similar (i.e. not statistically different) fuel loads in these instances. For fuel bed depth, TL3 and TL8 were equal to each other but surpassed the measured values, while ponderosa sites and sugar pine sites did not differ from each other. The TL3 and TL8 models did not include values for 1000-hr fuels because large logs generally do not have as much influence on fire behavior, although they are included in the Fire-Danger Rating System (Bradshaw et al. 1983).

2.3.2 Stand structure and fuels

In general, stand structure did not vary significantly between sugar pine plots and ponderosa pine plots (Table 2.4). Both had similar average quadratic mean diameter (QMD), basal area (BA), stand density index (SDI), focal tree DBH, crown base height (CBH), live crown ratio (LCR), and snag percentages. The one place where stands did differ was in the average number of trees per hectare. Sugar pine sites tended to have more trees per hectare (322.9 trees/ha for sugar pine, and only 248.1 trees/ha for ponderosa pine).

Some significant correlations were found between stand structure variables and fuel loads (Table 2.5). For sugar pine, there was a negative relationship between trees per hectare (TPH) and 1-hr fuels (p = 0.046), and a negative relationship between QMD and 1000-hr fuels (p = 0.0060). For ponderosa, there was a significant negative correlation between basal area and 10-hr fuels (p = 0.045) and a positive relationship between TPH and 1000-hr fuels (p = 0.015, Spearman's rank correlation). When both species were combined, TPH had a positive relationship to 1000-hr fuels (p = 0.0055). QMD had a negative relationship to 1000-hr fuels (p = 0.0090).

2.3.3 Surface fire

The 97th percentile weather condition inputs resulted in more severe fire behavior than the 50th percentile weather conditions (Table 2.6). Overall, TL8 and PILA tended to show more extreme fire behavior, while TL3 and PIPO were less extreme. The main exceptions are rate of spread and reaction intensity, where TL3 surpassed PILA. PILA also showed an extremely high heat per unit area, with TL8 in second, followed by PIPO and lastly TL3. For fireline intensity, flame length, and scorch height, the ranking was TL8, PILA, TL3, and lastly PIPO (in order from highest to lowest). PIPO scorch height actually decreased under 97th percentile conditions (the only value that decreased under more extreme fire weather). Rankings stayed constant across weather conditions, with PIPO consistently showing the least severe fire behavior and TL8 showing the most severe – except for heat per unit area, where TL3 was the least severe and PILA was most severe. The PIPO model tended to be the least sensitive to changes in weather conditions, often showing little change between 50th percentile weather and 97th percentile. Models could be de as fast burning and high heat (TL8), slow burning and high heat (PILA), fast burning but low heat (TL3), or slow burning and low heat (PIPO).

2.3.4 Crown fire

Crown fire models based on the 50th or 97th percentile wind speeds and moisture indicated that no crown fire would occur. Under 97th percentile conditions, critical surface intensity (the fire intensity needed for a surface fire to transition to a crown fire) was 2335 kW/m for sugar pine, and 2323 kW/m for ponderosa pine. This is much higher than the fireline intensity that the surface models suggested was likely (97.4 kW/m for sugar pine and 15.8 kW/m for ponderosa pine under 97th percentile conditions).

2.4 Discussion

2.4.1 Fuel loads and stand structure

Fuel loads measured here were similar to those measured by Kauffman and Martin (1989) in Quincy Experimental Area and in Challenge Experimental Forest, both slightly south of the sites used here. The chief exception is that Kauffman and Martin (1989) reported higher loads of 1000-hr fuels, which are not included in the fuel model. Overall, 1000-hr fuel loads seemed to be affected by stand structure more often than other, smaller fuel classes were. Thousand hour fuels are logs or large branches; higher loads of 1000-hr fuels therefore may indicate higher tree mortality/damage or higher levels of self-pruning. Thousand-hour fuel loads were positively correlated with TPH for ponderosa plots and for all plots combined, but negatively correlated with QMD for sugar pine sites and for all sites. This may indicate that more crowded stands with smaller trees are at a higher risk for damage and mortality that leads to deposition of large fuels. This is somewhat contrary to van Wagtendonk and Moore (2010), who found that 1000-hr fuel loads were highly variable between sites and therefore were not well predicted by stand structure variables. Van Wagendonk and Moore (2010) also found that crown height and live crown ratio were good predictors of fuel deposition for many Sierra Nevada conifers, but no relationship was found here between crown characteristics and fuel loads.

Comparing fuel loads to stand structure yielded some counter-intuitive results. Overall, for the variables that are included in fuel models, the data suggests that a higher basal area may mean lower 10-hr fuel loads for ponderosa stands, while more trees per acre may mean lower 1-hr fuel loads for sugar pine stands. This is somewhat consistent with the finding in Lydersen et al. (2015) that basal area of pines was negatively correlated with loads of 1-hr and 10-hr fuels (although total basal area showed a positive relationship with fine fuels). Fry and Stephens

(2010) also found negative correlations between density of Jeffrey pine (*Pinus jeffreyi*) and fine fuels, but positive correlations between white fir and fine fuels. However, these past studies simply found that stands with high densities of pines had fewer fine fuels than stands with low densities of pines and high densities of firs; they did not find that stands with high overall densities had fewer fine fuels than stands with low densities. This makes the finding of negative relationships between basal area or trees/hectare and fine fuels novel, and potentially deserving of further research. It is possible that the higher levels of fine fuels may be related to higher effective wind speeds in less dense stands (Reinhardt et al. 2006).

The differences in fuel loads between ponderosa sites and sugar pine sites in this study do not seem to be driven by differences in stand structure, unlike in some other studies (Lydersen et al. 2015). The two focal species had similar stand structures in terms of basal area, stand density index, quadratic mean diameter, and focal tree DBH. There was some difference in trees/hectare between the two species, with sugar pine sites having significantly higher trees/hectare. However, trees/hectare was negatively correlated with 1-hr fuel loads for sugar pine sites; therefore the higher value for trees/hectare in sugar pine sites does not explain the higher value for 1-hr fuels. Trees/hectare showed a positive relationship with 1000-hr fuels for both ponderosa and for all sites combined, but 1000-hr fuel loads were not significantly different between species despite the difference in trees/hectare.

Rather than being driven by stand structure, then, it seems reasonable to conclude that differences in fuel loads may have been caused directly by differences between the species. This is somewhat contradictory to some previous research that did find relationships between stand structure and fuels: Lydersen et al. (2015) found that overstory variables such as basal area and canopy cover explained around 23% of the variation in fuel loads in a Sierra Nevada mixed-

conifer forest – a small but significant amount. However, they also found that species composition had an impact on fuel loads – an idea that is supported by other research. Keane (2008) found that ponderosa pines tend to drop fewer 1-hr fuels than other Rocky Mountain conifer species, as well as somewhat low loads of 10-hr fuels. Ponderosa pines in Yosemite National Park have also been found to deposit fewer 1-hr fuels (g m⁻² year⁻¹) than sugar pines in the same area. This was especially true for "large" and "very large" trees (60 cm-120 cm, and >120 cm DBH, respectively) (van Wagtendonk and Moore 2010). However, van Wagtendonk and Moore (2010) also found that sugar pines deposit fewer 10-hr fuels than ponderosa pines do, which is inconsistent with the fuel loads observed here. Low deposition of fine fuels from ponderosa pines is often attributed to branch morphology – ponderosa simply has fewer fine twigs than other species do (Brown 1978; Brown and Bevins 1986; van Wagtendonk and Moore 2010; Lydersen et al. 2015).

Overall, there is support for the idea that species alone can drive differences in fuel loads, which may be something that future fuel models could incorporate more. Standard fuel models are somewhat generic – mostly by necessity, due to the limited number of fuel models and the great diversity of tree species that exist. Options for conifer forests are restricted to "Short needle litter" and "Long needle or hardwood litter" from the original 13 fuel models (Albini 1976), and "Low load, compact conifer litter," "Moderate load conifer litter," "High load conifer litter" and "Long-needle litter" from the more recent fuel model additions (Scott and Burgan 2005). A natural consequence of having standard fuel models is that they will not exactly capture every area and species – but having more species-specific and site-specific models for extremely fire-prone areas could certainly be of use to foresters.

2.4.2 Surface fire

Rothermel's rate of spread equation is somewhat complicated to unpack due to the large number of variables included in it (and the large number of variables included in calculating those variables). For discussion of the specifics of Rothermel's equations, see Rothermel (1972) and Burgan (1987). Also see Appendix B, Equations 2.5-2.13. Rather than exploring every variable in the equations here, this discussion will focus mainly on the variables that seem to best explain the observed differences between fuel models.

The question that emerges from the results is what drives the differences in fire behavior between the models. For example, why does the PILA model show lower rate of spread and reaction intensity than the TL3 model, and yet higher heat per unit area, fireline intensity, flame length, and scorch height? Why is the PILA model often more severe than the TL3 model even though it has similar or lower fuel loads and a much lower surface area/volume ratio (Table 2.7)? Typically surface area/volume (SAV) is an important factor in fire behavior, with higher SAV (i.e. a greater portion of smaller fuels) leading to more extreme fire behavior (Burgan 1987; Liu et al. 2015). In order to answer this question and explain the results, it is necessary to examine the equations used to calculate the output values.

Reaction intensity and rate of spread are both somewhat complicated factors, but they are a good place to begin because they go into calculating many other factors. Reaction intensity (Equation 2.5) is the total energy produced per square meter of combustion per second. It is partly based on potential reaction velocity (Γ'), which is a measure of the rate of fuel consumption (Equation 2.6). Potential reaction velocity is highly sensitive to relative packing ratio ($\frac{\beta}{\beta_{op}}$). β is the actual packing ratio, while β_{op} is the optimal packing ratio based on the SAV; the ratio between them is a measure of fuel bed density. Packing ratio is a value from 0 (no fuel;

all air) to 1 (all fuel; no air) that describes how open and porous the fuel bed is based on the fuel loads in different size classes. The optimal packing ratio is some intermediate value that balances the need for air flow with the need for fuel, and varies depending on the surface area/volume ratio (Burgan and Rothemel 1984). Γ' always peaks at $\frac{\beta}{\beta_{op}} = 1$ (i.e. when the actual packing ratio is the same as the optimal packing ratio), and begins decreasing from there (Burgan 1987). Of all the fuel models, the PILA fuel model has the relative packing ratio closest to 1 (Table 2.7), and therefore it has a high potential reaction velocity. Potential reaction velocity is an important factor in reaction intensity; therefore relative packing ratio explains why PILA has a high reaction intensity in spite of a low fuel load. However, reaction intensity is also based on net fuel load, which explains why TL3 and TL8 also have fairly high reaction intensities – they have the highest overall fuel loads of all the models. TL3 has a lower fuel load but a higher reaction intensity between the two; this is probably because its relative packing ratio is closer to 1. PIPO has both low fuel loads and a low relative packing ratio, which leads to a very low reaction intensity.

