THE PERSISTENCE OF OAK WOODLANDS IN ALTERED FIRE REGIMES OF THE PACIFIC NORTHWEST

DEBORAH GABRIELLE NEMENS

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Committee:

Ernesto Alvarado, Chair

J. Morgan Varner

Peter Dunwiddie

Janneke Hille Ris Lambers

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School of Environmental and Forest Sciences

University of Washington

Abstract

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Deborah Gabrielle Nemens

Chair of the Supervisory Committee:
Ernesto Alvarado, Research Associate Professor
School of Environmental and Forest Sciences

Pacific Northwest oak woodlands and savannas are fire-resilient communities dependent on frequent, low-severity fire to maintain their structure and understory species diversity, and to prevent encroachment by fire-sensitive competitors. These important ecosystems have been severely reduced in both extent and quality during more than a century of land use change and altered fire regimes. The re-introduction of fire into these transformed ecosystems is viewed as essential to their restoration, yet can be fraught with potential unintended consequences. We examined oak response following re-introduction of fire into two distinct oak ecosystems: formerly suppressed California black oak (*Quercus kelloggii* Newb.) woodlands subject to repeated wildfire, and Garry oak (*Quercus garryana* Douglas ex Hook.) woodlands experiencing "first entry" restoration burns. Both the black oak woodlands of Lassen National Forest, California, and

the Garry oak woodlands of Joint-Base Lewis-McChord, Washington have experienced shifts in vegetative structure and composition during long fire-free intervals. Black oak canopy dominance and vigor of resprouts were positively correlated with increased fire severity (R^2=0.41, 0.49, respectively), but black oaks that had sprouted following top-kill in the first fire were easily top-killed in the second fire, even at low severities, implying that long-term survival of regenerating black oaks in fire-prone regions is uncertain. Top-kill of Garry oak was rare (8%) in three prescribed burns, despite high levels (95%) of crown scorching and irrespective of proportional duff consumption around oak bases, demonstrating the high resilience of Garry oaks to first entry burns when compared to historic fires. Bud kill (as measured by lack of bud burst the spring following burns) in Garry oak crowns was correlated with crown scorching (R^2=0.42), but responses were highly variable, especially at high levels of scorching. The results of these studies indicate that fire adaptations may be specific to particular fire regimes, and that vegetative responses in oak woodlands are highly dependent on the adaptive traits of individual species. Restoration efforts in oak woodlands are more likely to be successful when reintroduction of fire is carefully tailored to target species, and modeled on characteristics of past disturbance, taking into account altered conditions of modern landscapes.

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DEDICATION

[For my father, Douglas, who always wondered when I would stop working for "some outfit or other" and go back to school. Sorry it took me so long, Dad; I know you would have been proud.]

INTRODUCTION

Fire plays a critical role in shaping plant communities and ecosystems worldwide (Bond and van Wilgen 1996, Bond and Keeley 2005, Bowman et al. 2009). A major earth system process, fire exerts a strong regulatory influence on vegetative diversity, species distribution, community structure, and landscape heterogeneity (Brockway and Lewis 1997, Schoennagel et al. 2008, Bowman et al. 2009). Frequent fire regimes can lead to the development and maintenance of unique plant communities, often surpassing the controlling influence of climate on vegetative growth, especially in fire-prone landscapes (Abrams 1992, Bond et al. 2004, Keeley and Rundel 2005).

Long a dominant force in plant evolutionary history in many of the world's biomes, fire has promoted the adoption of adaptive traits in many species that are subject to frequent and/or severe fire regimes (Bond and Midgley 2001, Schwilk and Ackerly 2001, Keeley et al. 2011). Over time, the existence of these traits in plant populations can result in species assemblages that are at least partially dependent on particular fire regimes for their persistence on the landscape. Frequent disturbance by fire can result in the preservation of early-seral vegetative stages by limiting the in-growth of fire-intolerant species in frequent-fire ecosystems (Vesk and Westoby 2004, Keeley et al. 2011).

Typical examples of fire-dependent ecosystems, woodlands and savannas have existed for millennia in concert with natural and anthropogenic fire (Swanson et al. 2011, Staver et al. 2011b). These ecosystems have thrived under frequent, low-severity fire regimes, which maintain their characteristic open canopy structure and often diverse herbaceous understories. Low-intensity fires are propagated in light "flashy" fuels, eliminating woody ingrowth of fire-

intolerant species, and opening areas of bare soil for germination of herbaceous plants. Without this regular disturbance, open woodlands and savannas in many regions would be replaced by closed-canopy forests through the normal processes of stand development.

During the last century, human intervention has resulted in dramatic changes to fire regimes in the western United States. The consequences of large-scale fire exclusion for western forests and woodlands are well documented (Brown and Arno 1991, Covington and Moore 1994, Peterson et al. 2005): increases in stand density and the resulting accumulation of fuels, and changes in structure and composition of forests. These novel, fuel-rich plant communities often burn at higher severities than the same landscapes under past fire regimes (Mallek et al. 2013, Steel et al. 2015). In long-unburned fire-adapted ecosystems, the consequences of returned fire after extended fire-free intervals can be dramatic. In areas where fire was historically a commonplace occurrence, the return of this key disturbance agent can be catastrophic, causing extensive mortality and potentially altering vegetative states (Varner et al. 2007, Hood 2010, O' Brien et al. 2010).

Oak woodlands are among the most fire-dependent ecosystems in the northwestern United States (Agee 1992). These early-seral vegetative communities are dependent on frequent, low-severity fire to maintain their open structure and high understory species diversity, as well as to prevent invasion by fire-sensitive competitors (Crawford and Hall 1997, Livingston et al. 2016). These habitats have high cultural and ecological values for people and wildlife, and harbor plant and animal diversity not found in adjacent conifer-dominated forests. Lacking fire, these ecosystems face increased degradation due to woody encroachment both in the canopy and in the understory, including invasion by non-native plants (Hanna and Dunn 1996, Livingston et al. 2016). The reintroduction of fire into oak habitats is considered to be critical to their

restoration (Agee 1996, Stanley et al. 2008, Dennehy et al. 2011, Engber and Varner 2012), however potential unintended consequences are poorly understood, and warrant further investigation.

Both California black oak and Garry oak woodlands have experienced recent declines due to the exclusion of natural fire, as well as the cessation of Native American burning practices that were used to manage these landscapes for millennia (Stewart et al. 2002, Anderson 2005, Storm and Shebitz 2006, Cocking et al. 2014, Crotteau et al. 2014, Long et al. 2016b). The absence of fire has allowed substantial encroachment of these communities by fire-sensitive plant species that compete directly with oaks and degrade the understories of these important habitats (California Partners in Flight 2002, Dunwiddie and Bakker 2011, Altman 2011, Cocking et al. 2014, Livingston et al. 2016). Both of these species exhibit varied fire-adaptive strategies, including protective bark, and the maintenance of latent buds that allow for prolific sprouting from root collars, stems and crowns following high-severity disturbance. These adaptations give a competitive advantage to oaks following fire events, and can be a mechanism of oak woodland restoration to landscapes where they have been largely extirpated (Cocking et al. 2014, Crotteau et al. 2014).

This thesis examines the outcomes of the reintroduction of fire to long-unburned oak woodlands in two distinct scenarios: mixed-severity wildfire and managed prescribed fire. The first chapter examines the impacts of recurring wildfire on formerly suppressed California black oak woodlands in the process of regeneration following a previous wildfire. The second chapter is a study of the effects of prescribed restoration fires in Garry oak woodlands, evaluating potential mechanisms of tree injury in “first entry” burns.

Chapter 1. CONSEQUENCES OF RECURRENT WILDFIRE FOR THE FUTURE OF CALILFORNIA BLACK OAK WOODLANDS IN LASSEN NATIONAL FOREST, CALIFORNIA

1.1 INTRODUCTION

Fire exerts a strong selective force on vegetation, interrupting successional processes. When fires are frequent, they maintain early-seral conditions and prevent the establishment of fire-intolerant species (Bond and Van Wilgen 1996, Bond and Keeley 2005). In response, some species have developed characteristics such as resistant bark, fire-stimulated germination, adventitious buds, and vegetative regeneration that confer tolerance to surface fires that are lethal to species lacking these adaptations (Keeley 1991, Bond and Midgley 2001, Vesk and Westoby 2004). Some fire-tolerant species are hypothesized to have evolved enhanced flammability in order to promote fire (Mutch 1970, Fonda 2001, Engber and Varner 2012), thus enhancing conditions ideal for their proliferation, and conferring competitive advantages over fire-intolerant species. Woodland and savanna plant communities have evolved over millennia to withstand the effects of frequent, low-severity fire regimes. These ecosystems exist worldwide largely due to the role that fire plays in the regulation of their community structure and composition (Bond and Van Wilgen 1996, Bond and Keeley 2005). These regular patterns of disturbance have created unique vegetative communities that support diverse species assemblages (Swanson et al. 2011).

Formerly extensive, California's oak woodlands have suffered substantial losses in both area and habitat quality since Euro-American settlement. The state's oak woodlands are threatened primarily by development at lower-elevations, but even in protected areas and at higher-elevations, these habitats are in decline (California Partners in Flight 2002). One significant contributing

factor to this decline has been the removal of frequent fire from California's wildlands. More than a century of fire exclusion throughout the western U.S. has interrupted historic patterns of fire activity on the landscape (Agee 1996, Sugihara et al. 2006), resulting in conifer invasion into formerly oak-dominated landscapes. As ecosystems that are reliant on fire to maintain early-seral vegetative conditions, oak woodlands have consequently experienced dramatic changes in plant community structure, function and composition. This has resulted in significant habitat and biodiversity losses (Dunwiddie and Bakker 2011, Altman 2011, Livingston et al. 2016).

Montane California black oak (*Quercus kelloggii* Newb.) woodlands of the Pacific northwest have not escaped the repercussions of shifting fire regimes, and have experienced a slow yet dramatic decline since the advent of large-scale fire exclusion (Cocking et al. 2014, Crotteau et al. 2014, Long et al. 2016a). Since the turn of the last century, fire return intervals in this region have increased dramatically. Dendrochronological studies indicate that frequent fire (between-fire intervals of less than 20 years) was common in many Pacific Northwest landscapes that have not burned in the most recent century (Taylor 2000, Sugihara et al. 2006, Bekker and Taylor 2010, Van De Water and Safford 2011). Historically, these ecosystems were elements of a complex mosaic of oak and pine-dominated woodlands and savannas, conifer forests, and shrublands (Collins et al. 2016). This heterogeneous landscape was shaped by both natural and human-influenced fire regimes. Frequent fire was used by the indigenous people of California over millennia to maintain critical resources found in oak woodlands and savannas (Stewart et al. 2002a, Anderson 2005, Long et al. 2016a). Historically, frequent fires in oak woodlands were driven largely by litter and grass fuels, and often burned at low intensities unlikely to kill overstory trees (Skinner and Taylor 2006, Cocking et al. 2014, Long et al. 2016b). Frequent burning prevented the accumulation of heavy fuels in oak woodlands, and maintained an open canopy that allowed

for herbaceous understory development, perpetuating the surface fires that maintained oaks as overstory dominants while preventing the recruitment of competing conifers. When fire is absent, shade intolerant early-seral species such as oaks decline due to increased competition from encroaching (shade-tolerant) native conifers. Continued suppression from neighboring conifers can weaken oaks and ultimately cause mortality (Cocking et al. 2012). Conifer encroachment also causes fundamental shifts in the structure and function of oak woodlands, engendering a more pyrophobic system that excludes low-severity fire, and is more vulnerable to stand-replacing wildfire under extreme conditions. In disturbance-dependent ecosystems, fire exclusion can eventually lead to conversion into distinct vegetative communities (van Wagtendonk 1984, Crotteau et al. 2013).

Over thousands of years, California black oaks have sustained both human and wildlife populations, providing a wide array of ecological resources. California black oak was arguably the most important oak species for many of California's native peoples (Plumb 1981, Long et al. 2016b). Black oak was highly prized for the edibility of its acorns and the utility of its wood, and is considered by anthropologists to be a "cultural keystone" species. Black oak savannas and woodlands were maintained by tribes through regular burning to facilitate acorn harvesting, clear undergrowth and competing plants, remove acorn pests, increase the production of acorns and understory plants and fungi, increase forage for wildlife, and stimulate shoots for construction and craft materials (Stewart et al. 2002b, Anderson 2005). Large, open-grown oaks provide the greatest quantities of acorns, and are most valued by tribes for harvesting purposes (Long et al. 2016a). Oak woodlands in California are key contributors to the state's biodiversity, harboring 48 plant species that are listed as rare, threatened or endangered by the state, as well as eight species that are federally listed (California Partners in Flight 2002). The habitat values of black oak woodlands

for birds and wildlife are also diverse. Mature oak trees provide large nesting cavities used by numerous species of birds and mammals and produce mast that is a critical food source for many varieties of wildlife (Long et al. 2016b).