Rate of spread is easy to describe: it is a measure of how quickly the fire front advances, in m/min. However, it is potentially the most complicated factor to calculate (Equation 2.7). It is based partly on reaction intensity, but in the results seen here, rate of spread is not very sensitive to reaction intensity. It also increases based on the wind factor (Table 2.7) – but here, the models with the highest wind factor have the lowest rate of spread. What, then, is causing the differences in rate of spread? One key factor may be the propagating flux ratio (ξ), which is an indicator of preheating of adjacent fuels (Equation 2.8) (Burgan and Rothermel 1984; Burgan 1987). It is based on the SAV and the packing ratio (β). From the results, it does indeed seem that models with the highest SAV also have the highest rate of spread, particularly when they also have a

high packing ratio (Table 2.7). Hence rate of spread was found to be sensitive to differences in SAV and packing ratio, because these factors impact preheating of fuels (ξ).

Once rate of spread and reaction intensity are calculated, it is easy to determine fireline intensity. Fireline intensity is a similar concept to reaction intensity, but rather than measuring the power of combustion over an area, it measures the reaction's power along the line of the advancing firefront. It is calculated from Byram's equation (Byram 1959), which can be reformulated to show that fireline intensity is directly proportional to reaction intensity and rate of spread, and inversely proportional to SAV (Burgan 1987) (Equation 2.9). In this case a low SAV actually contributes somewhat to a higher fireline intensity, which explains the high fireline intensity for the PILA model (although for the PIPO model, a low SAV is not enough to offset a very low reaction intensity and low rate of spread). The TL8 model has the highest fireline intensity, probably because it has by far the highest rate of spread, and a high reaction intensity.

Heat per unit area differs from reaction intensity in that it measures energy produced over an area, rather than power produced over an area (power is energy/time). Possibly the most salient result is the extremely high heat per unit area that the PILA model shows compared to the other models. The reason in this case is fairly simple: heat per unit area is calculated as a ratio between the fireline intensity and the rate of spread multiplied by a constant (Andrews and Rothermel 1982) (Equation 2.10), and the PILA model has the greatest ratio between these values. The PILA model suggests a fire that burns relatively slowly, but with high intensity and therefore great heat per area.

Flame length is closely related to fireline intensity according to Byram (1959), which explains why rankings for fireline intensity match rankings for flame length, and models with similar fireline intensity have similar flame length (Equation 2.11). Scorch height is related to

but distinct from flame length: it is the height at which the air is hot enough to kill live foliage, based on wind speed, temperature, and flame length or fireline intensity (because flame length is directly related to fireline intensity, it is difficult to separate the two) (Wagner 1973; Andrews 2009) (Equation 2.12). Therefore scorch height varies with flame length and fireline intensity, but may decrease with wind speed, as higher wind speed leads to great flame tilt. The impact of wind speed explains why the PIPO model, which shows only a small change in fireline intensity between the two weather scenarios, actually shows a decrease in scorch height under more extreme fire weather.

The PIPO model may be less sensitive to weather than the other models are because it has a much higher wind factor than the other models do (Table 2.7). The wind factor is based on wind speed, SAV, and relative packing ratio (Equation 2.13). Wind factor increases as relative packing ratio decreases, which explains why the PIPO model has the highest wind factor (Burgan 1987). (Wind factor also increases as SAV increases, but in this case the differences in relative packing ratio have a larger impact.) A slight increase in the wind factor may cause less of a change when the wind factor is already high, compared to when it is low. The TL8 model, in contrast, has the lowest wind factor, and seems to be most impacted by changes in the weather conditions and corresponding changes in the wind factor. While the wind factor for TL8 is more than doubled by weather changes (from 1.7 under 50th percentile weather to 4.1 under 97th percentile), the PIPO model shows an increase of similar magnitude but much smaller proportion (from 11.2 to 14.0); this small proportional increase has much less impact on fire behavior.

One revelation from these results is that higher fuel loads do not mean more extreme fire behavior, per se. The size distribution of the fuels may make a larger difference – i.e. the surface area/volume ratio and the relative packing ratio. These factors can have a large influence on the

rate of spread and the potential reaction velocity, which in turn can impact reaction intensity, fireline intensity, and heat per unit area. Overall these results show that high packing ratio and SAV lead to a faster spreading fire, while high fuel loads and relative packing ratio lead to a higher reaction intensity. Models that have a low rate of spread and a high reaction intensity will produce very hot fires, while a high rate of spread and low reaction intensity will produce cooler fires.

It should be noted that predicting or even explaining the outputs of fire models can be complicated, because the models depend on so many factors. This is why numerous studies exist on the sensitivity of the Rothermel model to different factors (Sylvester and Wein 1981; Liu et al. 2015), as well as other publications that exist to help explain and interpret the model (Burgan 1987), or to re-formulate it for different conditions (Wilson 1990; Sandberg et al. 2007). Genetic algorithms have even been used to attempt to optimize fuel models (Ascoli et al. 2015). The impact of relative packing ratio has not generally been a focus of the literature; instead factors such as SAV, fuel moisture, fuel load, and fuel depth have generally been considered to have more of an impact (Sylvester and Wein 1981; Jolly 2007; Liu et al. 2015). The results of this modeling experiment highlight the potential importance of relative packing ratio, which may deserve more attention in future modeling studies.

These models may be an under-prediction of actual fire behavior. Late spring prescribed burnings in Challenge and Quincy showed average rates of spread of 1.0 m/min and 1.9 m/min, respectively, with fireline intensities of 126 kW/m and 64 kW/m, and flame lengths of 0.71 m and 0.49 m (Kauffman and Martin 1989). This suggests the possibility that the TL8 model, which predicted the most extreme fire behavior, may be the best match for these sites of the ones tested. The PILA model also matches reasonably well with these results, despite a lack of sugar

pine in the area – Kauffman and Martin (1989) characterize the Challenge site as dominated by Douglas-fir, incense cedar, and ponderosa pine, while the Quincy site is dominated by Jeffrey pine, Douglas fir, and incense cedar. Strong under-prediction bias is a common issue in uncalibrated custom fuel models (Cruz and Alexander 2010), which can be solved with further observations of actual fire behavior and corresponding calibration of the model. However, prescribed fires are generally not ignited in dense stands; re-introduction of fire is a multi-step process that begins with thinning treatments and gradually leads to re-establishment of natural fire regimes.

The accuracy of these specific custom models has not yet been verified with observations of fire behavior. There may be other factors that were not accounted for here that could make a difference in fire behavior - for example, sugar pine has shorter needles than ponderosa pine, so the differences in fuel bed density between the two models might be even greater than the difference predicted here (Cheek et al. 2012). White fir (Abies concolor) also has a significant presence in the area, and creates a much denser fuel bed than ponderosa pine does due to differences in the leaf morphology (Stephens et al. 2004). Therefore the concentration of white fir in an area could also impact the fuel bed density and potentially create very different fire behavior. Testing and calibration of fuel models through lab experiments or field observations is generally recommended and may be a subject for future research. Fire behavior modeling faces a tradeoff between accuracy and simplicity; a more accurate model will tend to be more complicated, while a simpler model may be less accurate (Scott et al. 2014). In general, a model may be considered good if it can get within $\pm 35\%$ error in its predictions for rate of spread (Cruz and Alexander 2013). However, Rothermel's fire spread model was developed empirically based on observations, and such models have been shown to be applicable even under different

conditions from the original dataset from which the model was developed (Cruz and Alexander 2013).

2.4.3 Crown fire

It should be noted, first, that crown fire models are known to chronically under-predict the potential for crown fire. In order to initiate crown fire, models often require extremely dry conditions, very low canopy base heights, high canopy bulk densities, strong winds, and an intense surface fire (Hall and Burke 2006; Cruz and Alexander 2010). This is often found to be at odds with observations.

Modeling of crown fires is also made difficult by the fact that there is no widely agreed upon method for measuring canopy base height. Ottmar et al. (1998) defined canopy base height from the height of the lowest continuous branches. Scott and Reinhardt (2001), however, note that it is difficult to represent an entire stand with either a minimum or an average. This is even further complicated by the fact that ladder fuels such as saplings or draping mosses are not accounted for when simply measuring the crown base height of a tree, and these ladder fuels may be important to fire behavior (Davis et al. 1959). Various approaches include using the 20th percentile height to live crown as done here (Hunter et al. 2011), reducing the canopy height to 2 m to account for irregular but fairly continuous ladder fuels (Van Wagner 1993), defining canopy base height as the height at which some minimum density of fine fuels is found (Sando and Wick 1972; Scott and Reinhardt 2001), or using equations or tables in place of measuring (Hall and Burke 2006; Alexander and Cruz 2014).

Given the tremendous amount of disagreement over the proper measurement of canopy base height, it is difficult to say whether the method of measurement used here was appropriate

or not. Photos of the plots show fairly continuous ladder fuels in almost all cases, so it is possible that a lower estimate would be more accurate for estimating crown fire potential, especially given the inherent under-prediction bias in the modeling system. The selection method for measuring crown heights may have also biased the estimate a bit high – only the focal tree and its competitors were measured for crown height, which tends to mean that mostly larger trees were measured, and taller trees naturally tend to have higher crowns. The estimate used for crown bulk density may have also been lower than necessary, given the high standard error reported with the value – mean crown bulk density was reported as 0.08 kg/m³ with a standard error of 1.11, indicating that some areas probably have much higher crown bulk density (Van de Water and North 2011*b*).

Test runs indicated that by reducing canopy base height to 0.5 m, increasing canopy bulk density to 0.5 kg/m³, increasing 20-ft wind speed to 25 km/h, and decreasing foliar moisture to an extremely dry 30%, crowning could be made to occur in the simulations for PIPO, with conditional crowning in the PILA model. However, this may say more about the underprediction bias of the model than it does about the actual conditions needed for crowning. Crown fire was slightly easier to initiate in the PIPO model because crown base height was slightly lower in the PIPO model. This is also why in the results, critical surface intensity was lower for PIPO than for PILA.