California black oak has several distinct fire-adaptive mechanisms. It has the ability to survive both low- and moderate-intensity surface fires, to reproduce from seed after fire, and to regenerate from latent buds after high-intensity fire has destroyed all of its above-ground vegetation. In this sense, it can be categorized as a fire resister, endurer, and an evader as classified by Rowe (1983). Because of black oak's protective bark, surface fires in frequently burned woodlands rarely generate enough heat to injure the cambium, and mature trees are generally able to survive these intensities. This characteristic may be enhanced by the production of flammable litter, which burns quickly, preventing more damaging long-duration smoldering fires (Engber and Varner 2012). In the case of more intense fires where above-ground vegetation is killed, black oak is able to resprout vigorously from its base, outpacing the growth of competing conifers, which must regenerate from nearby surviving seed sources (Donato et al. 2009, Cocking et al. 2012, Collins and Roller 2013, Crotteau et al. 2014). This process is made possible by the substantial carbohydrate reserves and basal bud banks maintained by black oak, which enable rapid post-fire recovery. This diverse array of adaptive strategies allows black oak not only to survive variable fire severities, but to gain a temporary competitive advantage over other tree species in a variety of fire regimes. As such, it is considered to be fire-dependent in all the ecosysytems in which it is found (Fryer 2007).

The shift in fire regimes over more than a century has resulted in the transition of oak woodlands and savannas to dense mixed conifer forests. Opportunities exist, however, for restoration of suppressed oaks in these forests following moderate and high-severity wildfires.

Previous studies (Cocking et al. 2014, Crotteau et al. 2014) have found that a single high-severity wildfire can re-establish oak overstory dominance following decades of ingrowth of competing fire-sensitive conifer species. These authors hypothesized that with recurring low-severity fire, oaks would remain dominant in the overstory, conifer regeneration would be inhibited, and pre-suppression era oak woodlands could be restored. Cocking et al. (2014) developed a conceptual model wherein suppressed oak woodlands are resurgent after stand-replacing fire, and are able return to former steady-states via negative feedbacks between fire and fuels, maintaining these communities. Here, we examine the effects of repeated fire in these altered landscapes in order to evaluate this model.

We examined black oak sprout vigor and shifts in patterns of species composition across a spectrum of fire severity combinations following two mixed-severity wildfires that burned over the same area in 2000 (Storrie Fire) and again in 2012 (Chips Fire) in California's Lassen National Forest. We asked the following questions: i. is the transition to oak dominance reinforced with a second wildfire? ii. did oaks that were subjected to repeated top-kill continue to sprout, and did their response vary across burn severities? iii. were there interactive effects on oaks between the two fires? iv. what are the effects of a second fire on regenerating oak stands, and how do these effects differ across burn severities? and v. what are the impacts of a second fire on conifer regeneration? Based on the results of previous studies (Cocking et al. 2014, Crotteau et al. 2014, Hammett et al. 2017), we hypothesized that successive wildfires would set oak woodlands on a trajectory of recovery, given their competitive advantages over native conifers in a recurrent fire scenario. These results have implications for the management and restoration of oak woodlands across northern California and perhaps more broadly where changes in fire regimes have impacted fire-dependent ecosystems.

1.2 METHODS

1.2.1 *Study Area*

The study site is located within the intersection of the Storrie and Chips Fire extents in the southern Cascade Range in the Lassen National Forest in northern California, USA (**Figure 1.1**). Soils of the site are typically young and of volcanic origin, but also include granitic soils in the southernmost portion of the study area, where the Cascades intersect the Sierra Nevada (Cocking et al, 2014). Climatic patterns are Mediterranean, with warm dry summers, and cool, wet winters, during which 95% of the annual precipitation is received. Elevations range from 900 to 1800 m above sea level (asl), with steep slopes dominating the terrain. Forest cover type in the study area is classified as Sierra Nevada Mixed Conifer (Eyre 1980); common overstory species were ponderosa pine (*Pinus ponderosa* var. *ponderosa* C. Lawson), sugar pine (*Pinus lambertiana* Douglas), coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), white fir

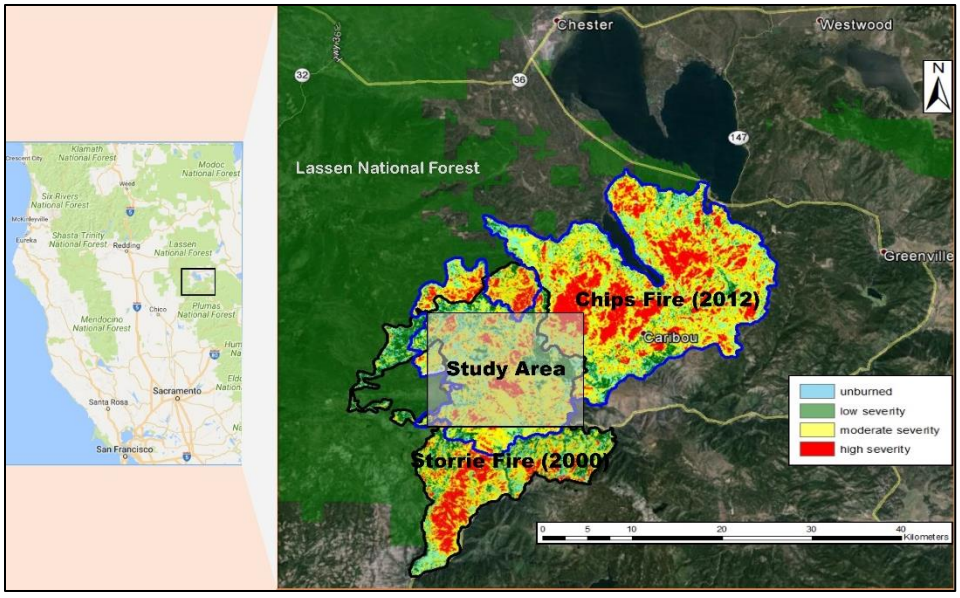

Figure 1.1: Study area in the Lassen National Forest, California. Study fires areas are color-coded by burn severity as classified by Monitoring Trends in Burn Severity.

(*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), and California black oak. Common shrub species were deerbrush (*Ceanothus integerrimus* Hook. & Arn.), greenleaf manzanita (*Arctostaphylos patula* Greene), snowbrush (*Ceanothus velutinus Douglas ex Hook.* var. *velutinus*), Sierra gooseberry (*Ribes roezlii* Regal var. *roezlii*), mountain whitethorn (*Ceanothus cordulatus* Kellogg), and trailing snowberry (*Symphoricarpos mollis* Nutt.).

The Storrie Fire burned approximately 23,000 ha in August of 2000 in both the Plumas and Lassen National Forests (hereafter "Plumas" and "Lassen"). The Chips Fire burned approximately 30,000 ha in the same area, beginning in the Feather River canyon of the Plumas, and quickly spreading onto the Lassen in August of 2012. The Chips Fire burned into the perimeter of the Storrie Fire, creating a reburn area approximately 9,900 ha in extent. Both fires burned at a mix of severities, allowing sampling across a spectrum of combined burn severity strata. Data collection occurred in the summer of 2015, three years after the Chips Fire, and 15 years after the Storrie Fire.

1.2.2 *Field Sampling*

Ninety-three randomly established fixed-area plots were established inside and adjacent to the 9,900 ha reburn area (**Figure 1.1**). Plots were evenly distributed across sixteen burn severity combinations (unburned in Storrie and unburned in Chips to high-severity in Storrie and high-severity in Chips, **Figure 1.2**), and ranged in elevation from 900 to 1400 m asl. When comparing fire effects on vegetation, severity categories used to classify plots represent the following changes to forest canopy: unburned (less than 10% overstory mortality), low (between 10 and 25% mortality), moderate (25-75% mortality), and high (greater than 75% mortality) (Miller et al. 2009). Plot locations were selected randomly within the previously defined strata using ArcGIS

(ESRI, Redlands, California, USA). Plots were located a minimum of 100 m from roads and trails. Areas with evidence of subsequent management activity (i.e. post-fire salvage, fuel mastication), which could bias our data, were avoided.

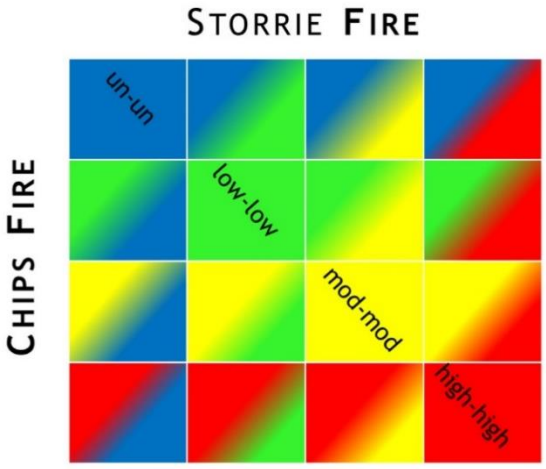

Figure 1.2: Visualization of factorial sampling method across the spectrum of burn severity strata combinations for both fires.

In order to characterize stand composition before and after each fire, a 0.045 ha fixed-area circular plot was established for measurement of overstory characteristics. Within each plot, we recorded the species, diameter at breast height (1.37 m, "DBH"), and percent live crown for all live trees > 2.5 cm DBH. Basal diameter, snag condition class (following Thomas, J.W.; Anderson, R.G., Maser, C. and Bull 1979) and fire history (i.e. killed in Chips Fire, top-killed in Storrie only, survived both fires) were recorded for all dead stems > 1.37 m tall. Designations of Storrie Fire, Chips Fire, and other causes of mortality were made based on snag condition class and other visual cues (e.g., presence of unconsumed bark on snags, substantial consumption of snags and stumps, considerable decay of old snags). Substantially burned snags and stumps were identified to species where possible using remnant bark or wood samples, and classified by genera where field identification was unreliable due to deterioration of samples. These field methods

have been used successfully in other post-fire mortality assessments in the study area (Cocking 2011, Cocking et al. 2014, Hammett et al. 2017). Locations for all measured stems within each plot were mapped and recorded using distance and azimuth from plot center.

Oak sprout vigor was assessed within each larger plot in a focal oak subplot. . We located the closest living California black oak to plot center above 1.37 m tall, and used that individual as the locus for a 10 m radius (314 m^2) circular plot. All living and dead sprouts emerging from the base of this "focal oak" were counted and their origin (sprouted post-Storrie Fire or sprouted post-Chips Fire) and diameter at 20 cm above ground level was recorded. Substantial size differences between 15-year old sprouts (Storrie Fire origin) and three-year old sprouts (Chips Fire origin), as well as minimal consumption of live (at the time of the Chips Fire) vegetation in the second fire made identifying each sprout generation unambiguous (Hammett et al. 2017). Live and dead oak sprout clump crown diameter and live emergent height were measured for this and two additional oaks per plot. Within each circular sub-plot, ocular estimates of percent cover for all shrub species were recorded in two equally sized opposing quadrants using the following cover classes: <1%, 1-10%, 11-25%, 26-50%, 51-75% and >76%. Diameter, species, and cause of mortality (where possible) were recorded for all stumps within the sub-plot.

We examined tree regeneration within a second sub-plot located in the center of the main plot across the spectrum of fire severity combinations. Within this 4.2 m radius (56.48 m^2) circular plot, all woody plant species were mapped using distance and azimuth from plot center. Tree seedlings and saplings greater than 10 cm tall were recorded in the following height categories: 10-25 cm; 25-50 cm; 50-75 cm; 75-137 cm; and >137 cm but less than 2.5 cm DBH. Seedlings < 10 cm tall were considered ephemeral and excluded from sampling due to their high mortality rates (Crotteau et al. 2013).

1.2.3 *Data Analysis*

We used Relative differenced Normalized Burn Ratio (RdNBR) values for each fire as our predictor variable in all analyses of vegetative response across the spectrum of fire severity combinations. RdNBR values are derived from satellite imagery using particular infrared spectra to detect and classify burn scars on the landscape by detecting differences in pre- and post-burn imagery, based primarily on changes to chlorophyll and moisture content in vegetation and soils (Miller and Thode 2007). This widely used continuous measure of burn severity has been shown to be sensitive to pre-fire stand condition, and an accurate burn severity metric across diverse vegetative types (Miller and Thode 2007, Miller et al. 2009).

In order to examine the effects of Chips Fire severity on continued oak dominance, compositional changes to the canopy across a spectrum of fire severities were measured. This was done by determining the species and fire history for each overstory stem (i.e. which fire caused mortality), and using these data to calculate pre- and post-fire live proportion of oaks and competing conifers (white fir and Douglas-fir) for each plot. Post-fire live canopy proportion was subtracted from pre-fire canopy proportion to produce a change in dominance for each classification (oak or competing conifer). Chips Fire severity (as measured by RdNBR values) was used as the explanatory variable, with change in dominance as response, in a generalized linear regression model examining their relationship.