2.4.4 Economic aspects

There is little doubt that wildfires can be costly. In addition to the destruction that they cause and the loss of property and timber, wildfires can decrease the numbers of recreational visitors to parks and forests (Duffield et al. 2013). Fire suppression costs billions each year, and

an individual fire may cost millions depending on its size and its location on public or private land (Liang et al. 2008, Liang et al. 2012). In the Pacific Southwest, a single fire costs an average of \$2.8 million (Thompson et al. 2013). Wildfires may also produce much more smoke than a controlled burn, leading to air quality issues and health costs from smoke exposure (Richardson et al. 2012). Severe fires also pose a more direct threat to human life, both for fire fighters and for residents of fire-prone areas. However, fire management also has its costs, so from an economic perspective, the question is whether the costs of reducing fire severity can equal or outweigh the costs of high-severity fires.

A risk-based approach to fuel reduction treatments allows the estimated cost of treatment to be weighed against the risk and the potential cost of a wildfire. In this way, areas that are highrisk for fire and low-cost for treatment are given priority, and fire managers are not rewarded for inefficient resource expenditure on overly aggressive fire suppression (Thompson et al. 2013). Otherwise, costs of fuel reduction treatments may be greater than the savings they provide for fire suppression (Taylor et al. 2015). In considering the cost of fuel treatments, there is also the possibility for timber sales and payment for ecosystem services to help cover the costs (Matzek et al. 2015). While higher fire risk decreases the optimal rotation period for thinning treatments, higher carbon prices increase the rotation period (Couture and Reynaud 2011); from an economics perspective, optimal rotation period balances these two factors.

Research also suggests that a thorough understanding of the value of fuel reduction treatments must also include nonmarket benefits such as fire prevention and suppression and habitat preservation and restoration (Huang et al. 2013), for which the public has shown a high willingness to pay (Loomis and González-Cabán 2010). This willingness to pay even extends to passive use values: many people are willing to pay just to know that a habitat is being protected,

even if they will never personally see it or directly benefit. For example, California households were willing to pay an average of \$79/household per year to protect spotted owl habitat, \$460/household for prescribed burning, and \$510/household for fuel reduction (for white populations – Hispanic populations were willing to pay even more to decrease risk) (Loomis and González-Cabán 2010). Therefore it is possible to implement fuel reduction treatments that are funded by some mixture of timber sales, carbon markets and other markets for ecosystem services, and the communities that benefit. If applied optimally, treatments may also serve to reduce costs of fire suppression and health-related costs of fire, increase revenues from park use, and avoid some of the costs of property damage and disruption of businesses. Forest protection in China has been projected to expand both the value of the forestry sector and the economy as a whole, while also leading to ecological benefits (Shen et al. 2006). If implemented correctly, preservation of natural resources can have a variety of social, economic, and environmental benefits.

2.5 Conclusions

Existing fuel models fail to reflect the fuel loads measured in Lassen National Forest, and lead to different predictions of fire behavior. Evidence also suggests that fuel loads and fuel bed density differ based on species composition. Fuel loads vary over time and are typically not spatially homogenous, but having detailed, high-resolution and up-to-date fuel maps for every fire-prone area is probably not a realistic goal. Instead, having more fuel models such as the ones in this study may help foresters to predict fuel loads and fire behavior based on the species of the largest trees in an area. This study also highlights the possible under-prediction bias found in many custom fuel models and models of crown fires. Directions for future research include

calibration of these fuel models from observations of actual fire behavior, and more detailed measurements of ladder fuels and crown characteristics for more accurate modeling of crown fire behavior. Studies of post-thinning fuel loads and fire behavior would also be beneficial in understanding the potential costs and benefits of thinning, and discovering optimal thinning practices. Fire behavior is also sensitive to climatic conditions, so there is potential for these models to also be used in predicting fire behavior under future climate change scenarios, although such models may also wish to account for differences in stand structure and fuel loads that might also be caused by climate change (Miller and Urban 1999). These models could also be incorporated into economic models of fire suppression costs. This study lays the groundwork for many of these potential future directions.

APPENDICES

APPENDIX A

TABLES

Treatment	Plot radius (m)	# large pines in plot	Focal tree DBH range (cm)	# plots
R30	9.144	1	92.2-127.5	4 PILA, 2 PIPO
R30C1	9.144	2	80.0-128.3	3 PILA, 2 PIPO
R30C2	9.144	3	91.9-117.6	3 PILA, 2 PIPO
RD	DBH of focal tree * 12	1	73.2-76.0	3 PILA, 2 PIPO
RD1.2	DBH of focal tree * 15	1-2	74.7-120.7	7 PILA, 4 PIPO
Control	DBH of focal tree * 15	1-2	63.5-117.6	5 PILA, 3 PIPO
Overall			63.5-128.3	25 PILA, 15 PIPO

Table 2.1 Plot types. PILA sites are dominated by at least 1 large sugar pine, while PIPO sites are dominated by at least 1 large ponderosa pine. Treatments vary based on the plot radius and the number of large pines in the plot.

Table 2.2 Non-fuel load inputs for each fuel model. PILA is the sugar pine model, PIPO is the
ponderosa pine model, TL3 is the moderate load conifer model, and TL8 is the long needle pine
model. All other non-fuel load inputs were the same for all fuel models and therefore are not
shown here.

Fuel model	1-hr SAV	Dead fuel moisture of extinction
PILA	1729	35%
PIPO	1575	35%
TL3	6562	20%
TL8	5906	35%

Table 2.3 Fuel loads by focal tree species, and for the two standard models (TL3 – Moderate load conifer and TL8 – Long needle litter) fuel model. Values followed by the same letter are not significantly different from other values in the same column (p < 0.05). All fuel load measurements are in Tonnes/hectare. The standard fuel models could not be compared to each other with statistics, due to only having a single value for each rather than a distribution. Therefore letters apply only to comparisons between the standard and the custom fuel models, or between the two custom fuel models.

Focal tree species	Litter- duff	1-hr fuels	10-hr fuels	100-hr fuels	1000-hr fuels	Total fuels	Fuel bed depth (m)
Pinus lambertiana	115.5 ^a	0.7023 ^a	4.999 ^a	3.368 ^a	2.729 ^a	127.3 ^a	0.04389 ^a
Pinus ponderosa	147.9 ^a	0.1285 ^b	2.159 ^b	4.287 ^a	2.771 ^a	157.3 ^a	0.05017 ^a
TL3	NA	1.121 ^c	4.932 ^a	6.277 ^b	NA	NA	0.09 ^b
TL8	NA	13.002 ^d	3.138 ^c	2.466 ^a	NA	NA	0.09 ^b

Table 2.4 Stand characteristics by focal tree species. QMD is the quadratic mean diameter at breast height for all live trees in the plot. DBH is the diameter at breast height. Tree height and live crown ratio are averages for the focal tree and competitors only. Values followed by the same letter are not statistically different from other values in the same column (p < 0.05).

Species of	QMD	Basal area	Trees/hectare	Stand density	Focal tree	Crown	Live crown	% snags
dominant tree	(cm)	(m^2/ha)		index	DBH (cm)	height (m)	ratio	
Pinus	49.99 ^a	61.68 ^a	322.9 ^a	924.8 ^a	96.75 ^a	10.31 ^a	0.35 ^a	7.0 ^a
lambertiana								
Pinus	52.50^{a}	53.15 ^a	248.1 ^b	784.0^{a}	89.15 ^a	12.05 ^a	0.38 ^a	5.0^{a}
ponderosa								

Table 2.5 Correlation table for all relationships between plot structure and fuels. *Indicates a significant relationship. **Indicates that Spearman rank correlation test was used due to inability to normalize data. For all other correlations, Pearson correlation was used on normalized data. QMD is quadratic mean diameter, BA is basal area, SDI is stand density index, and TPH is trees per hectare.

Group	QMD	BA	SDI	TPH	Crown ratio	Crown height
PIPO						
1-hr fuels	-0.040	0.345	0.229	0.460	-0.046	0.110
10-hr fuels	-0.351	-0.508*	-0.413	-0.399	-0.011	-0.141
100-hr fuels	-0.291	0.230	0.319	0.362	0.237	0.241
1000-hr fuels**	-0.239	0.355	0.331	0.593*	0.209	0.236
All fuels	-0.274	-0.075	-0.088	0.031	-0.061	-0.154
PILA						
1-hr fuels	0.205	-0.171	-0.227	-0.411*	-0.028	0.064
10-hr fuels	0.362	0.269	0.232	-0.062	0.158	0.211
100-hr fuels	-0.340	-0.188	-0.134	0.201	-0.096	0.159
1000-hr fuels	-0.474*	-0.130	-0.031	0.359	-0.059	-0.143
All fuels	-0.349	-0.173	-0.113	0.210	-0.380	-0.252
Overall						
1-hr fuels	-0.061	0.147	0.168	0.207	-0.015	-0.008
10-hr fuels	0.024	0.141	0.147	0.114	0.003	-0.040
100-hr fuels	-0.284	-0.062	0.003	0.237	0.140	0.136
1000-hr fuels	-0.361*	0.064	0.150	0.431*	0.100	0.037
All fuels	-0.275	-0.191	-0.149	0.057	-0.187	-0.172

Fuel	Weather	Max ROS	Heat/area	Fireline	Flame	Reaction	Scorch
mode	%	(m/min)	(kJ/m^2)	intensity	length (m)	intensity	height (m)
1				(kW/m)		(kW/m^2)	
PILA	50%	0.21	15,130	54.0	0.49	166.4	1.33
PIPO	50%	0.12	5241	10.9	0.23	31.6	0.31
TL3	50%	0.27	2532	11.3	0.24	168.4	0.32
TL8	50%	0.89	8921	131.6	0.73	685.5	2.63
PILA	97%	0.34	17,157	97.4	0.64	188.7	1.77
PIPO	97%	0.16	5943	15.8	0.28	35.8	0.26
TL3	97%	0.62	3034	31.4	0.38	201.8	0.56
TL8	97%	1.97	10,116	332.6	1.12	777.3	5.24

Table 2.6 Summary of BehavePlus outputs under different weather conditions and different fuel models. ROS = rate of spread.

Table 2.7 Values of select intermediates for the Rothermel model. Most values are not impacted by weather scenarios, with the exception of wind factor. For wind factor, the value in parentheses is for 50^{th} percentile weather conditions, while the regular value is for 97^{th} percentile weather conditions.

Fuel model	Characteristic	Relative packing	Packing ratio	Wind factor
	SAV (m^2/m^3)	ratio		
PILA	831	1.120	0.0403	7.4 (5.4)
PIPO	456	0.434	0.0256	14.0 (11.2)
TL3	5028	3.190	0.0263	4.8 (2.1)
TL8	5808	5.417	0.0397	4.1 (1.7)

APPENDIX B

EQUATIONS

Tonnes/hectare = $\frac{26.09*n*d^2*s*a*c}{Nl}$ Equation 2.1

n = number of fuels

c = slope correction factor $d^2 =$ squared average diameter

s = specific gravity

a = non-horizontal angle correction factor

l = length of sampling plane

N = number of sampling planes

$$d^{2} = \text{squared average diameter} = \frac{P_{1}d_{1}^{2} + P_{2}d_{2}^{2} + P_{3}d_{3}^{2}}{P_{1} + P_{2} + P_{3}}$$
Equation 2.2

 P_1 = portion of plot that is species 1 d_1^2 = squared average diameter for species 1 P_2 = portion of plot that is species 2 d_2^2 = squared average diameter for species 2 P_3 = portion of plot that is species 3 d_3^2 = squared average diameter for species 3

Litter and duff weight (tonnes/ha) =
$$C_{ld}$$
 * depth (cm) * 10 Equation 2.3

 C_{ld} = species-specific litter and duff coefficient

Competition Index =
$$\frac{D_j/D_i}{DIST_{ij}}$$
 Equation 2.4

 D_j = diameter of competitor tree D_i = diameter of focal tree $DIST_{ij}$ = distance between focal tree and competitor

$$I_R$$
 = reaction intensity = $\Gamma' w_n h \eta_s \eta_M$ Equation 2.5

 Γ' = potential reaction velocity $w_n = net fuel load$ h = heat content η_s = mineral damping coefficient η_M = moisture damping coefficient

$$\Gamma' = \text{potential reaction velocity} = \Gamma'_{\max} \left(\frac{\beta}{\beta_{op}}\right)^A \exp\left[A(1 - \frac{\beta}{\beta_{op}})\right]$$
 Equation 2.6

 Γ'_{max} = rate of fuel consumption at optimal fuel bed packing ratio $\frac{\beta}{\beta_{op}}$ = relative packing ratio A = 1/(4.77\sigma^{0.1} - 7.27) σ = surface area/volume

R = Rate of spread =
$$\frac{I_R \xi (1 + \phi_w + \phi_S)}{\rho_b \varepsilon Q_{ig}}$$
 Equation 2.7

$$\begin{split} I_R &= \text{reaction intensity} \\ \xi &= \text{propagating flux ratio} \\ \phi_w &= \text{wind coefficient} \\ \phi_s &= \text{slope factor} \\ \rho_b &= \text{ovendry bulk density} \\ \epsilon &= \text{effective heating number} \\ Q_{ig} &= \text{heat of preignition} \end{split}$$

 $\xi = \text{propagating flux ratio} = (192 + 0.2595\sigma)^{-1} \exp[(0.792 + 0.681\sigma^{0.5})(\beta + 0.1)]$ Equation 2.8

 σ = surface area/volume β = packing ratio

$$I_B = \text{fireline intensity} = 384 I_R R/(60\sigma)$$
 Equation 2.9

 I_R = reaction intensity R = rate of spread σ = surface area/volume

$$H_A = heat per unit area = \frac{55I_B}{R}$$
 Equation 2.10

 I_B = fireline intensity R = rate of spread

$$FL = flame length = 0.45I_B^{0.46}$$
 Equation 2.11

FL = flame length $I_B =$ fireline intensity

h_s = scorch height =
$$\frac{3.94I_B^{7/6}}{(0.107I_B + U^3)^{0.5}(60-T)}$$

Equation 2.12

 I_B = fireline intensity U = wind speed T = temperature

$$\phi_{\rm w} = \text{wind factor} = \text{CU}^{\rm B} \left(\frac{\beta}{\beta_{op}}\right)^{-\rm E}$$
 Equation 2.13

 $C = 7.47 \exp(-0.133\sigma^{0.55})$ $\sigma = \text{surface area/volume}$ U = wind speed $B = 0.02526\sigma^{0.55}$ $\frac{\beta}{\beta_{op}} = \text{relative packing ratio}$ $E = 0.715 \exp(-3.59 * 10^{-4}\sigma)$ REFERENCES

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CHAPTER 3

EFFECTS OF CLIMATE AND COMPETITION ON DOMINANT TREES

3.1 Introduction

The fact that competition from other trees can have a limiting effect on tree growth has been well established (e.g. Gómez-Aparicio et al. 2011; Das 2012; Ruiz-Benito et al. 2013). This suppression of growth may be particularly harmful to older trees. Although competition is often not the primary factor in the mortality of old-growth trees, old-growth trees in more competitive environments may be at a higher risk of mortality (Das et al. 2011). In a ponderosa pine forest of north eastern California, old-growth trees have been shown to have significantly elevated mortality in un-thinned stands vs. thinned stands (Ritchie et al. 2008). Thinning treatments (in addition to decreasing the risk of high-intensity fire) are beneficial in limiting competition and thereby promoting the growth of the residual trees (Magruder et al. 2013; van Mantgem and Das 2014; Pukkala et al. 2015). Thinning has been shown to reduce mortality from Dendroctonus bark beetles without harming stand productivity (Zhang et al. 2013), and applying thinning treatments to reduce competition may also increase a stand's resiliency to climate stresses (Misson et al. 2003; Linares et al. 2010; Magruder et al. 2013; Guillemot et al. 2015). Just as competition may affect sensitivity to climate, climatic conditions can also affect how sensitive trees are to the effects of competition. Factors such as temperature and precipitation can have a large influence on which species have the competitive advantage in an area, because different conditions may favor different species (Gómez-Aparicio et al. 2011; Cavin et al. 2013). Climate and competition are both important factors that may help or hinder tree growth, but interactions between climate and competition can be complex, and effects may vary by species, region, tree age, and tree size.

Effects of past climate and competition can be studied through dendrochronological analysis. By comparing ring width data to past climate data, the response of radial growth to climatic conditions can be inferred over many years (e.g. Chhin et al. 2008a). Dendrochronology may also be used to determine establishment dates and trends in regeneration (Baker 1992; Chhin and Wang 2002), or to estimate when past fires occurred and their influence on recruitment (North et al. 2005). In this way, a picture can be formed of how the stand has changed over time, and how it has responded to disturbances, yearly variations in weather, and changes in competition.

Studies that use dendroclimatology (i.e. use tree rings to study past impacts of climate) often examine how both the current year's weather and the past year's weather impact growth in the present. For example, Gedalof and Smith (2001) found that for mountain hemlock (*Tsuga mertensiana*), warm summer temperatures were associated with positive growth in the present year, but negative growth in the following year. They attributed this to warm summers being favorable for initiating large crops of cones, which then matured in the following year at a significant energetic cost to the tree. Other studies have noted that different site conditions may result in different dendroclimatic responses – for example, trees that are located near bodies of water may show less response to drought stress in dry years, but be more susceptible to harm from flooding in wet years (Potito and MacDonald 2008; Chhin et al. 2013). Response may also vary by species. Hurteau et al. (2007) found that for Sierra Nevada conifers under high-density conditions, white fir (*Abies concolor*) showed the strongest and most consistent response to climate, with most species (including white fir) showing stronger responses under more open conditions.

Larger trees may show different responses than smaller trees (Castagneri et al. 2012;

Rozas 2014), because larger trees have greater non-structural carbon pools to draw on (Niinemets 2010) and better access to sunlight (Thomas and Winner 2002), but are also slower growing in general. Differences in drought response between saplings and mature trees may also depend on species; in a deciduous forest, He et al. (2005) found that some species showed little difference in drought response between old trees and young ones, while other species showed greater drought-related growth reductions in older trees. Individual trees may also show different responses to climate than the population does as a whole, due to differences in microclimate, competition, and tree age and size (Rozas and Olano 2013). To control for age and size effects, some dendrochronology studies have chosen to study even-age plantations (de Luis et al. 2009), to separate trees out into different size classes before analysis (Chhin et al. 2008b), or to focus on a particular age group such as seedlings of 0.5-2 m in height (Chhin and Wang 2008).

While most studies in dendrochronology focus on establishment dates and responses to climate, there is some existing research that has used dendrochronology to study interactions between climate and competition. Results to date have shown that competition cannot be neglected in studying tree growth over time. For example, fires that reduce competition can have a benefit to the growth of surviving trees, especially smaller trees, in spite of the cost of fire damage (Valor et al. 2013). Additionally, while trees with low competition may show strong climatic signals in their yearly growth, trees that are more suppressed due to competition do not have much sensitivity to climate (Piutti and Cescatti 1997; Gea-Izquierdo et al. 2009; Rozas 2014). Instead, their growth is more dependent on the previous year's growth (Rozas and Olano 2013). Competition can be a more important factor in tree growth than climate is, although climate can influence a tree's sensitivity to competition and can affect which species are the dominant competitors (Gómez-Aparicio et al. 2011).

Dendrochronology studies in the Sierra Nevada mainly focus on fire history and reconstructing stands from the pre-fire suppression era (e.g. Taylor 2010; Van de Water and North 2011; Fry et al. 2014; Barth et al. 2015). Dendrochronology has also been used to determine timing of bark beetle outbreaks and relationships between beetle outbreaks and fire (Simard et al. 2011). Some dendrochronology studies of fire in the Sierra Nevada also consider climate, looking at effects of El Niño/La Niña years on fire size and occurrence (North et al. 2005), or relationships between fire and climate indices (Fry and Stephens 2006), or incorporating both El Niño/La Niña and other climate indices (Taylor and Beaty 2005; Beaty and Taylor 2008). One study examined relationships between pre-fire tree growth and likelihood of mortality following a fire (Nesmith et al. 2015). It was found that radial growth did not relate to immediate postfire mortality; however, trees showed better survivorship five years after a fire if they had higher mean growth and fewer sharp declines in growth over the past 30 years.

Other studies have also attempted to determine which Sierra Nevada conifers give the most reliable records of climate: Hurteau et al. (2007) found that of Sierra Nevada mixed-conifer species growing in high-density conditions, white fir (*Abies concolor*) growth showed the closest correspondence with the Palmer drought severity index (PDSI); incorporating lagged climate effects generally did not improve chronologies' alignment with PDSI, except for Jeffrey pine (*Pinus jeffreyi*). Potito and MacDonald (2008), on the other hand, found that Jeffrey pine growth corresponded with winter (October-February) PDSI better than western juniper (*Juniperus occidentalis*) or lodgepole pine (*Pinus contorta*). For certain Sierra Nevada conifers (*Sequoiadendron giganteum, Pinus balfouriana, Pinus albicaulis*), high growth is associated with warm and wet winters (November-March), while low growth is associated with cool and dry winters for the pine species studied, and warm and dry winters for the giant sequoia (Garfin

1998). Effort has also been given to constructing long-term chronologies for some of California's longest living tree species: the giant sequoia (*Sequoiadendron giganteum*) (Brown et al. 1992), the coastal redwood (*Sequoia sempervirens*) (Carroll et al. 2014), and the bristlecone pine (*Pinus longaeva*) (Ferguson 1968) – species which are not found at the sites used in this study.