Black oak sprouting response was quantified using sprout density for each measured oak sprout clump (number of stems per clump), sprout basal area (cm^2 per clump), maximum sprout height (m), and mean clump crown area (m^2 per clump). The relationships between the various sprout response metrics and Chips Fire burn severity, as well as potential interactions between the

two fires on sprout vigor, were analyzed using generalized linear modeling. Goodness-of-fit was tested using chi-squared tests (Huntsberger and Billingsley 1981).

Logistic regression modelling was used to analyze the impact on sprout top-kill of Chips Fire severity. Goodness-of-fit was evaluated using a likelihood ratio test, and predictive ability of the model by calculating the area under the receiver operating characteristic curve (ROC) for the model (Egan 1975, Saveland and Neuenschwander 1990, Pearce and Ferrier 2000). Density of conifer regeneration was analyzed using ANOVA, with burn severity as treatment. All analyses were conducted using the R statistical program (The R Core Development Team 2014).

1.3 RESULTS

Following the second wildfire, canopy composition shifted towards greater dominance of oak in the overstory with increasing burn severity ($P<0.0001$, $R^2=0.43$). Competing conifers were killed at higher burn severities, while the majority of oaks survived or resprouted after the fire. Shifts in overstory dominance led to the creation of oak-dominated stands at higher Chips Fire burn severity values (**Figure 1.3**). In plots that had burned at higher severities in the Storrie Fire (i.e. all overstory conifers were killed), relative dominance was unchanged (no conifers were added to the overstory, and extant oaks either were not top-killed or resprouted following top-kill). This phenomenon was observed across a range of Chips Fire severity values, and occurred in 20 of our plots. These were excluded from analysis, due to the potential for misinterpretation of these null values.

Table 1.1: Black oak sprout clump metrics for measured live post-Storrie Fire and post-Chips Fire sprouts. Mean and (standard deviation) values are given for each metric. Plots which did not have measurable sprouts resulting from each fire event are excluded from calculations.

	Storrie Fire sprouts	Chips Fire sprouts
Frequency	18	60
Basal area (cm²/clump)	1,014.58(745.70)	78.04(62.24)
Height (m)	4.06(1.56)	2.18(0.56)
Density (stems/clump)	10.95(6.93)	40.18(26.88)

More than 99% of oaks that sprouted after the Storrie Fire resprouted after being top-killed in the Chips Fire. Post-Chips Fire sprout vigor was positively correlated with Chips Fire burn severity. Both emergent sprout height ($P<0.0001$, $R^2 = 0.26$) and sprout basal area ($P<0.0001$, $R^2 = 0.49$)

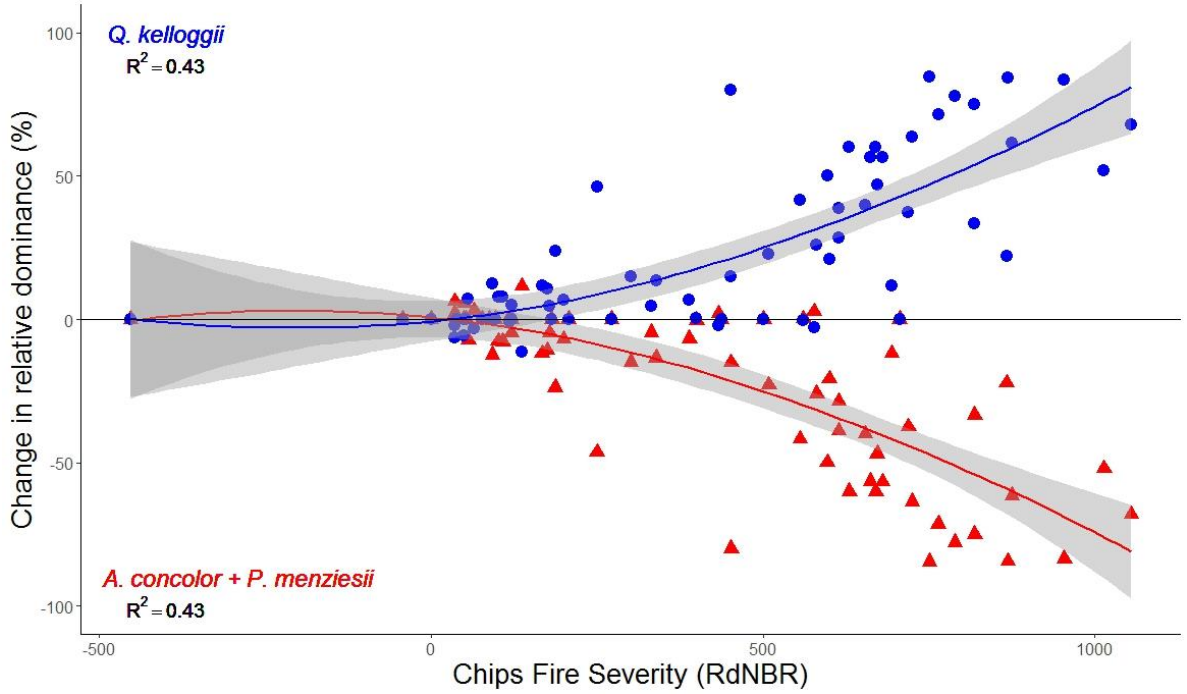

Figure 1.3: Change in overstory proportional dominance after Chips Fire by fire severity. Circles represent oaks, triangles represent conifer competitors (*A. concolor* and *P. menziesii*).

increased with fire severity (**Figure 1.4**). Surviving post-Storrie Fire sprout clumps (n=19) had a maximum height of 7.9 m, while post-Chips Fire sprouts (n=60) reached 4.2 m in height in three growing seasons after the fire. Sprouts of Chips Fire origin were more abundant, but smaller in stature than those that sprouted following the Storrie Fire (**Table 1.1**). Measurements presented here are for live sprouts; i.e.: post-Storrie sprouts that were not burned in the Chips Fire (as these were top-killed in the second event), and post-Chips sprouts that generated either from pre-Storrie oaks or post-Storrie sprouts that had been top-killed (as fire-induced mortality was the mechanism that induced the sprout response).

Generalized linear modeling of post-Chips Fire sprout metrics stratified by categorized Storrie Fire severity yielded no significant interactive effects between burn severities in the two fires (Appendix, **Fig. A**). Two measurements of sprout vigor (sprout basal area and emergent sprout height) were modeled; neither model demonstrated significant interactions (P=0.24 and P=0.62, respectively).

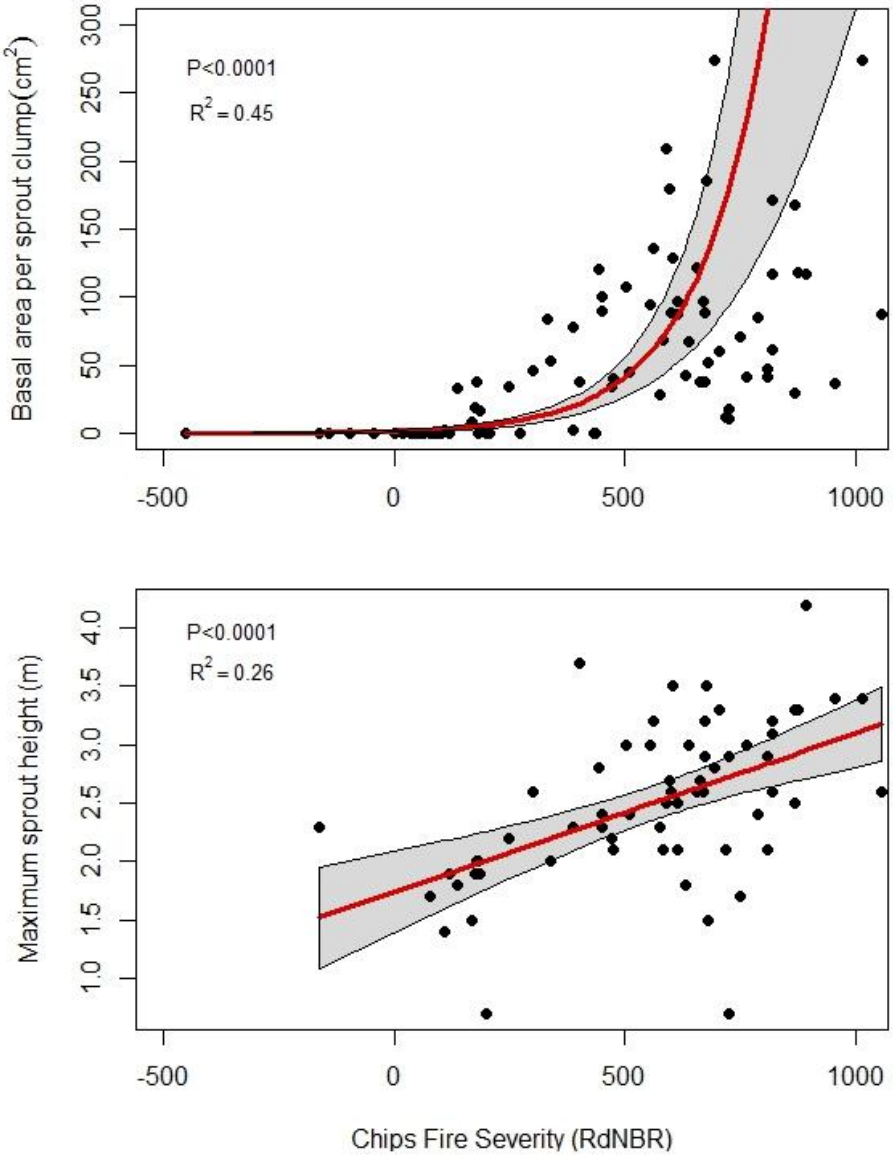

Figure 1.4: Basal area and maximum height of post-Chips Fire sprouts by fire severity. Zero values were removed from sprout height analyses in order to meet model assumptions.

A total of 51 plots (55%) had live post-Storrie Fire sprouts at the time of the Chips Fire. Of these plots, approximately 33% (17 plots) experienced complete oak sprout mortality in the Chips Fire (**Figure 1.5**a). Post-Storrie Fire sprout survival rates were binomially distributed, with nearly all plots experiencing either 0 or 100% mortality of measured post-Storrie fire sprouts. A

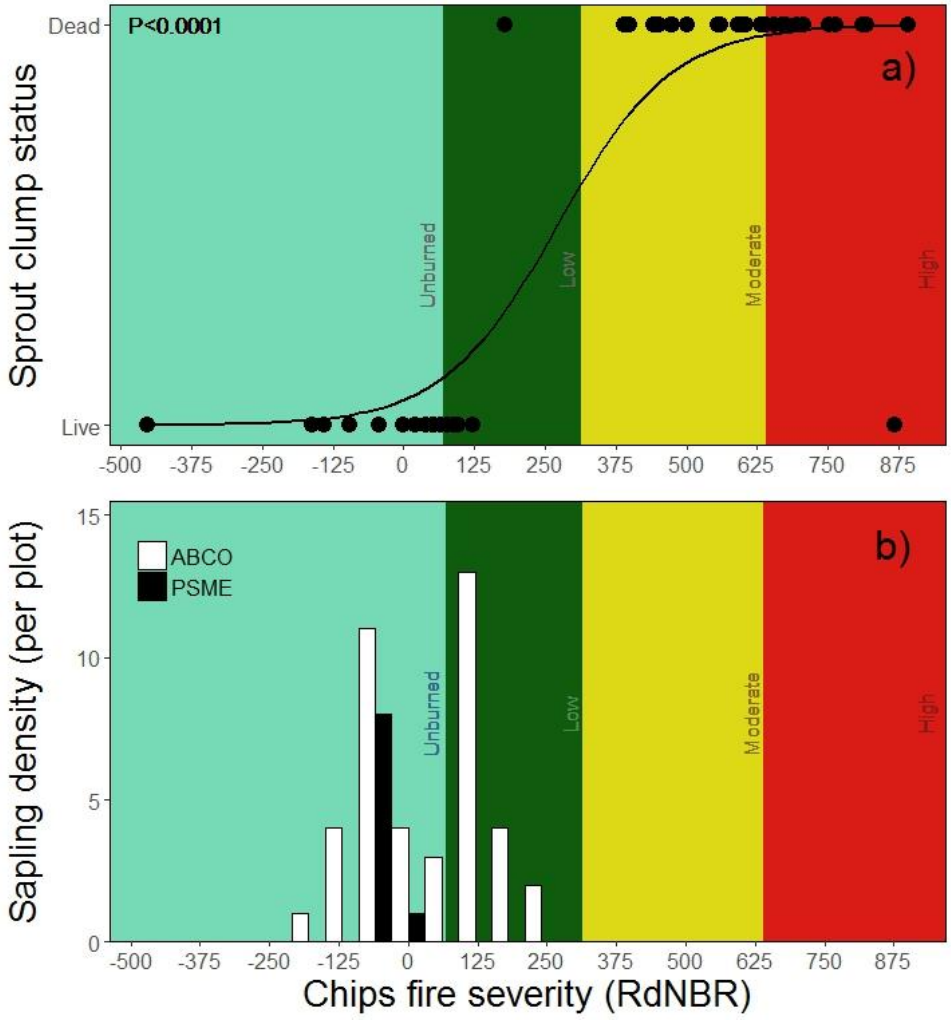

Figure 1.5: Survival of post-Storrie Fire sprouts in Chips Fire (a) and post-Storrie Fire regeneration of competing conifers by burn severity (b). Excepting a single outlier, maximum burn severity (RdNBR) value at which a majority of oak sprouts in each clump survived a second fire was 121. Maximum burn severity at which competing conifer regeneration was removed was approximately 250.

threshold value of 70% stem mortality within each clump was used to categorize "live" and "dead" status for remaining plots. Post Storrie-Fire sprouts were top-killed at low burn severities in the Chips Fire (nearly all sprout clumps experienced complete or near-complete aboveground mortality at values greater than 167 RdNBR). Fire severity was able to explain oak sprout survival with a high level of accuracy ($P<0.0001$, area under ROC curve = 0.95). All measured sprout clumps that were top-killed in the Chips Fire had resprouted by the time of measurement, as post-fire mortality was confined to aboveground vegetation.