While many studies exist on dendrochronology in the Sierra Nevada as well as the impacts of weather patterns on growth, or the impacts of competition on growth, studies that cover interactions between these factors are lacking for the Sierra Nevada. This is in spite of the fact that factors such as temperature and precipitation may influence which species are most competitive. Higher competition, in turn, may decrease sensitivity to climate and increase tree mortality in old-growth forests (Smith et al. 2005). Dendrochronology provides a method by which to study decades of growth responses, and to draw conclusions about how growth has been impacted by factors such as climate and competition – and by interactions between these two factors. In this study, dendrochronology is used to study species-specific effects of monthly and seasonal weather trends on growth for four common Sierra Nevada mixed-conifer species (*Abies concolor, Pinus ponderosa, Pinus lambertiana*, and *Calocedrus decurrens*). Ring width data is also used to examine whether monthly and seasonal weather impacts trees differently based on their dominance in the stand.

3.2 Methods

3.2.1 Study site

Study sites were located in Lassen National Forest at an elevation of approximately 1525 m (Figures 3.1 and 3.2). The climate for this area is considered Mediterranean, with cool wet winters and hot dry summers (Grantham et al. 2010). In approximate order of abundance, the most common tree species in the area are white fir (*Abies concolor* or ABCO), sugar pine (*Pinus*

lambertiana or PILA), ponderosa pine (*Pinus ponderosa* or PIPO), and incense cedar (*Calocedrus decurrens* or CADE). Average basal area for the plots used in this study was 58.27 m²/ha, with a quadratic mean diameter of 50.99 cm (Table 3.1). Of the species found at these sites, ponderosa pine is the least shade tolerant, followed by sugar pine. Incense cedar is somewhat shade tolerant, and white fir is by far the most shade tolerant. Older trees also tend to be less shade-tolerant than young trees (Kinloch and Scheuner, 1990).

The Sierra Nevada is something of a unique ecosystem in that it has very large trees and high productivity despite growth that is limited by extremely dry conditions in the summer, and cold conditions in the winter. Based on data from the PRISM climate group (Daly et al. 2008), average daily temperature for December-February was 1.4°C for 1980-2010. Average precipitation for June-August was only 1.25 cm per month. The main growing season begins in the spring but continues throughout the summer, with growth continuing to occur to a lesser extent even in the fall and winter. Kelly and Goulden (2016) measured gross ecosystem productivity and found that 32% occurs in the spring, 32% in the summer, 21% in the fall, and 15% even in the winter. Spring tends to be the most favorable time for growth; in other seasons it is more limited by temperature and precipitation/moisture availability.

The season for radial growth begins in mid-April for sugar pine, ponderosa pine, and incense cedar, and in early May for white fir at sites with a similar location and elevation to the ones studied here (Fowells 1941). Radial growth lasts until August or September (Fowells 1941). Shoot growth tends to begin after radial growth, some time in June, and needle growth begins even later in late June or early July (Royce and Barbour 2001). Shoot growth may also begin at the same time as radial growth, but may proceed very slowly until June when rapid growth begins (Historical data file in Pacific Southwest Research Station – Redding). Radial growth may

be based on water availability, beginning with snow melt and ending when water potentials drop after summer drought (Royce and Barbour 2001). Shoot growth instead may be based on photoperiod and temperature (Royce and Barbour 2001).

3.2.2 Field methods

Sites were selected based on the presence of at least one old-growth pine, which here was defined as a pine with a diameter at breast height (DBH) of at least 63.5 cm. Some trees in this study were upwards of 300 years old and/or 120 cm in DBH. A total of 40 plots were sampled, with 25 where sugar pine was the dominant old-growth tree and 15 where ponderosa pine was dominant, due to the greater relative abundance of large sugar pine in the area. Plots were centered on a focal tree, which was the largest pine in the plot. Within each plot, all live trees greater than 20.3 cm in DBH were cored. Plot radius varied; 16 plots had a set radius of 9.1 m, 5 plots had a radius of 8.8-9.0 m based on the focal tree diameter * 12; 19 plots had a radius of 9.1-18.0 m based on the focal tree diameter * 15.

For each plot, 1-3 competitors were selected based on visual assessment of which trees in the plot were providing the most competition for the focal tree. Assessment was based on size and distance from the focal tree. Competitor trees all meet at least two out of three of the following criteria: they have a DBH that is at least 1/3 of the DBH of the focal tree; they are at least 1/3 of the height of the focal tree; the gap between the tree's crown and the crown of the focal tree is less than the crown width of the focal tree. Two trees were selected when possible; three plots only had one acceptable competitor, while one other had three approximately equal competitors. When the previous criteria were not enough to decide between several possible competitors, the Lorimer Competition Index was used. The Lorimer Competition Index

quantifies competition using the following equation (Lorimer 1983):

$$CI = \frac{D_j/D_i}{DIST_{ij}}$$
(Equation 3.1)

In this equation, CI is the competition index, D_j is the diameter of the competitor tree, D_i is the diameter of the focal tree, and $DIST_{ij}$ is the distance between the two trees.

The focal tree and each competitor were all cored twice at stump height (0.5 m). These cores were used as the basis for quantifying the impacts of climate and competition on the growth of dominant pines.

3.2.3 Laboratory methods

In the lab, cores were dried, mounted, sanded, and cross-dated using standard dendrochronological methods (Stokes and Smiley 1996; Speer 2010). Ring widths were cross-dated using the list method (Yamaguchi 1991), measured in CooRecorder, and verified with statistical cross-dating in COFECHA (Holmes 1983), and standardized in ARSTAN (Cook 1985). Each species was standardized separately (Table 3.2). For studying climate effects, each species was standardized with either a linear regression or a cubic smoothing spline. For white fir, a 40-year cubic smoothing spline was used; for sugar pine and ponderosa pine, a 60-year cubic smoothing spline was used; and for incense cedar, a linear regression was used. For studying competition, a conservative linear regression was used in order to preserve short-term and medium-term effects of climate and competition while smoothing out long-term effects from factors such as age (ring widths may decrease on larger trees due to the increased bole area that the ring must cover) (Gersonde and O'Hara 2005; Speer 2010). From this, a standard ring width chronology was created for each species (Figure 3.3).

Weather data was obtained from the PRISM climate group at Oregon State University, which triangulates data from multiple weather stations and accounts for geographical and

topographical variations in order to give site-specific weather records dating back to 1895 (Daly et al. 2008). These climate data include precipitation, average temperature, minimum temperature, and maximum temperature on a monthly scale. These values can then be used to calculate the climatic moisture index as well (Hogg 1997). In addition to monthly data, threemonth seasonal climate data was also calculated as the average of temperature and the sum of precipitation over three months. Climate data for successive 19-month periods (April-October of the following year) were related with tree ring chronologies using a specialized R program as in Chhin et al. (2008b). This program used the stepAIC function to perform a stepwise forward selection, designed to select models with the lowest Akaike Information Criteria (AIC) (Venables and Ripley 2002). AIC is a measure of the "distance" between the values predicted by a model and the values that were measured; hence a low AIC indicates a better model for the dataset (Burnham and Anderson 2002). AIC penalizes models for adding more parameters, so variables were only added if they lowered the AIC by at least 2 (Akaike 1974). This produced species-specific results for relationships between climate and tree growth, on a monthly scale as well as a three-month seasonal scale. When models had multiple time periods that were significant to growth, they were ranked in order of importance using standardized partial regression coefficients (Zar 1999).

To study interactions between climate and competition, competitive chronologies were also calculated between focal trees and competitor trees using the formula

Competition Ratio =
$$\frac{\text{Focal tree radial growth index}}{\text{Competitor radial growth index}}$$
 (Equation 3.2)

Therefore, a competition ratio > 1 means that conditions favor the growth of the focal tree more than the growth of the competitor. A competition ratio < 1 means that conditions favor the competitor over the focal tree. These competition ratios were used as the basis for studying dendroclimatology and competition. In cases of missing rings, a value of 0.1 was substituted for the missing ring in order to avoid dividing by zero in calculating the competition ratio. Competitive chronologies were then averaged together with other chronologies of the same category. Categories of competitive chronologies were based on which species were competing: PIPO-PIPO, PIPO-ABCO, PILA-PILA, PILA-ABCO, or PILA-CADE, where the first species is the dominant focal tree. Other competition categories (PILA-PIPO, PIPO-CADE, PIPO-PILA) did not have a large enough sample size to be included. Additional categories were also created for PIPO-interspecific and PILA-interspecific, which included all interspecific competition chronologies for each focal tree species. Competitive chronologies were created back to 1920, which ensured that all categories had a sample size of at least 8 instances of competition for the entire chronology. Competitive chronologies for each category were then related with climate data using the same methods that were applied for the species chronologies

3.3 Results

3.3.1 Species specific dendroclimatology

In general, cooler average temperatures in the summer and warmer average temperatures in the winter were most favorable for growth of all species (Figure 3.4 A). Incense cedar (CADE) showed no response to summer temperatures in the current year, but was sensitive to summer temperatures from the past year. The two pine species (PILA and PIPO) also showed negative responses to warmer temperatures in May of the previous year. For the sugar pine and white fir, average temperature in June of the current year was the most important variable, with a negative impact from high averages. Ponderosa was also negatively impacted by high averages in May-July of the current year. However, this effect was less important than the positive effect

from warm temperatures in December-February, or the negative effect of warm temperatures in May of the previous year. December-February temperature was second most important for sugar pine and white fir. Incense cedar was unique in that it was most negatively affected by high average temperatures in July of the previous year, followed by November of the previous year, and lastly it was positively impacted by warmer Februarys in the current year. In terms of the coefficient of determination (\mathbb{R}^2), ponderosa showed the highest \mathbb{R}^2 , followed by sugar pine, then white fir, with incense cedar showing the weakest determination.

Higher minimum temperatures tended to be beneficial in the winter but harmful in the summer (Table 3.4 B). Winter minimums (December-February) were more important than summer minimums for sugar pine, ponderosa, and white fir. July minimums in the current year were the second most important time for sugar pine and white fir; ponderosa pine showed an additional negative impact from high minimums in May of the previous year, which was more important than the impact from July of the current year. The chief exception to minimum temperature trends was incense cedar, which showed very little response to minimum temperatures and was only impacted by minimums in April of the previous year. Higher minimums in the past April had a negative impact on incense cedar. Once again ponderosa pine showed the highest coefficient of determination and incense cedar showed the lowest.