Table 1.2: Mean shrub cover by categorized severity rating for both fires.

Fire severity category	Storrie Fire	Chips Fire
Unchanged	23.9	31.1
Low	25.5	32.9
Moderate	36.8	30.7
High	59.7	51.6

Regeneration of competing conifer species was compared across Chips Fire severities. Sapling density per plot was considered to be of particular importance, since these had presumably established before the Chips Fire occurred, and could be used to measure the effects of fire severity on conifer regeneration. A size threshold of 50 cm in height was used to distinguish saplings from seedlings, as conifers in the study area will not attain this height in less than three growing seasons (J. Crotteau, pers. comm.), and thus are presumed to have been present at the time the Chips Fire occured. Live conifer saplings were observed only below RdNBR values of approximately 250 in the Chips Fire (**Figure 1.5**b). No saplings of either conifer species were observed at moderate or high burn severities, and density was significantly higher at lower burn severities ($P<0.0001$).

1.4 DISCUSSION

In the mixed-conifer forests of northern California, wildfire can shift the competitive environment to favor oak dominance, releasing oaks from suppression due to overtopping conifers (McDonald et al. 2002, Cocking et al. 2014, Hammett et al. 2017). Our study found that after a second fire, this trajectory toward oak dominance is reinforced, as higher severities in the Chips Fire eliminated post-fire conifer regeneration and killed remaining overstory conifers, while oaks continued to resprout (Hammett et al. 2017). This outcome is similar to the scenario proposed in a conceptual model by Cocking et al. (2014), where, once reestablished, oak-sprout stands transition into oak woodlands with the stabilizing influence of frequent fire. While high-severity wildfire confers a temporary competitive advantage to oaks, the significant conifer regeneration that occurred after both the Storrie (Crotteau et al. 2013) and Chips fires demonstrates the need for frequent fire intervals in order for this early-seral community to be maintained. While resprouting oaks can quickly gain a height advantage over regenerating conifers, they will eventually be shaded by faster-growing conifers as their height growth slows in maturity (McDonald 1969). Thus, a continual process of disturbance is necessary for oaks to maintain overstory dominance in the long-term.

Prolific and rapid sprouting allows oaks to recover quickly from top-kill after wildfire (Bond and Midgley 2001, Cocking et al. 2012, Hammett et al. 2017). Resprouting black oaks utilize underground carbohydrate reserves to support rapid height growth, and have been observed to allocate resources to height growth at the expense of both diameter growth and bark thickness (McDonald 1969, Kidd et al., submitted manuscript). Black oak's vigorous post-fire height growth confers an advantage when competing with regenerating conifers, but it leaves young stems susceptible to cambial injury in subsequent fires. McDonald (1980) stated that California black

oak needs approximately 60 years to attain sufficient bark thickness to withstand cambial injury in low-severity burns. This delay in fire-resistance presents a challenge for oak woodlands recovering from high-severity fire in conifer-dominated regions. While resprouting oak clumps were more prevalent than regenerating conifers in areas that experienced higher burn severities in both fires, few had oaks that recruited into the overstory, despite the lack of competition from conifers. This shrub-like growth of oaks was due to the high sensitivity of post-fire growth to fire, as individuals that resprouted after the Storrie Fire were vulnerable to top-kill even at lower fire severities (**Figure 1.5a)**. This pattern supports the "goldilocks principle" referred to by Long (2016): California black oak is highly dependent on fire to maintain early seral stand conditions, but its above-ground growth is paradoxically sensitive to fire. While oaks made gains in relative dominance post-fire (**Figure 1.3**), this was at the expense of overstory recruitment, as recurrent oak top-kill preserved oaks in a shrub form.

Twelve years after the initial fire, oaks in previously burned areas underwent vigorous regrowth after a second fire, with a more robust response in higher-severity plots. Surprisingly, this response was unrelated to previous burn severity in the Storrie Fire (Appendix**, Figure A**), indicating that underground carbohydrate storage was either not substantially depleted after a single resprouting event, or that the 12-year interval between fires was sufficient for plants to rebuild these reserves (Donato et al. 2009b). These results provide further support for the finding that California black oaks are resilient in the face of multiple fires (Hammett et al. 2017). However, it is unknown if this capacity to regenerate is interval-dependent. If the intervening time between wildfires is insufficient for carbohydrate reserves to be replenished, resprouting ability of an individual may be diminished (Delitti et al. 2005). While this phenomenon has not yet been observed in California black oak, predicted increases in fire frequency may provide further

opportunities to study this species' capacity for repeated regeneration over short fire return intervals.

Current vegetation and corresponding fuel conditions preclude the frequent, low-intensity fire regimes that sustained California black oak woodlands in the past. Evidence from historical accounts (Stewart et al. 2002b, Anderson 2005), as well as dendrochronological studies (Taylor 2000, Bekker and Taylor 2010), point to a previously beta-diverse, heterogeneous landscape in the region, created and maintained by mixed-severity fire. This matrix of vegetative communities was a relatively stable system, whose structural and vegetative diversity likely protected many areas from severe wildfire (Hessburg et al. 2005, Perry et al. 2011). After decades of fire exclusion, ingrowth of fire-sensitive conifer species has changed the structure of vegetation and fuels in encroached woodlands. Dense conifer growth provides ladder fuels into the canopy, promotes greater fuel loading, excludes herbaceous fuels from the understory, and generates fuelbeds with higher bulk densities than those found in open oak woodlands (Engber et al. 2011). These shifts in fuel density and arrangement, as well increased homogeneity of fuels, create significant changes to wildland fire behavior, greatly increasing the risk of large-scale, stand-replacing wildfires (Perry et al. 2011, Mallek et al. 2013).

This departure from historic conditions at the stand- as well as landscape-level sets the stage for further vegetative change, as the consequences of the catastrophic wildfires that result are exhibited on the landscape. Studies of high-severity reburns in California have found that dry forests are experiencing dramatic post-fire state-shifts (Collins and Roller 2013, Coppoletta et al. 2016, Lauvaux et al. 2016). In this region's dry mixed conifer forests, prolific regeneration of montane chaparral shrublands often occurs after stand-replacing fire (Nagel and Taylor 2005, Collins and Roller 2013, Lauvaux et al. 2016). Chaparral shrub species are well adapted to high

severity fire, often regenerating vegetatively (as in the case of greenleaf manzanita and snowbrush), from prolific fire-stimulated seed banks (such as deerbrush), or employing both strategies (mountain whitethorn) (Keeley 1991, Howard 1997, Anderson 2001, Reeves 2006, Hauser 2007). In our study, dense shrub regrowth was common three seasons after the Chips Fire, with mean cover greater than 50% in plots that burned at high severities (**Table 1.2**). As a wildland fuel, chaparral is often self-perpetuating, as it is highly flammable under dry conditions, has many strategies for repopulating severely burned areas, and most commonly burns at high intensities and severities (Anderson 1982, Barro and Conard 1991, Nagel and Taylor 2005, Collins and Roller 2013, Lauvaux et al. 2016). While chaparral can convert to forest along normal successional pathways in the absence of fire, current research indicates that predicted future increases in fire frequency and severity will maintain chaparral stands long into the future (Steel et al. 2015, Coppoletta et al. 2016, Lauvaux et al. 2016).

The resulting alternate vegetative states thus have the potential to alter the future fire regime, from a regime of mixed-severity, with large areas of low-intensity fire, to that of repeated high-severity fire fueled by large, unbroken expanses of shrublands. The outcome of this second type-shift may be a positive feedback of high-severity fire promoting further high-severity fire, in stark contrast to other authors' (Cocking et al. 2014, Hammett et al. 2017) predictions of negative feedbacks provoked by increased fire frequency. The key difference between these scenarios is the fuel type that is promoted under these novel contemporary fire regimes. California black oaks regenerating within a matrix of dense shrub regeneration are unlikely to withstand the high intensities that are typically produced in chaparral fires. If these high-severity fire regimes persist, above-ground vegetation of California black oak will be continually top-killed in these events, and

the species will persist solely as small-statured mid-story component across these altered landscapes.

The results of our study, when placed within the context of others' work, suggest that in California's fire-excluded oak woodlands, a single wildfire event may be insufficient to restore pre-European settlement conditions. It is possible that currently regenerating black oak stands, if allowed to develop without further disturbance by fire, could eventually reach maturity to regain their lost ecological functions and cultural values. Indeed, the presence of even-aged stands of mature California black oak are evidence that woodlands have reestablished after stand-replacing fires in the past (McDonald 1969). However, stand-replacing fire origin was likely not the dominant mechanism for oak establishment in past landscapes, as fire, both natural and anthropogenic, was likely much more frequent and less intense than current regimes (Stewart et al. 2002, Anderson 2005, Taylor 2010, Cocking et al. 2014), and many remnant black oak stands are multi-aged (Garrison et al. 2002, Cocking et al. 2012). Continued encroachment by native conifers is will be an ever-present threat to these regenerating stands if fire is completely excluded. Hammett et al. (2017) surmise from their data that the return of "historically normal fire return intervals" subsequent to high-severity fire events may aid in the restoration of mature black oak woodlands; our results, however, cast this prediction into doubt.

The legacy of long-term fire exclusion in dry forests, coupled with a changing climate, may endure well into the future. An increasing body of evidence indicates that changing patterns of disturbance are impacting vegetation, and thus, fire regimes, in the dry forests of California. Repeated fires accelerate conversion to distinct plant communities and maintain these state shifts on the landscape (Nagel and Taylor 2005, Steel et al. 2015, Coppoletta et al. 2016, Lauvaux et al. 2016). Regenerating black oaks will not be tolerant of the larger, more contiguous, and higher-

severity fires that are propagated in these fuels. The altered fire regimes that are increasingly replacing disturbance regimes of the past may preclude the development of mature oak woodlands. Oaks may thus be forever caught in a "fire trap" (sensu Grady and Hoffmann 2012): despite their resilience to high-severity fire, the sprouts produced following these fires are highly vulnerable in reburns. Future frequent fire, instead of maintaining mature oaks woodlands as in the past, may suppress oaks in a form that lacks the characteristics important for wildlife habitat and cultural practices. As the repercussions of long-term fire exclusion are expressed in current wildfire activity, old paradigms are no longer relevant, and new ones must be carefully studied before predictions can be made about their implications for restoration of historic plant communities.

1.5 Management Implications

California's black oak woodlands have existed in concert with human activity for thousands of years. The historic extent and dominance of mature oak savannas and woodlands was dependent on natural fire regimes as well as anthropogenic management, particularly tribal burning practices (Stewart et al. 2002, Anderson 2005, Long et al. 2016b). The current decline of montane oak woodlands across their range is in large part a consequence of recent human disruptions to these fire regimes of the past. The future of these important landscape elements is dependent on current and future land management decisions. Our research suggests that large wildfires alone fail to promote the recovery and persistence of these critical communities. The structure and composition of vegetation (and thus, fuels) across the landscape is so dramatically altered from historic conditions as to render such a result unlikely. Wildfire can reestablish temporary oak dominance on a severely burned landscape; these fires can even maintain this dominance by killing all surviving or regenerating conifers in the case of a re-burn. However, the restoration of oak

woodland structure and function is difficult to achieve solely via an increase in the relative cover of oaks, as this does not necessarily lead to the development of the ecological features that give oak woodlands their value.

Given this reality, additional post-fire treatments may be necessary in order to break the cycle of resprouting and top-kill that was observed in this study. Managers can take advantage of post-wildfire oak recovery by protecting regenerating oaks from both conifer encroachment and recurring wildfire. In order to achieve this, it may be necessary to use methods such as herbicide treatment, mastication, or manual removal (Conard and Radosevich 1982, Potts et al. 2010), in order to interrupt the continuity of shrub fuels around resprouting oaks. Following shrub control, seeding of herbaceous species and regular application of prescribed fire can be utilized in order to re-establish historic flashy fuels and understory biodiversity. Restoration efforts may be most effective in large patches of high-severity reburn, as these are less likely to experience substantial natural conifer regeneration due to lack of nearby seed sources (Donato et al. 2009a, Pierce and Taylor 2010, Lauvaux et al. 2016), especially for heavier-seeded competitors such as white fir. These management practices have the added benefit of promoting resilience to future wildfire by reducing fuel densities and increasing landscape heterogeneity. These management interventions will be of increasing importance in the context of predicted and on-going increases in fire size, frequency, and severity in the western United States (Westerling et al. 2006, Barbero et al. 2015, Parks et al. 2016, Abatzoglou and Williams 2016).

Chapter 2. EFFECTS OF PRESCRIBED FIRES ON CROWN INJURY IN MATURE GARRY OAK WOODLANDS ON JOINT BASE LEWIS-MCCHORD, WASHINGTON

2.1 INTRODUCTION

Frequent fire has maintained woodlands and savannas for millennia, sustaining unique plant communities on many continents (Swanson et al. 2011). The regular disturbance provided by frequent fire regimes preserves many of these ecosystems in an early-seral state which would otherwise transition into forests or shrublands (Bond and van Wilgen 1996, Bond and Keeley 2005). Due to characteristic high fire frequency, these fire-dependent ecosystems typically burn at low severities, allowing a stable vegetative state of fire-tolerant species, and preventing encroachment by fire-intolerant plants (Staver et al. 2011a, 2011b).

Once common across the Willamette Valley-Puget Trough-Georgia Basin ecoregion, Garry oak (*Quercus garryana* Douglas ex Hook.) woodlands, savannas, and associated prairies have been substantially reduced in both quality and extent in the years since Euro-American settlement (Chappell and Crawford 1997, Crawford and Hall 1997). A legacy of the last glacial period, oak woodlands were sustained for millennia by indigenous burning and lightning-ignited fires that favored fire-adapted oaks and prevented the encroachment of the rapidly growing native competitor Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) and other woody species (Agee 1993, 1996, Sprenger and Dunwiddie 2011). During the past century and a half, Garry oak woodlands have been degraded and eliminated by a suite of human disturbances: conversion to agriculture, domestic grazing, human development, and fire exclusion (Thilenius 1968, Crawford and Hall 1997, Regan and Agee 2004). Invasion by both native and non-native plants further threaten the remaining fragments of oak woodland and savanna. Encroachment of

woody species into these formerly sparsely vegetated sites increases mid-story density, reduces native understory diversity, degrades habitat quality, and causes the decline of remnant oaks (Thysell and Carey 2001, Regan and Agee 2004, Livingston et al. 2016).

The range of Garry oak covers much of the western coast of the United States, extending from southern British Columbia to California. Garry oak is found growing as isolated individuals in savannas, as well as in both pure and mixed-species woodlands. Under ideal growing conditions, oaks can attain a height of approximately 30 m, with an equivalent crown spread (Thilenius 1968). Mature oak trees, with their characteristic spreading growth form, provide nesting platforms and cavities, abundant acorn crops, and other highly valuable habitat components not available in adjacent conifer-dominated forests (Larsen and Morgan 1998). Oak woodlands support an array of rare invertebrates, birds, and mammals, including such oak-obligates as the Washington state Threatened western gray squirrel (*Sciurus griseus*) and the Propertius' duskywing (*Erynnis propertius*) (Anderson 1972, Larsen and Morgan 1998). As such, oak woodlands provide critically important habitat in central and western Washington. Lack of recruitment of oaks from the understory has become a concern for managers in recent years, making the protection of existing oaks even more crucial.

In response to the restoration need in Garry oak ecosystems, managers are increasingly using prescribed fire in order to return historic disturbance patterns to the landscape (Sugihara and Reed 1987, Tveten and Fonda 1999, Dunwiddie and Bakker 2011). Prescribed burning is implemented in restoration efforts in order to control invasive woody species, increase bare ground for native herbaceous plant establishment, and prepare sites for herbicide application to control non-native understory species (Agee 1996, Stanley et al. 2008, Dennehy et al. 2011, Engber and Varner 2012, Livingston et al. 2016). Common practices aim for a fire return

interval of 3-5 years, a frequency necessary to maintain native-dominated understories largely free of the two greatest threats to oak habitat quality: the non-native shrub Scot's broom (*Cytisus scoparius* (L.) Link) and Douglas-fir (Tveten and Fonda 1999, Regan and Agee 2004, Engber and Varner 2012). This burn frequency attempts to replicate historic burning patterns, as fire-stable systems tolerated this disturbance where it had been consistent on the landscape (Agee 1993). Garry oak is considered to be a fire-resistant species, employing survival strategies such as protective bark and adventitious buds that can quickly resprout following damage in fire (Agee 1993, Gucker 2007). Most Garry oak woodlands in the Pacific Northwest, however, have experienced long periods of fire exclusion (Cole 1977, Agee 1993, Taylor and Skinner 2003, Sugihara et al. 2006, Sprenger and Dunwiddie 2011), and re-introducing fire into these long-unburned stands may have unintended consequences (Agee 1996). Of particular concern are greater fuel loadings and lower fuel strata gaps due to Douglas-fir and Scot's broom invasion, as well as accumulated forest floor duff (Oe and Oa organic soil horizons) around the bases of mature oaks. Higher densities of fuels, lower canopy base heights, and accumulated ground fuels can increase fire severity in an ecosystem that is adapted to low-severity fire that was largely propagated in light, herbaceous fuels and a shorter, sparser shrub strata (Agee 1993, 1996).

Managers, concerned about injury to oaks during prescribed fires, often attempt to limit fire intensity around remnant trees during burns by reducing surrounding fuels during burn unit preparation, managing firing techniques, and conducting burns under moderate weather conditions in order to regulate flame lengths (J. Richardson, pers. comm.). These actions are taken under the presumption that scorching in the crown will injure or even kill above-ground vegetative growth. Previous studies have found that extensive crown scorch can cause mortality

in a variety of conifer species (Hood 2010), as well as top-kill in some oak species (Babb 1992), but this relationship has not been well examined for Garry oaks. Long duration smoldering can also injure and kill trees via cambial injury or injury to fine roots (Swezy and Agee 1991, Varner et al. 2009). Large quantities of basal duff that accumulate in the continued absence of fire provide fuel for long-duration smoldering (Miyanishi and Johnson 2002), with greater depth and lower moisture content contributing to greater consumption and heat transfer to mineral soil (Hungerford et al. 1995). Considerable evidence exists for smoldering-induced mortality of pines in long-unburned sites due to basal duff consumption (Stephens and Finney 2002, Varner et al. 2005, 2009). All of these studies, however, examined below-ground fire effects on conifers, and to our knowledge, no studies of duff consumption and its potential causal relationship to tree injury have been conducted in oak-dominated systems. Oaks' tolerance of smoldering ground fires is unknown, as is the effect of duff consumption on the below-ground carbohydrate stores that facilitate post-fire sprouting.

Garry oaks are highly tolerant of low and moderate severity surface fires, and, even when injured, are capable of sprouting both from the crown and base of the tree (Fry 2002, Gucker 2007). As such, Garry oaks are rarely killed under conditions typical in prescribed burns, although top-kill and even mortality can occur at higher intensities (Sugihara and Reed 1987). While post-fire sprouting is a common mechanism for regeneration following disturbance, Garry oaks have also been observed to sustain a late-season flush of crown foliage following burns (Peter et al. 2011). This additional expenditure of carbohydrates at the end of the growing season may diminish reserves available for crown repair in the spring following underburning. To our knowledge, this phenomenon has not been studied, and the impact of fall bud burst on oak vigor and spring leafing response is unknown.

Joint Base Lewis-McChord (JBLM), a military training facility in the southern Puget Sound region of Washington state, contains the most extensive Garry oak habitats remaining in the south Puget Sound region (Crawford and Hall 1997, Dunwiddie and Bakker 2011). The unique land use history of the military installation distinguishes JBLM's oak ecosystems from others in the Pacific Northwest. While fire regimes and plant communities have certainly experienced perturbations in the time since Euro-American settlement, as well as following the establishment of Fort Lewis in 1918 (Blazina 2017), oak and prairie ecosystems on the base have experienced less fragmentation and more regular fire incursion (both from prescribed fires as well as wildfires resulting from munitions training) than most oak landscapes in the western United States (Regan and Agee 2004). JBLM maintains an active prescribed fire program, currently burning an average of 650 ha of prairie and oak communities annually (J. Richardson, pers. comm.). JBLM's program has achieved success in restoring prairie habitat on the base, and is increasing its activities in remnant oak woodlands, with the objectives of controlling invasive shrubs, preventing conifer encroachment, and increasing oak regeneration. Potential mortality and top-kill of mature oaks in these burn units is a major concern to managers.

In order to better understand the drivers of fire-induced oak injury and to provide relevant data to managers on the military installation, we examined Garry oak response to prescribed burning, with specific focus on the differential and interactive impacts of above- and below-ground fire on oak crowns. We asked if either below-ground smoldering, above-ground flaming, or a combination of effects influenced dieback in Garry oaks. Given the potential of smoldering duff to harm fine roots that may be present, we looked for drivers of greater duff consumption during prescribed fires in Garry oak habitats. Post-fire tree mortality can be delayed by years and even decades (Ryan and Reinhardt 1988, Agee 1996), and a short-duration study such as this

one is unlikely to capture fire-induced tree mortality, especially in a fire-resistant species such as Garry oak. Additionally, managers take steps to protect oaks during prescribed burn operations, such as maintaining shorter flame lengths and lower fire intensities. As such, mortality of measured trees was not expected; canopy dieback (crown bud kill) was used instead as a metric of tree injury. As the phenomenon of late-season bud burst is not well understood, we also examined the relationships between fire effects, late-season leaf flush and subsequent bud death in oak crowns. Additionally, we examined the impact of extant scars on bole injury, as many trees in our study site had pre-existing fire and mechanical scars. This work has direct implications for fire management on JBLM and perhaps more widely in Garry oak woodlands where restoration burning is frequently employed for ecosystem restoration.

2.2 METHODS

2.2.1 *Study Area*

The study sites were located on Joint Base Lewis-McChord, a 34,802 ha military installation located in Thurston and Pierce Counties, Washington. The dominant soil type on the oak woodland sites is Spanaway gravelly sandy loam, a typical glacial outwash soil of the region (Zulauf 1979). Topography is flat to undulating, with an average elevation of 90 m above sea level (Thysell and Carey 2001). Climate in this region is Mediterranean, with warm, dry summers (summer high temperatures average 25 °C), and cool, wet winters. Annual precipitation averages 997 mm, most of which falls between the months of October and May (Pringle 1990).

2.2.2 *Field Data Collection*

Three burn units were selected for measurement in two non-adjacent areas on the military installation. Two units were located in the Upper Weir Prairies, also known as the Rainier Training Area, near the town of Rainier, Washington (46.91655517, -122.7094762). A third unit was located in Holden Woods, closer to the center of the installation (47.059179, -122.5099519). The most recent records of burning at this site date to a likely pile burn approximately 15 years prior to the study. Two adjacent burn units with distinct vegetation were selected in the Upper Weir area. The 2.8 ha UWTT unit had been burned twice in the last decade, and had an herbaceous understory comprised largely of non-native perennial grasses (*Agrostis capillaris*, *Arrhenatherum elatius*, and *Dactylis glomerata*), with few shrubs. UWTB, which was 2 ha in area, had not burned in several decades, and had a shrub-dominated understory. A short west-facing slope connects the two units. Dominant shrubs in both sites were Scot's broom, snowberry (*Symphoricarpos albus* (L.) S.F. Blake), and Himalayan blackberry (*Rubus armeniacus* Focke). The Holden Woods unit (HLD01) was 8.9 ha in area, with a mixed herbaceous understory dominated by exotic grasses and forbs, with approximately one-third of the site covered with a mix of snowberry and low Oregon-grape (*Mahonia nervosa* (Pursh) Nutt.). Similar fuels reduction and non-native species control treatments had been recently conducted in all burn units prior to our study. These treatments largely took the form of brush-cutting of mature Scot's broom throughout each unit, and served to reduce, but not eliminate, this invasive species from these sites (T. Zuchowski, per. comm). All units had a similar Garry oak-dominated overstory and woodland structure, and, with the exception of UWTT, had scattered conifers present. Douglas-fir was a minor component in both UWTB and Holden Woods, with the latter also

containing a small number of ponderosa pines (*Pinus ponderosa* Douglas ex C.Lawson). Mean diameter of oaks in both Upper Weir units was 18 cm, and 22.8 cm at the Holden Woods unit.