Higher maximum temperatures tended to be negative for growth, particularly in summer of the present year and late spring or early fall of the past year (Table 3.4 C). Incense cedar again showed effects from hot summers in the previous year but not in the current year, while other species were most impacted by hot summers in the current year. For the two pine species, higher maximums in May of the previous year were also a negative; ponderosa additionally showed a negative relationship with maximums in September-November, and a positive relationship with

January maximums. White fir was only impacted by July maximums in the current year, with no impacts from the past year. Incense cedar, on the other hand, had a negative relationship to maximums in July and November both of the previous year, mirroring its negative relationship to July and November averages for the previous year. Ponderosa pine had the highest R^2 value and incense cedar was tied with white fir for lowest R^2 .

More precipitation was almost always a positive for all species (Figure 3.4 D). Fall precipitation was generally not beneficial to growth in the current year, but did show benefits for growth in the next year. Winter precipitation from the past year and summer precipitation in the current year tended to have the largest impact on growth, with the exception of ponderosa pine. Ponderosa was most positively impacted by precipitation in the late fall/early winter of the past year (October-December), followed by May of the past year, and lastly early spring of the current year (February-April). Unlike the other species, ponderosa did not show a response to summer precipitation. Sugar pine and white fir showed identical responses to precipitation: both were most impacted by precipitation in December-February, then precipitation in May-July of the past year. Incense cedar was most impacted by August precipitation in the current year, followed by August-October of the past year, then November-January. All relationships to precipitation were positive. This time ponderosa showed the weakest coefficient of determination, followed by incense cedar.

Like precipitation, a higher climate moisture index was generally positive for all species in most months and seasonal periods. This seemed to be especially true in the summer (both current and prior year) and the fall-winter of the past year, and less true in the spring and fall of the current year (Table 3.4 E). Ponderosa was most impacted by CMI in July of the current year;

incense cedar was most impacted by CMI in July of the past year. Sugar pine and white fir showed the greatest impact from CMI for May-July of the current year. Sugar pine had the second strongest effect from October-December, and then May-July of the previous year. Ponderosa's second greatest effect was from May-July of the previous year, then September-November. White fir had the most effects from CMI. Its second greatest effect was for December-February, then September-November, and lastly May-July of the previous year. Incense cedar had the second strongest effect for June-August of the current year, and lastly October-December. For R² value, white fir was highest, then ponderosa, then sugar pine, and last of all incense cedar.

All species showed fairly high inter-core correlations, ranging from 0.274 for ponderosa pine up to 0.385 for incense cedar (Table 3.2). The average core was missing less than 0.3% of rings for each species. Mean sensitivity was between 0.1067 and 0.1618, with sugar pine at the low end and incense cedar at the high end.

3.3.2 Intraspecific and interspecific competition and climate

Overall, climate in the past year seemed to have more of an impact on competition than climate in the present year did (Figure 3.5). For average temperature, the most consistent effects were for temperature in the spring of the past year, and temperatures in July of the past year (Figure 3.5 A). Warm spring temperatures in the past year favored competitors over focal trees for PIPO-interspecific, PIPO-ABCO, PILA-interspecific, and PILA-ABCO competition. The influence of past spring temperatures was the most significant effect for PIPO-Interspecific and PILA-ABCO; for PILA-Interspecific and PIPO-ABCO, it was the only significant effect. The second most significant effect for PIPO-Interspecific was that higher October averages in the

past year favored competitors. For PILA-ABCO, the second largest effect was from October of the current year, where higher averages instead favored focal trees. For PILA-CADE competition, the number one effect was from February averages, with higher averages favoring competitors. The second most important factor was temperatures in July of the previous year, with warmer temperatures favoring focal trees. Overall, PIPO-PIPO competition showed the highest R² value, while PILA-PILA had no significant effects at all and PILA-Interspecific, PILA-ABCO, and PIPO-ABCO all had R² values under 0.1.

Minimum temperatures mostly showed different trends for each competition category (Table 3.5 B). Lower minimums in August (beta coefficient (b) = -0.417) and higher minimums in December (b = 0.235) benefited ponderosa focal trees over interspecific competitors (a higher beta coefficient (b) indicates a stronger relationship). Lower minimums for September-November of the previous year also benefited sugar pine focal trees over intraspecific competitors (b = -0.261). Lower minimums for May of the previous year benefited sugar pine focal trees over interspecific competitors (b = -0.229), and ponderosa pine focal trees over white fir competitors (b = -0.223) (the only minimum temperature effect that showed up in more than one category). PILA-CADE showed mixed trends, with high August minimums benefiting incense cedar competitors (b = -0.448), and high July minimums benefiting sugar pine focal trees (b = 0.297) in the current year. R² values for minimum temperature were highest for PIPO-Interspecific, followed by PILA-CADE. Other R² were <0.1 (PILA-PILA, PILA-Interspecific, PIPO-ABCO), or else no significant effects were found (PIPO-PIPO, PILA-ABCO).

Maximum temperature showed some of the highest R² values of any of the climatecompetition variables (Table 3.5 C), with the exception of PILA-PILA (which showed no significant relationship to maximum temperature) and PIPO-Interspecific (which showed

stronger determination from minimum and average temperature). The highest R^2 value was for PIPO-PIPO, while the lowest were for PILA-PILA (no effect) and PILA-ABCO (the only one <0.1, but still the highest R² value seen for PILA-ABCO). Higher maximum temperatures in the past July benefited focal trees for PILA-interspecific (b = 0.275) and PILA-CADE (b = 0.314), and was the top effect for both. Meanwhile, higher temperatures in the past spring tended to benefit interspecific competitors for PIPO-interspecific (b = -0.244), PILA-ABCO (b = -0.201), and PIPO-ABCO (b = -0.305). Higher temperatures in the past fall seemed to benefit focal trees at sugar pine sites (#1 effect for PILA-ABCO, #2 effect for PILA-Interspecific and PILA-CADE), but benefited interspecific competitors at ponderosa sites (#2 effect for PIPO-Interspecific and PIPO-CADE). For intraspecific ponderosa competition, though, the focal tree seemed better able to withstand the warm fall temperatures (b = 0.302). PIPO-PIPO competition showed the most effects, including a benefit to focal trees from high maximums in May of the past year (b = 0.344), and a benefit to competitors from high maximums in August (b = -0.263), April (b = -0.248), and July (b = 0.248) of the past year. Maximum temperatures in the current year showed little impact on competition ratios, other than for PILA-CADE which showed some benefit to competitors from high maximums in January-March (b = -0.245).

In examining precipitation and CMI, it seemed that competitors tended to benefit most from more moisture and precipitation, particularly in the past year (Table 3.5 D-E). Higher precipitation in July of the past year benefited competitors for PILA-PILA competition; higher CMI in July of the past year benefited competitors for PILA-PILA competition and PILAinterspecific competition. Higher precipitation and higher CMI in May and in September-November of the past year benefited competitors in PIPO-PIPO competition, but higher precipitation and higher CMI in August of the past year benefited focal trees. Incense cedar

benefited from wet summers in the current year as well as in the past year in PILA-CADE competition: incense cedar competitors benefited from more precipitation in July-September of the current year, and from higher CMI in July-September of the previous year as well as June-August of the current year. Precipitation did not affect competition for PILA-interspecific, PIPO-interspecific, PILA-ABCO, or PIPO-ABCO competition. PIPO-interspecific, PILA-ABCO, and PIPO-ABCO showed no impacts from CMI. The highest R² value was for PIPO-PIPO for both precipitation and CMI. PILA-CADE had the second highest R² for CMI only. All other R² vales were under 0.1.

3.4 Discussion

3.4.1 Species specific dendroclimatology

The method used here for studying competition is novel and effective for comparing the growth of two trees. Responses to temperature were as expected, and mostly consistent across species. Radial growth for all species tended to be positively impacted by warmer winters, which likely indicates that excessively cold conditions cause stress to trees. All vascular plants are prone to freezing-induced embolism (in which a tracheid is blocked by an air bubble) which can in turn lead to cavitation (in which a tracheid becomes filled entirely with air). This is caused by formation of ice crystals in the xylem which force air out of solution, then thaw and lead to bubbles and breaks in the water column (Tyree and Sperry 1989; Pittermann and Sperry 2006). Furthermore, while Sierra Nevada evergreens remain photosynthetically active year-round, temperatures below about 8°C can inhibit productivity by reducing CO₂ uptake (Fellows and Goulden 2013). At a temperature of 0°C, photosynthesis is reduced to half of maximum rates (Kelly and Goulden 2016).

Negative impacts of cold winters have been found before in dendroclimatology studies in mountainous regions (Johnson et al. 1988; Chhin et al. 2008*b*). However, studies of temperature effects on Sierra Nevada mixed-conifer forests are lacking, which makes this finding somewhat novel for this forest region. It is also partially contradictory to the finding in Garfin (1998) that the years with lowest tree growth had dry and warm winters for giant sequoias (*Sequoiadendron giganteum*), and dry and slightly cool winters for whitebark pine (*Pinus albicaulis*) and foxtail pine (*Pinus balfouriana*). Garfin attributed the negative influence of warm winters on giant sequoia to low snowpack in warm and dry winters, leading to less moisture availability later in the year.

Negative impacts of hot summers are an even more common finding (St. George 2014). While warmer summer temperatures are positive in some climates, they become a negative when they become high enough to increase evaporative water loss and slow photosynthesis (St. George 2014; St. George and Ault 2014). The Sierra Nevada tends to be very dry in the summer, so high summer temperatures may be harmful mainly in that they can induce or compound moisture stress, as in Reichstein et al. (2007). Higher temperatures contribute to a higher vapor-pressure deficit, which in turn contributes to drought stress (Williams et al. 2012). Higher temperature also leads to increased respiration and loss of carbohydrates, which can make carbohydrate reserves from the previous year important for growth in the current year (Pallardy 2007). This may explain why temperature in the past summer and spring are important for growth in the current year for sugar pine, ponderosa pine, and incense cedar. Spring and summer are the time when radial growth and height growth occur in California, which makes growing conditions particularly important during this time (Fowells 1941).

The chief exception to temperature trends was incense cedar, which showed weaker relationships to temperature and seemed to be more sensitive to temperature in the previous summer than in the current year. It is not entirely surprising that incense cedar shows different trends from other Sierra Nevada conifers; while pines and firs are all part of the Pinaceae family, incense cedar is more distantly related, in the Cupressaceae family. Hurteau et al. (2007) suggest that incense cedar is less sensitive to annual climate because it concentrates less of its growth into photosynthetic tissue, which leads to lower growth efficiency (Gersonde and O'Hara 2005). Fowells (1941) similarly suggested that incense cedar may be slower growing than other mixedconifer species, because it does not have an over-wintering bud but instead must continually invest in leaf elongation. Incense cedar was also unique in that it was negatively impacted by higher mean and maximum temperatures in November (although ponderosa was also negatively impacted by high maximums in September-November). This may be because warm periods that are followed by a large drop in temperature can be damaging to trees (Scharpf 1978). Incense cedars are also particularly vulnerable to sun scorch, which occurs when there are sunny days following cold and snow fall. This causes the leaves that are exposed to sun to desiccate and die, as the rest of the tree is still too cold for effective water transport (Scharpf 1978). Hence warm winter temperatures may be harmful if they are followed by or preceded by much colder temperatures.

A higher climate moisture index and higher precipitation were generally positive yearround for all species. In some moist climates, winter precipitation may have a negative effect as heavy snow loads may damage trees and persistent snowpack may delay the growing season (Chhin et al. 2008*a*). However, it is more common for winter precipitation to have a positive impact on growth as seen here, because winter snowfall has the largest impact on moisture

availability (St. George 2014). In California especially, precipitation is highly variable and most of the precipitation for the year falls in the winter (Dettinger et al. 2011). Snowmelt is an important determinant of water availability well into the warm season (Hamlet et al. 2007). Hence winter tended to be the most important time for precipitation for sugar pine, ponderosa pine, and white fir. While winter precipitation still impacted the growth of incense cedar, for this species the most critical time for precipitation was August of the present year and August-October of the past year. This is consistent with research showing that shoot growth in incense cedar continues until October, and increases significantly with more watering (Harry 1987).

Moisture availability (i.e. CMI) tended to be more critical during the summer growing season. This is consistent with a climate where most of the precipitation falls in the winter and most evapotranspiration occurs in the summer (Kelly and Goulden 2016). In such a moisturelimited climate, more precipitation and higher CMI tend to be beneficial almost year-round. Incense cedar again tended to be most impacted by CMI in summer of the previous year, while other species were most impact by CMI in summer of the current year. This may again be explained by the key role that summer and fall moisture play in shoot elongation for incense cedar (Harry 1987): more shoot growth in the previous year leads to benefits in the following year as photosynthetic ability is increased.

Past studies of ponderosa pine have underscored the importance of precipitation and moisture availability (especially summer precipitation and moisture) in determining growth (Watson and Luckman 2002, Peterson et al. 1993). Growth of ponderosa pines in western Canada showed positive correlations to both precipitation and the Palmer Drought Severity Index (PDSI), with the strongest effects from yearly precipitation and July precipitation for the current year (Watson and Luckman 2002). While the climate at Watson and Luckman's (2002) sites was

considered arid to semi-arid, they note that maximum precipitation tended to fall in June-July, with minimums in February-April (Watson and Luckman 2002). This is a very different weather pattern from the one in the Sierra Nevada, which means that the monthly/seasonal results are not necessarily directly comparable, although the positive impact of precipitation and PDSI in a moisture-limited climate likely still applies. In Colorado ponderosa pines, growth also showed positive relationships to both precipitation and PDSI, particularly in the summer (Peterson et al. 1993). Spring temperature was negatively correlated with growth (Peterson et al. 1993) - similar to the negative relationship found here between temperature in the past May and pine growth in the Sierra Nevada. The negative impact of warm springs may be related to snow pack. Guarín and Taylor (2005) found that April snowpack depth in Yosemite National Park had a significant negative correlation to tree mortality (i.e. more trees died in years with lower April snowpack), at sites that contained all the species present in this study. The association between mortality and low April snowpack was likely due to the reduced moisture availability later in the season. This may also explain the negative relationship that incense cedar and ponderosa pine both showed to higher minimum temperatures in the previous spring.

Studies of other Sierra Nevada mixed-conifer species are more lacking, probably because the species are less common outside the Sierra Nevada. After ponderosa pine, white fir has the broadest range outside the mountains of California. White fir in Utah have also been shown to exhibit the best growth under cooler and wetter conditions (Shane and Harper 1979). Studies that examine the dendroclimatology of a mixed-conifer Sierra Nevada forest are rare, though, which makes the research presented here novel. Bigelow et al. (2014) present the most similar research to the work conducted here: their research on the dendroclimatology of large Sierra Nevada conifers revealed responses to climate much like the ones found here. Namely, they found

generally positive responses to precipitation from all species, positive responses to winter minimums, negative responses to summer maximums, and a negative response to spring maximums in the past year (Bigelow et al. 2014). However, Bigelow et al. (2014) only found negative responses to summer temperature in white fir and incense cedar, and spring temperatures in the previous year were only found to impact ponderosa pine. The research presented here suggests that these effects may impact more species than previously thought. Bigelow et al. (2014) also limited their study only to trees >76 cm in DBH, while the average QMD for the competitor trees in this study was only 61 cm (Table 3.1). This suggests that these climatic effects also extend to somewhat smaller trees.

3.4.2 Intraspecific and interspecific competition and climate

Climatic conditions that were unsuitable for pines but neutral for other species tended to favor interspecific competitors. For example, ponderosa pine was the only species that showed a negative response to high maximums in September-November of the previous year, and therefore interspecific competitors gained an advantage from high October maximums at ponderosa sites. With intraspecific competition, however, ponderosa focal trees fared better than ponderosa competitors with high September-November maximums. Likewise, higher averages and higher maximums in May of the past year were shown to be negative for both pine species, but only for the pines; hence, interspecific competitors tended to far better under warm temperatures in the past spring (with the exception of PILA-CADE competition, which showed no effect). Intraspecific competition, however, once again showed a different trend, as both the focal tree and the competitor were negatively affected by warmer temperatures. While intraspecific competition between sugar pines showed no significant relationship to average

temperature at all, intraspecific ponderosa competition showed that warm temperatures in the past May favored the focal tree over the competitor. This may indicate that under adverse conditions, dominant trees show more resilience than their less dominant conspecifics.

Several other results also suggest that when conditions are generally favorable for all species, competitors show greater growth, while under generally negative conditions, focal trees show more growth. Competitors seem to benefit more from increased moisture and precipitation (i.e. conditions which were generally found to be beneficial). Focal trees fared better with high July averages in the previous year (PIPO-PIPO and PILA-CADE), high July maximums in the previous year (PILA-Interspecific, PILA-CADE, and PIPO-PIPO), low February averages in the present year (PILA-CADE), and low January-March maximums (PILA-CADE). One possible exception is December minimums: low December minimums favored competitors over focal trees for PIPO-Interspecific competition, which may indicate that large trees are more sensitive to extreme cold. Other trends were more mixed and difficult to interpret.

Overall this suggests that competitors fare comparatively better with more moisture and precipitation, cooler summers, and warmer winters. The inverse is also true: dominant trees fare comparatively better with and less moisture and precipitation, hotter summers, and cooler winters. This could be because older and larger trees tend to show slower growth than a smaller competitor does, so under positive conditions a small competitor will tend to grow more than a large focal tree. Under negative conditions, however, the focal tree will not suffer as much as the competitors will, because it will tend to have a more established root system (Van Lear and Kapeluck 1995), a better canopy position translating into a wider canopy, and thicker bark to protect it. Younger trees may also begin the growing season earlier and thus tend to show more overall growth, but with greater sensitivity to environmental signals (Rossi et al. 2008; Vieira et

al. 2009).

This interpretation has mixed support from the literature. While some studies have found that larger and/or older trees show more uniform growth and are less sensitive to climate (Vieira et al. 2009; Olivar et al. 2014), other studies have found that large trees are more sensitive (Guillemot et al. 2015) or equally sensitive (Chhin et al. 2008*b*; Linares et al. 2010). De Luis et al. (2009) suggest that these differences may be due to the fact that some studies compare climate sensitivity on the basis of age, while others compare on the basis of size, and these factors are difficult to separate. In an even-age plantation, de Luis et al. (2009) found that small trees were more sensitive to climate than large trees. Effects of size and age may also be confounded by effects of competition and suppression, as suppressed trees may be less sensitive to climate (Rozas and Olano 2013).

Another possible explanation is suggested by Piutti and Cescatti's (1997) finding that European beech trees (*Fagus sylvatica*) with high competition showed opposite responses to temperature and precipitation compared to trees with low competition. Trees with low competition responded positively to increased temperature and negatively to increased water availability, while trees with high competition responded negatively to increased temperature and positively to increased water availability. In this study of Sierra Nevada conifers, dominant focal trees may be less impacted by competition than their smaller competitors are. Therefore, due to the lower competition, focal trees respond more favorably to high temperatures and low moisture (which also fits with evidence that focal trees are more sensitive to low minimum temperatures). This is consistent with studies that have found that large trees fare better than small trees do in competitive environments (de-Dios-García et al. 2015), and that decreasing competition also decreases drought stress (Misson et al. 2003).

Another noteworthy finding was that intraspecific competition ratios between ponderosa pines showed the biggest effects (that is, the highest coefficient of determination) from all climate variables, except minimum temperature. The same cannot be said for competition between sugar pines, which indicates that intraspecific competition is not stronger per se than interspecific competition, but rather is species-specific. It is possible that the low significance of intraspecific competition between sugar pines is due to more extensive root grafting in this species, which reduces competition. While little is known about how common root grafting is in sugar pine vs. ponderosa pine or other species, sugar pine is in the same subgenus (Strobus) as eastern white pine (*Pinus strobus*), which is known to show frequent root grafting (Bormann and Graham 1959).

Root grafts may be detected by hydraulic excavation (e.g. McMinn 1963, Tarroux and DesRochers 2011), by transfer of chemicals between trees (e.g. Graham 1960), or their existence may be inferred by the presence of living stumps that continue to grow long after felling (e.g. Fraser et al. 2007). Living stumps have been recorded for all of the species that were included in this study (Lanner 1961), which suggests that at least some amount of root grafting may occur at these study sites, although the extent of potential root grafts is unknown. Root grafts can reduce intraspecific competition by allowing trees more equal access to water and nutrients through the shared root system (Tarroux and DesRochers 2011). Interspecific grafts may also occur, but are much rarer (Loehle and Jones 1990). Root grafts may also be more likely to form between larger and more dominant trees, because the process of forming a root graft is energetically expensive and requires large roots that are extensive enough to contact other roots (Tarroux and DesRochers 2011). Lev-Yadun 2011). However, suppressed trees may also be involved in root grafts (Lanner 1961), in which case, root grafts will tend to benefit the smaller tree(s) in the

relationship more than the larger one(s) (Loehle and Jones 1990, Lev-Yadun 2011).