Prior to each burn, we randomly selected approximately 50 oaks per burn unit (n = 151) which were at least 5 cm in diameter at 137 cm from ground level ("dbh"). In order to examine fire effects on individual trees, we recorded each tree's location with GPS, dbh, height, crown base height, and extent of any prior scarring. To facilitate post-burn proportional duff consumption measurement, we installed eight metal welding rods around the base of each tree at each of the cardinal and ordinal points 10 cm from the bole. These rods were driven into mineral soil, and cut to be flush with the upper surface of the duff.

Fuels collections were made within an hour prior to ignition in each unit. Samples consisted of 1- and 10-hour timelag woody fuels (dead wood less than 1/4 inch and 1 inch in diameter, respectively), live shrubs, live grasses, oak litter, and duff (combining Oe and Oa horizons from the bases of nearby unsampled oaks). Samples were sealed in polyethylene bags and transported to the laboratory for analyses. Each fuel sample was weighed wet and then oven-dried for 72 hours at 60 °C. Final dry weights were used to calculate mean gravimetric moisture content for each fuel type (**Table 2.2**)

Fire effects on selected oaks in each unit were measured approximately two weeks after burns were conducted (**Table 2.1**). For each tree, we recorded the following above-ground fire effects metrics: maximum height of charring on the bole (cm); percent circumference charred at the base (BCC) and at 137 cm (DBHCC); percent of crown volume scorched (PCVS); and percent of crown volume consumed (PCVC); following methods employed by Kobziar et al. (2006). Foliage was considered scorched if leaves were prematurely brown and wilted within two weeks of each burn (measurements of crown scorch were taken before seasonal leaf drop),

and consumed if leaves were blackened or completely consumed in the fire. In order to assess effects of below-ground (smoldering) fire on measured trees, we measured depth of the pre-burn duff layer and depth of duff consumed at each welding rod location where consumption had occurred.

Table 2.1: Field measurements used in analyses of prescribed fire effects on *Q. garryana* at Joint Base Lewis-McChord, Washington.

Pre-burn	**Post-burn**
Tree characteristic predictors	*Above-ground predictors*
Height	Bole char height
Diameter at breast height (dbh)	Bole char at base (BCC)
Crown base height	Bole char at dbh (DBHCC)
Prior scarring	Percent crown volume scorched (PCVS)
	Percent crown volume consumed (PCVC)
	Percent crown volume flushing (PCVF)
	Below-ground predictors
	Proportional duff consumption
	Response metric
	Crown dieback (%)

We then used these measurement to calculate mean proportional duff consumption for each tree. We examined quantity of late-season foliage production in oak crowns three months post-burn, measured as proportion of crown volume flushing (PCVF). In order to assess Garry oak response to measured fire effects, we measured crown dieback as the proportion of the crown volume not producing leaves (assumed bud kill) nine months post-burn (May 2017); trees with no visible spring bud break were considered top-killed.

2.2.3 *Day-of-burn Fire Conditions*

Both Upper Weir units were burned on 01 August 2016. Firing began in UWTB, and proceeded up the slope to the UWTT unit approximately 30 minutes later. Air temperatures ranged from 18 °C at time of ignition (1215) to 28 °C when ignition ceased, at approximately 1600. Winds averaged 4.8 km hour^{-1}, with gusts up to 13.7 km hour^{-1}. Relative humidity at time of ignition was 56%, and dropped to a low of 42% at 1524. Flame lengths in both Upper Weir units ranged from 0.3 m in backing fires, to a maximum of 3 m in head fires. Rates of spread ranged from 0.02 m sec^{-1} in backing fires to 0.13 m sec^{-1} in head fires.

Table 2.2: Average day-of-burn fuel moisture values in three *Q. garryana* woodland burn units at Joint Base Lewis-McChord, Washington.

	HLD 01	UWTB	UWTT
1 hr. time lag	13%	33%	5%
10 hr. time lag	12%	10%	6%
live shrubs	94%	103%	87%
live grasses	61%	61%	115%
litter	12%	9%	3%
duff	20%	11%	14%

The Holden Woods unit was burned on 11 August 2016. Air temperature at the time of ignition (1200) was 23 °C, increasing to 28 °C an hour later, when ignition ceased. Relative humidity decreased from 54 to 36% over the course of the burn. Winds during the burn were light, ranging from 1.6 to 6.4 km hour^{-1}. Flame lengths ranged from 0.3 m in backing fires to 2.5 m in head fires. Rates of spread ranged from 0.01 m sec^{-1} in backing fires to 0.1 m sec^{-1} in head fires.

2.2.4 *Data Analysis*

All analyses were conducted using pre- and post-burn data pooled from all measured trees, regardless of unit location. Due to the close proximity of measured trees in this study, spatial autocorrelation was a potential concern in the analysis of response data. Trees were grouped by location on the landscape, and Mantel tests of each group were used to test for spatial autocorrelation in response data related to study tree location in R (The R Core Development Team 2014) using the vegan package (Oksanen et al. 2007, version 3.3.2). For each location, a distance matrix of response variables (fire effects) was compared to a distance matrix created from spatial coordinates for each tree location. Spatial coordinates were standardized by subtracting the minimum value from both latitude and longitude values before analysis, and response variables not already in proportional form were relativized by their maximum values in order to give each equal weight in the analysis. Euclidean distance calculations were used to create both dissimilarity matrices. Mantel tests yielded low correlations and non-significant results for both Holden Woods ($P = 0.428$) and the Upper Weir sites ($P = 0.629$). This allowed the remainder of the analyses to continue without the need to add additional terms to models in order to account for the effect of tree location within a unit.

Linear modeling was used to evaluate the impacts of above and below-ground fire effects on crown dieback observed in Garry oak crowns. All measured fire effects variables (bole char height, BCC, DBHCC, PCVS, proportional duff consumption), as well as late-season flushing, were modeled against crown dieback using backwards stepwise regression in order to determine which effects were significantly correlated with post-fire crown dieback. Differences in diameter between top-killed vs. non-top-killed trees were evaluated using Welch's two-sample t-tests. Due to unbalance sample sizes and non-parametric distribution of data, bole charring on

scarred and unscarred trees was compared using a Wilcoxon ranked sum test (Huntsberger and Billingsley 1981). We compared duff consumption with pre-burn duff depth using generalized linear modeling, and variation in duff consumption within and between trees using ANOVA.

2.3 RESULTS

In the three prescribed burns at JBLM, only 12 Garry oaks (8%) were top-killed, and mean crown dieback values were less than 30% of crown volume. Ten percent of trees experienced some consumption of leaves, with only two of those having more than 10% of their crown consumed. Due to the rarity of this phenomenon, crown consumption was discarded from further analyses. Scorching of oak crowns was common in all three burn units, with more than 95% of trees experiencing some level of leaf scorch; of scorched trees, mean quantity of scorch was 71% of

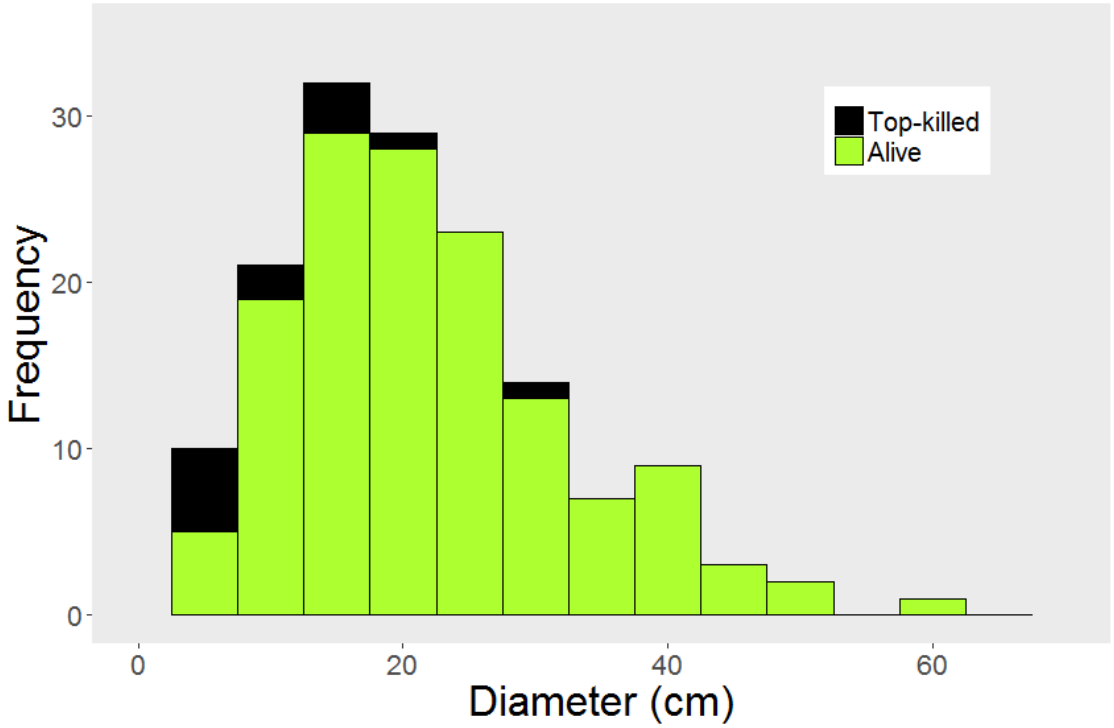

Figure 2.1: Diameter distributions of live and top-killed oaks following prescribed burns at Joint Base Lewis-McChord, Washington.

crown volume. Eighty-seven percent of trees had their boles charred in the burns; mean char height across all three units was 58.4 cm. Late-season bud burst was minimal, with a mean of 10% crown volume producing fall foliage across sites, and only 23% of trees exhibiting this effect.

Smaller diameter oaks were top-killed more readily: top-killed trees had a mean dbh of 11.4 cm, mean dbh of trees with live above-ground vegetation was 22.2 cm (**Figure 2.1**, P=0.0002).

Quantity of scorching was related to late-season bud burst, with flushing trees having experienced higher volumes of scorch (P=0.011), but effect size was small (model coefficient = -0.16). Late-season leaf flush did not occur in trees that had less than 60% of their crowns scorched in burns.

Table 2.3: Fire effects on measured *Q. garryana* in three burn units at Joint Base Lewis-McChord. Means are given, with standard deviations in parentheses.

	HLD01	UWTB	UWTT
Bole char height (cm)	55.6 (48.9)	91.6 (108.8)	28.8 (37.6)
BCC (%)	70.1 (33.9)	50.3 (31.8)	19.7 (26.3)
DBHCC (%)	0.9 (5.7)	15.8 (25.6)	2.0 (8.3)
Crown scorch (%)	70.2 (31.5)	67.3 (40.3)	66.1 (36.4)
Duff consumed (cm)	3.3 (2.8)	1.6 (1.5)	0.3 (0.7)
Duff consumed (%)	38.1 (31.3)	28.5 (22.8)	9.1 (16.6)
Flushing (%)	9.2 (21.7)	11.3 (22.8)	10.0 (23.7)

The majority of recorded fire effects were variable across the three oak woodland burn units, even between Upper Weir sites, which were adjacent. The UWTT unit had lower values for char height along the bole and at the base of trees, as well as quantity and proportion of duff

consumption. Volumes of crown scorching and post-fire sprouting were largely consistent between sites (**Table 2.3**).

Table 2.4: Summary of multiple linear regression model fits of *Q. garryana* crown dieback.

	Evaluation criteria		
Model predictors	RMSE	R^2	AIC
PCVS	24.7	0.36	1388
PCVS+Bole char ht	24.5	0.37	1402
PCVS+Bole char ht+DBHCC	24.4	0.37	1403
PCVS+Bole char ht+DBHCC+BCC	24.4	0.37	1405
PCVS+Bole char ht+DBHCC+BCC+Duff cons (%)	24.4	0.36	1407
PCVS+Bole char ht+DBHCC+BCC+Duff cons (%)	24.4	0.36	1407
PCVS+Bole char ht+DBHCC+BCC+Duff cons (%)+Height	21.8	0.49	1374
PCVS+Bole char ht+DBHCC+BCC+Duff cons (%)+Height+DBH	21.6	0.5	1373
PCVS+Bole char ht+DBHCC+BCC+Duff cons (%)+Height+DBH+PCVF	21.3	0.5	1372
PCVS+Height+PCVSP	21.9	0.5	1370
$PCVS^2$+PCVS+Height+PCVF (final model)	21.4	0.52	1363

Of all measured fire effects, crown scorching was the strongest single predictor of subsequent crown dieback ($P<0.0001$, $R^2=0.36$). Below 80% of crown volume scorched, dieback was minimal, ranging from 0 to 40% with a mean value of 9%. While top-kill only occurred where entire oak crowns were scorched, high levels of scorching had widely variable effects in oak dieback response (ranging from 0 to 100%). Stepwise multiple linear regression comparing crown dieback with all meaured fire effects resulted in the strongest model including the following three predictors: scorch volume, height, and flushing (**Table 2.4**, $P<0.0001$, $R^2 = 0.52$). As tree height and dbh were correlated ($R^2=0.54$), only height was used in this model, as it had a stronger individual effect on crown dieback (model coefficient = -1.94) than dbh (coefficient = -1.54) when compared in a linear regression model. A box-cox transformation sugessted the addition of the squared term for scorching, and this improved both model fit and

selection criteria (AIC and RMSE). Similar quadratic relationships have been found between

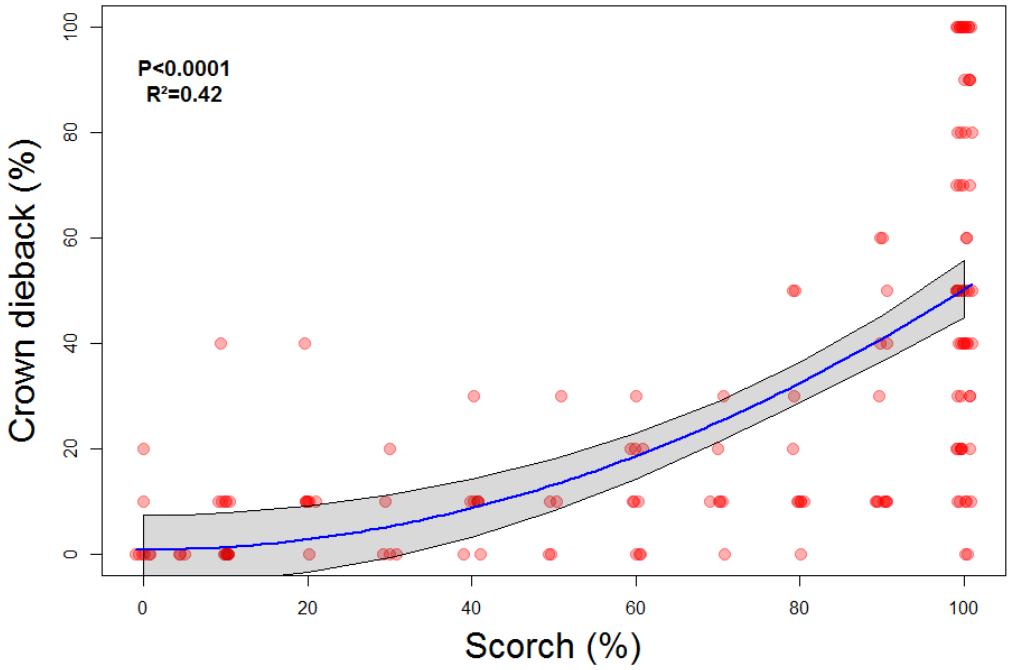

Figure 2.2: *Q. garryana* crown dieback as related to quantity of crown volume scorched in prescribed burns.

tree mortality and crown scorching in previous studies (Peterson and Ryan 1986, Ryan and Reinhardt 1988). Higher levels of scorching were correlated with increasing dieback, while height and late-season flushing mitigated this relationship, with a negative influence on magnitude of dieback (**Figure 2.3**: Crown dieback of measured *Q. garryana* trees. Symbols are sized relative to tree height values, density is scaled according to volume of post-fire sprouting.). Below-ground fire effects (proportional duff consumption) were not correlated with crown dieback (P=0.161).

While per-tree duff consumption depths were greater in the UWTB and HLD01 units (**Table 2.3**), overall consumption (mean of 8 measurements per tree) was not extensive: mean

percent consumed was 25%, representing a mean depth of consumption of 1.7 cm (Appendix, **Figure B**). Within-tree variance in consumption was 3.35, and variance between trees was 3.33. Depth of duff consumption increased significantly with greater pre-burn duff depths (**Figure 2.4**, $P<0.0001$, $R^2 = 0.72$).

Per-rod duff consumption was more variable, ranging from 0 to 16 cm, with a mean of 2.4 cm (mean percentage consumed equaled 67.9 %) across all sites (**Table 2.3**). Depth of per-rod duff consumption was also positively correlated with deeper pre-burn duff depths (**Figure 2.5**, $P<0.0001$, $R^2=0.79$).

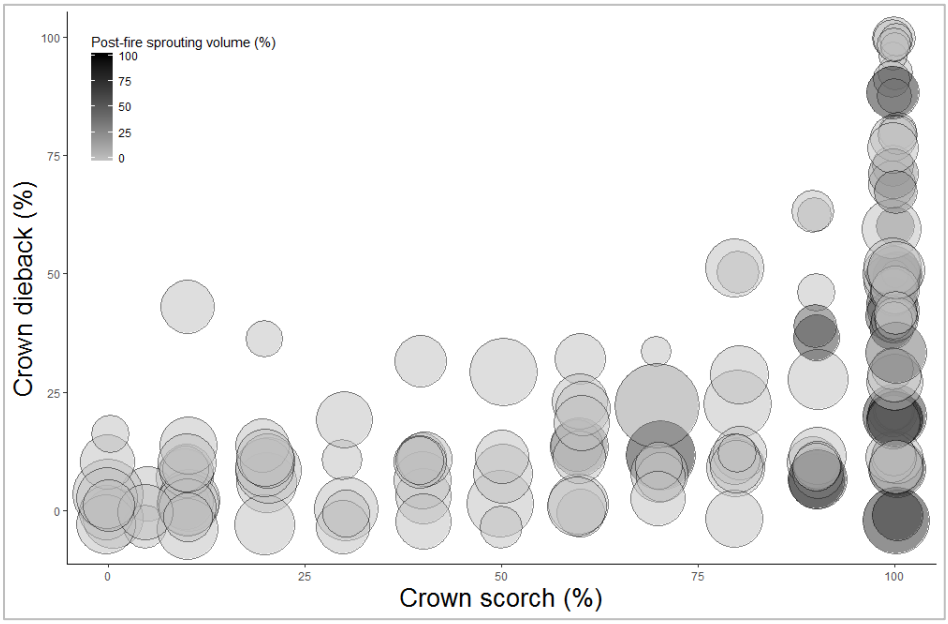

Figure 2.3: Crown dieback of measured *Q. garryana* trees. Symbols are sized relative to tree height values, density is scaled according to volume of post-fire sprouting.

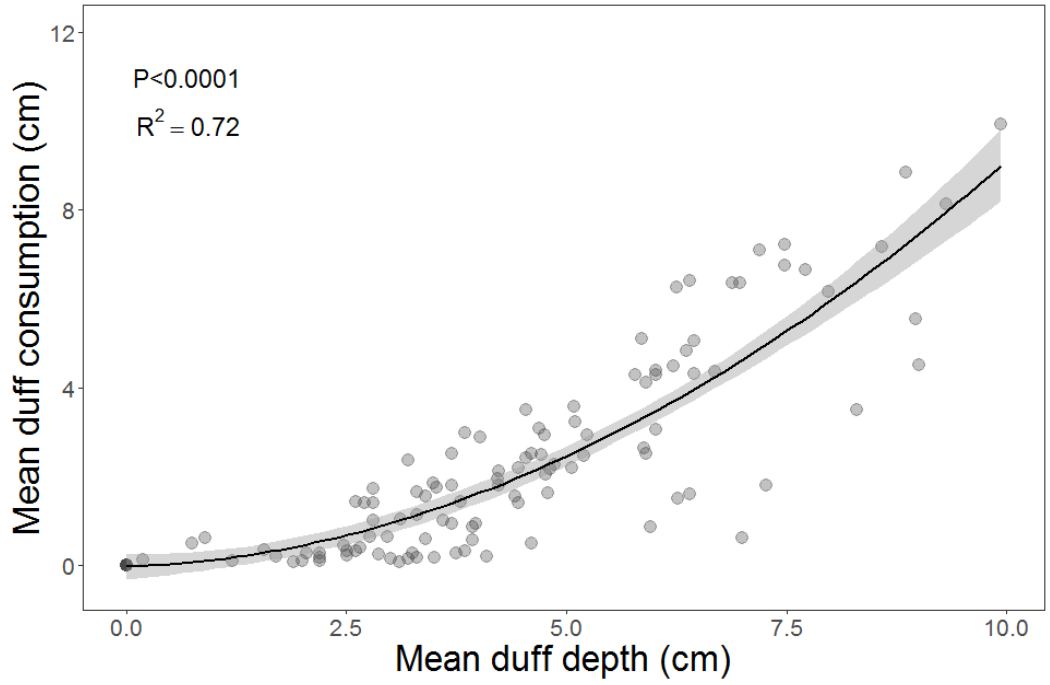

Figure 2.4: Mean per-tree duff consumption as a function of mean duff depth.

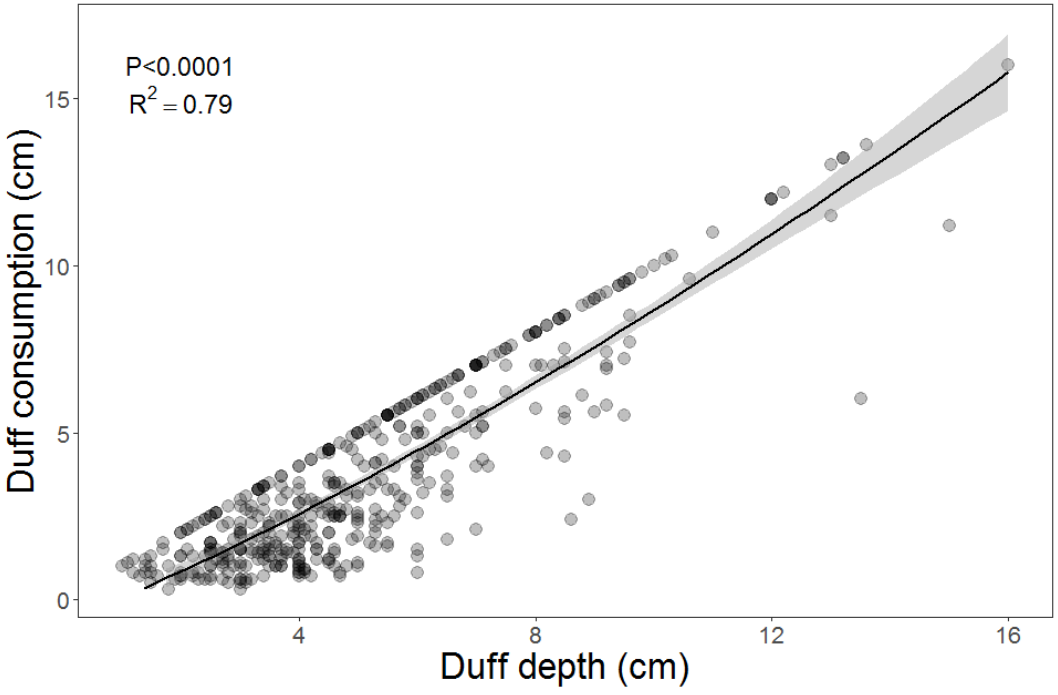

Figure 2.5: Point duff consumption as a function of pre-burn duff depth. Only rods with measureable consumption were included for analysis.

Results of a Wilcoxon rank-sum test found pre-existing scars to be a significant predictor of increased charring on tree boles, with mean bole char heights on scarred trees 2.6 times greater than on unscarred trees (**Figure 2.6,** P=0.002).

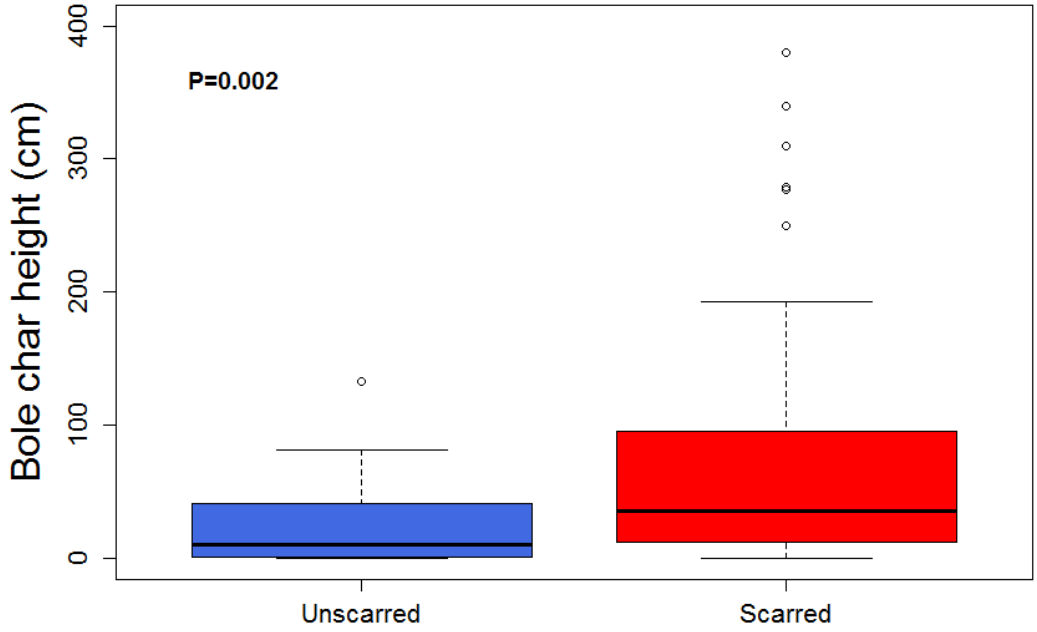

Figure 2.6: Prior bole scars were linked to greater charring on the boles of trees during burns. Trees that had evidence of previous scarring (n=120) had charring at greater heights than unscarred trees (n=31).