The effects of root grafts on responses to thinning is somewhat debated. On the one hand, grafts that support living stumps after thinning may prevent residual trees from showing as much of a response to release, although thinning may still be beneficial (Tarroux et al. 2010). On the other hand, having access to a larger root system may allow trees to show even greater growth after thinning (Graham and Bormann 1966); Lev-Yadun (2011) even suggests that one of the reasons why trees form root grafts may be in order to take advantage of a neighbor's root systems after that neighbor dies. It may be that thinning shows increased benefits to large trees which are grafted to suppressed stumps, and decreased benefits to suppressed trees that are grafted to large stumps (Eis 1972). The potential effects of root grafts on competition and thinning responses should be considered in any study of these factors.

In the absence of such cooperative relationships, it is common to find stronger effects for intraspecific competition vs. interspecific (Perot and Picard 2012; de-Dios-García et al. 2015). This is consistent with the idea that decreases in species diversity lead to less diversity in resource use, which ultimately leads to intensified resource competition and a decrease in productivity (Loreau et al. 2001). However, different species may be differently impacted by climate and competition (Fernàndez-de-Uña et al. 2015), and while greater diversity may reduce stress from some sources, it does not necessarily reduce drought stress (Grossiord et al. 2014).

Competition ratios were also generally less impacted by conditions in the current year than conditions in the past year. This seems to fit with the idea that suppressed trees are more influenced by growth in the past year than by climate in the current year (Rozas and Olano 2013). This finding also seems reasonable in light of the idea that stem growth responses to changes in competition are expected to have some lag (Vincent et al. 2009). A suppressed tree

may need time to build up its root system, improve its canopy position, and increase its carbohydrate stores before it can show an increase in radial growth. Therefore positive conditions in the previous year tend to make more of a difference for competitors than conditions in the current year.

3.5 Conclusions

The dendroclimatic findings were consistent with the climate of the Sierra Nevada, which is moisture-limited and features cold winters and hot summers. More precipitation and more moisture availability were generally positive in all seasons, and growth was favored by more mild temperatures in the winter and summer. Competitive dynamics were affected to some extent by species – e.g. conditions that tended to be harmful for pines but not for other species naturally tended to benefit other species at the expense of the pines. On the other hand, conditions that were positive for both focal trees and competitors tended to benefit competitors more, while focal trees were better able to maintain consistent growth under negative conditions. These findings imply that large pines may be very resistant to future increasing temperatures and decreasing moisture, while smaller trees may fare worse. Findings also suggest that sensitivity to climate can vary with tree size, age, and/or dominance and canopy position, along with species. Not only that, but trees that are less affected by competition may even show opposite effects from trees that are heavily affected by competition, as suggested by Piutti and Cescatti (1997). There was also evidence that, while ponderosa pine shows relatively strong intraspecific competition, sugar pine shows little intraspecific competition, which suggests the possibility of root grafting. These results should be taken into account in future dendroclimatic studies, and in making management decisions about mixed-age stands. This research suggests many potential

future research directions, including examining impacts of varying levels of competition, impacts of climate post-thinning compared to pre-thinning, impacts of tree species diversity on climate sensitivity, and studies of the extent of root grafting in Sierra Nevada species.

APPENDIX

	ABCO	CADE	PIPO	PILA	All
BA (m ² /ha)	18.11	5.48	13.87	20.47	58.27 ¹
QMD all (cm)	37.40	45.02	65.14	78.89	50.99
QMD competitors (cm)	55.87	55.74	67.83	72.78	61.39
QMD focal (cm)	NA ²	NA ²	90.55	98.71	95.53
Competitor height (m)	26.0	21.2	29.3	26.0	25.8
Focal height (m)	NA ²	NA ²	34.1	34.7	34.4
Competitor crown diameter (m)	6.99	6.05	7.83	6.56	6.91
Focal crown diameter (m)	NA^2	NA ²	9.19	10.6	10.0

Table 3.1 The average basal area per plot, quadratic mean diameter, height, and crown diameter for each tree species, and for focal trees and competitor trees, respectively. The 'All' column contains a total for BA and an average for other values.

¹Some stands contained small numbers of Jeffrey pine (*Pinus jeffreyi*) or red fir (*Abies magnifica*), which accounts for the slight difference between the sum of the basal areas for the species listed, and the total basal area.

 2 NA = not applicable. No white fir (ABCO) or incense cedar (CADE) were selected as focal trees.

Species	Chronology	# trees	Mean	Standard	Absent	Common interval	# trees in	Intercore			
	time span		sensitivity	deviation	rings (%)	time span	common interval	correlation			
ABCO	1846-2014	34	0.1135	0.1315	0.045	1951-2013	30	0.312			
CADE	1812-2014	13	0.1618	0.2680	0.207	1903-2014	8	0.385			
PIPO	1718-2014	30	0.1343	0.1681	0.293	1872-2013	21	0.274			
PILA	1785-2014	34	0.1067	0.1356	0.048	1902-2014	25	0.294			

Table 3.2 Statistics for standard tree ring chronologies for each tree species. ABCO = *Abies concolor*, CADE = *Calocedrus decurrens*, PIPO = *Pinus ponderosa*, PILA = *Pinus lambertiana*.



Figure 3.1 The study site was located in northern California, marked with a star on the inset map. Plots were located in several different but closely spaced study areas as shown.



Figure 3.2 Standardized ring width chronologies for each species. PIPO = *Pinus ponderosa*, PILA = *Pinus lambertiana*, ABCO = *Abies concolor*, CADE = *Calocedrus decurrens*.

A. Mean temperature



Figure 3.3 Tree response to mean temperature, climate moisture index, precipitation, minimum temperature, and maximum temperature by species. Dark coloring indicates a negative relationship with growth, while light coloring indicates a positive relationship according to a linear regression model. Numbers indicate order of significance (1 is the most important relationship according to standardized partial regression coefficients). All relationships that are shown are statistically significant (p < 0.05). PILA = *Pinus lambertiana*, PIPO = *Pinus ponderosa*, ABCO = *Abies concolor*, CADE = *Calocedrus decurrens*.
A. Mean temperature



Figure 3.4 Competition ratio response by species. Dark coloring indicates that conditions favored competitor growth, while light coloring indicates that conditions favored focal tree growth. Numbers indicate order of significance (1 is the most important relationship according to standardized partial regression coefficients). All relationships that are shown are statistically significant according to a linear regression model (p < 0.05). N.S. indicates that no relationships were significant. PILA = Pinus lambertiana, PIPO = Pinus ponderosa, ABCO = Abies concolor, CADE = Calocedrus decurrens. IR = Interspecific, and includes all trees of a different species from the focal tree.

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CHAPTER 4

CONCLUSIONS

Sierra Nevada mixed-conifer forests present an ecosystem that has been shaped by fire and fire suppression, and that will be shaped by climate change and management decisions. Fire suppression has increased both levels of fuel and levels of competition in many forests of the American west. Future management may be able to restore historical stand structures and fire regimes, but the climate will be changed beyond historical means. In order to understand the past, present, and future of these forests, it is necessary to understand potential fire behavior, responses to climate, and responses to competition.

In Chapter 2, custom fuel models were built in order to better understand current conditions and potential fire behavior in the northern Sierra Nevada. These models revealed differences in fuel loads and fire behavior based on the dominant tree in a stand. Plots where a ponderosa pine was the dominant tree showed lower loads of fine fuels than sugar pine sites – a difference that was better explained by focal tree species than by differences in stand structure. This difference in fine fuels corresponded to a difference in fire behavior: the sugar pine fuel model tended to show more extreme fire behavior. Compared to potentially applicable standard fuel models, the custom fuel models showed significantly different fuel loads. Of the all the models that were run, the TL8 model (long needle litter) tended to show the most extreme fire behavior, while the TL3 model (moderate load conifer litter) tended to be intermediate between the ponderosa model and the sugar pine model. Further research is needed in order to calibrate fuel models and verify their ability to predict and model fire behavior; however, this research suggests that standard fuel models may fail to reflect actual conditions in the Sierra Nevada, and that species-specific fuel models may be called for in this area.

In Chapter 3, dendroclimatology was used to study how climate impacted each Sierra Nevada mixed-conifer species, and how competitive interactions between dominant trees and their smaller competitors (both interspecific and intraspecific) were impacted by climate. Each species tended to show consistently positive responses to higher precipitation, higher Climate Moisture Index (CMI), and higher winter temperatures. Pines showed negative effects from warm spring temperatures in the past year, likely because warmer spring temperatures lead to lower spring snowpack, which leads to greater drought stress later in the year. Ponderosa pine, sugar pine, and white fir were all negatively impacted by hot summers in the present year, while incense cedar was instead negatively impacted by hot summers in the past year.

Competitive interactions tended to show that climate could impact which species had a competitive advantage, through one of two observed mechanisms. Conditions could either favor one species over another (e.g. warm temperatures in the past May benefited interspecific competitors over pines), or conditions could favor one dominance class over another (i.e. favor focal trees over competitors or vice versa). There was some tendency for harsher conditions to favor dominant trees, while milder conditions favored competitors. For minimum temperatures, though, this trend was reversed and milder conditions tended to favor focal trees, which may indicate that large trees are more sensitive to extreme cold. Conditions in the past year also tended to influence competitive dynamics more than conditions in the present year.

Results help to underscore the importance of fire, climate, and competition in California ecosystems. Thinning treatments are expected to be beneficial in reducing competitive stress and potentially allowing for greater climatic resilience. Paired with prescribed fire, thinning treatments are also expected to reduce fuel loads and restore stand structure to something closer to historical conditions. Future research will examine the effects of thinning treatments on the

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plots used in this study.

Future studies of these plots will incorporate physiological measurements of tree water use into studies of competition and species differences in the Sierra Nevada. Data will also be collected on post-thinning stand structure, understory vegetation, fuel loads, and radial growth. The fuel models developed here will allow ready comparison of pre-thinning and post-thinning fuels and predicted fire behavior. The dendrochronology employed here will facilitate studies of growth responses to radial release, and of the effects of thinning on competition and climatic resilience. In time, prescribed burns may be conducted to reduce fuel loads and promote a natural fire regime, allowing a chance for more accurate fire modeling. These data also leave ample room for modeling responses to climate change scenarios – both in terms of modeling fire behavior and modeling tree growth and possible shifts in species composition. This research provides a part of an important foundation from which many future studies will be built.