2.4 DISCUSSION

Various mechanisms control plant response to fire, with the maintenance of latent bud reserves and carbohydrate storage acting as effective methods of survival in fire-prone ecosystems (Clarke et al. 2013, Pausas and Keeley 2014). Our results demonstrate Garry oaks' high resilience to fire, utilizing strategies of both fire-resisters (protective bark, heat-tolerant buds) and endurers (adventitious bud banks, below-ground carbohydrate storage) (Rowe 1983). The characteristic low severity of prescribed fires creates difficulty in modelling mortality for fire-tolerant species under these management regimes. However, top-kill and excessive crown dieback are also important impacts for managers seeking to maintain habitat values provided by mature oak woodlands.

Garry oak tolerance to crown scorching is commonly assumed to be high, but few studies have established this with certainty. Several authors have examined prescribed fire effects on Garry oak regeneration (Tveten and Fonda 1999, Regan and Agee 2004), and one of these measured crown scorch in trees (Regan and Agee 2004), but did not attempt to relate this effect to oak injury. Peter et al. (2009) found buds of Garry oaks to be highly resistant to heating, suffering very low bud mortality at even the highest treatment level (133 seconds of heating at 60 °C, a threshold temperature commonly associated with plant tissue mortality). Thus, visible scorching of leaves in the crown may not indicate subsequent bud death with any certainty, in accordance with the findings of a previous study of prescribed fire in Garry oak woodlands (Peter et al. 2011). If this is the case, it might explain the highly variable dieback response at higher levels of crown scorching observed in this study (**Figure 2.2**). If scorching in oak crowns does not necessarily result in bud mortality, it may be of limited value as a field assessment of post-fire injury in highly fire-resistant species such as Garry oak. Additionally, the wide

variation in crown dieback may indicate that managers' efforts to protect oaks from crown scorching may not be warranted, especially for mature trees.

Our results hint at the existence of other factors, unmeasured in this study, which may influence outcomes for oaks exposed to understory burning. Unaccounted-for sources of variation in response could include pre-burn vegetation management, competition, and canopy position, none of which were examined as part of this study. Additionally, one of the study units (UWTT), had a more recent burn history than the others, which could have an influence on fire effects. However, it is important to consider that crown scorch, the fire effect with the strongest predictive ability in our model of crown injury, did not differ significantly between study units ($P=0.918$, **Table 2.3**), despite the disparity in fire history, and the resulting reduction in fuel density and height. Proportional duff consumption did vary across units, and was significantly lower in the recently burned UWTT unit ($P<0.0001$, **Table 2.3**), likely due to previous reductions of ground fuels in recent burns. This variable, however, did not have a significant effect on crown dieback (see Results). Longer-term monitoring, as well as additional studies, may reveal better predictors of Garry oak injury in prescribed burns.

As our strongest model predicting quantity of crown dieback included terms for late-season bud burst and tree height as well as crown scorch, it is necessary to examine how the two former variables might mitigate the impacts of scorching on tree vigor. As Garry oaks in our study produced new leaves after the start of the dormant season, it would be reasonable to surmise that this would result in a net reduction of carbohydrate reserves, and a consequent decrease in spring leaf-out: leaves produced this late in the season could feasibly drop before producing sufficient carbohydrates to replenish the stores used to produce them. However, while the effect was small, trees in this study that produced late-season leaves had a significantly

greater spring bud break response than those which did not. As such, late season foliage could provide a readily available source of carbohydrates that allow for the rapid restoration of lost crown volume in spring.

While both height and diameter were negatively correlated with crown dieback in our study (**Table 2.4**), these correlated variables did not contribute equally to our final model (see Results). It is unsurprising that height would have a greater effect on crown injury than diameter, as protection from heating in aerial buds is conferred via attainment of escape height (Higgins et al. 2000, Bond 2008, Burrows et al. 2008), while the added bark thickness associated with increased diameter offers greater protection to adventitious buds along the stem and base of plants (Pyke et al. 2010, Clarke et al. 2013).

While we were unable to precisely predict post-fire crown injury based on effects of understory burns on oaks, there were some clear thresholds of tree response. Post-fire crown sprouting did not occur below scorch volumes of 60%, and more than 80% scorch was necessary for substantial (50% or greater) crown dieback to occur. These results imply the existence of a high tolerance in Garry oaks for fire-induced injury, only beyond which will a response be observable in impacted trees. It appears that substantial injury must occur before imbalances are created in the hormones that regulate plant growth such as to provoke a sprouting response in adventitious buds (Anderson et al. 2001, Pyke et al. 2010). Correspondingly, bud death is also unlikely unless very high volumes of scorching occur in oak crowns.

The connection between basal duff consumption and oak vigor is much less clear. Our results indicate that duff consumption in Garry oak woodlands is greater with deeper duff depths, in accordance with other studied systems (Frandsen 1987, Hungerford et al. 1995, Kreye et al. 2017). Duff accumulation is greater in long-unburned stands, and thus these stands are at higher

risk if fine roots are present in duff or on the surface of the soil. While Garry oak is generally considered to be a deep-rooted species with a long tap root, Devine and Harrington (2005) found that in the coarse-textured glacial outwash soils of JBLM, the majority of fine lateral roots were located within the top 40 cm of the mineral soil profile. We did not observe fine oak roots embedded in duff prior to burns (logistical and safety concerns precluded extensive digging in our study units); the quantity of fine roots underlying duff in the surficial mineral soil, and the amount of heating that occurred at these depths during burns, is not known. To our knowledge, no research in Garry oak has measured root ingrowth into deep organic duff, as has been recorded in other long-unburned ecosystems (Swezy and Agee 1991, O'Brien et al. 2010). We found no apparent negative impacts on oak mortality within nine months of prescribed burns, even on oaks that experienced considerable proportional duff consumption (see Results). Similarly, while Kobziar et al. (2006) found that basal charring was a significant predictor of California black oak mortality following prescribed burns, they concluded that duff consumption did not predict oak mortality eight months after burning. These unknown factors obscure our ability to determine whether smoldering and duff consumption represent a significant risk of injury to trees in long-unburned oak stands.

We found that increased stem charring on oaks was strongly correlated with the existence of previous scars on tree boles. This was a predictable result, given the increased likelihood of ignition of scarred boles due to exposure of dry dead wood (Hood 2010). Once injured, scarred trees are more likely to be re-injured in a subsequent fire due to exposure of dry wood (Arno and Sneck 1977). The high level of injury due to ignition of old bole scars (and the large proportion of scarred trees) in this study may indicate that current prescribed burns are more intense than historic fires. Past fires are hypothesized to have been of low intensity, due to the predominance

of grass fuels that promote "flashy" short-duration flame fronts (Agee 1996, Engber et al. 2011). Contemporary oak stands are likely to have a greater density of shrub fuels due to prolonged fire exclusion and the encroachment of Scot's broom and other invasive woody plants in oak understories. Where these heavier fuels are present, protection of scarred trees may be required to avoid substantial oak injury. Manual clearing of fuels from around the base of trees can prevent ignition and ameliorate fire effects (Williams et al. 2006), and thus offers some protection from injury and mortality.

Their high level of resilience to fire, coupled with great variability in post-fire response, make the prediction of fire-caused Garry oak mortality problematic. Our results demonstrate the difficulty in predicting crown dieback based on short-term observations of fire effects, and suggests that crown scorch, while an effective predictor of mortality in many conifer species, may not be as definitive a tool for modelling mortality or top-kill of fire-tolerant oaks. Some of this difficulty may arise from the limited time-span of our study. The limitations of a short-duration study of tree injury are substantial, since many trees will not show signs of injury for several years after fire (Ryan and Reinhardt 1988, Agee 2003). However, Garry oak mortality is uncommon following understory burns (Thysell and Carey 2001, Regan and Agee 2004), indicating that while substantial injury to mature Garry oaks is possible in during underburning, the risk is quite low. Our results validate this supposition; nevertheless, as it is challenging in the short term to assess non-lethal impacts to trees (such as decreased radial growth, or reduced acorn production), further post-burn monitoring should document these additional metrics of injury, and preferably continue for several years.

2.5 Management Implications

The re-introduction of fire into long-unburned fire-adapted ecosystems is a process mired in uncertainty. While many studies have been conducted in long-unburned conifer-dominated systems (Hood 2010), to our knowledge this is the first study to compare both above and below-ground fire effects in restoration burns in Garry oak woodlands. The short term nature of this study, coupled with the high variability in outcomes, creates difficulties in drawing conclusions about the long-term vigor of oaks after understory burning in units that have experienced long fire-free intervals. However, preliminary results presented here may guide management decisions in the near future. While our findings did not identify any negative impacts of basal duff consumption, longer-term monitoring of selected trees may be necessary for these effects to manifest. Additionally, our results indicate that while oaks are highly resilient to understory burning, previously scarred trees are more vulnerable than others to injury in fires. Managers wishing to protect oaks in burn units may choose to focus efforts on removing fuels via raking and/or brush-cutting around trees with basal scars before burns are conducted (as in Williams et al. 2006).

One intention with this work was to establish a study that can be elaborated upon in the future. This effort will require continued monitoring of measured trees, as well as the addition of more units, especially ones that can be established to have a long fire-free history. It is reasonable to assume that based on broader studies of fire effects on Garry oaks, recommendations can be made to managers looking to meet understory restoration goals while limiting tree injury and mortality during prescribed fire operations.

CONCLUSIONS

After having undergone more than a century of the combined negative impacts of development, cattle grazing, non-native species invasion, and fire exclusion on their habitats, oaks continue to persist in Pacific Northwestern landscapes. Both of our study species exhibit extraordinary resilience to fire, suggesting that, despite considerable landscape alteration, potential for the restoration of these oak woodlands exists. However, the extensive departure of some of these formerly oak-dominated ecosystems from their historic conditions will necessitate substantial intervention in order to restore historic ecological processes. The degree of disjunction from historic ranges of variability has implications for the magnitude of intervention required in order to restore key habitat functions (Morgan et al. 1994, Landres et al. 1999). Deviations from past patterns of disturbance wrought by human intervention in natural fire regimes, coupled with the cessation of anthropogenic burning, aggravate the challenges present in oak woodland restoration.

Disruption of disturbance processes in fire-dependent oak ecosystems has consequences not only for stand development in the absence of fire, but for future vegetative states as fire returns to these systems. While fire is a mechanism critical to the maintenance of oak ecosystems, fire alone is unlikely to restore their functionality. The results of our studies indicate that fire-adaptive traits are specific to particular fire regimes, and that even species considered to be tolerant of fire (such as California black oak) can be susceptible when modern intensities exceed levels experienced in past fire regimes. Restoration efforts in oak woodlands are more likely to be successful when methods, especially the reintroduction of fire, are carefully tailored to model characteristics of past disturbance, and consideration is given to the landscape context within which a project is situated. Where past fire exclusion and other land use changes

have caused regional fire regimes to be substantially altered, as in black oak landscape that we studied, the reintroduction of fire can have unintended consequences for target habitats and species. Where impacts of altered fire regimes on vegetative communities have been less severe, such as the case of Garry oak woodlands on JBLM, this process may be less complex. In either scenario, the reintroduction and future reapplication of fire will be essential for the maintenance of fire-dependent oak woodlands.

Predicted changes in climate, and the altered fire regimes that result, will continue to impact plant communities across the western United States. Increases in the magnitude and occurrence of high-severity fire, including patch size expansion, will result in a greater incidence of vegetative states that are tolerant of this novel disturbance regime. The resulting conversion to landscape patterns may be inevitable. Due to their resilience to fire, oaks will likely continue to persist in these novel landscapes as they have for millennia, albeit perhaps in a new form. This is especially true for California black oak in northeastern California, which is likely to endure as a component of montane chaparral shrublands in much of its former range. Garry oak woodlands may experience fewer short-term impacts due to climate change and shifting fire regimes, but will continue to require frequent burning to maintain these habitats. Restoration activities in both oak ecosystems are necessary in order to ensure the long-term resilience of these important ecosystems in the future.

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APPENDIX

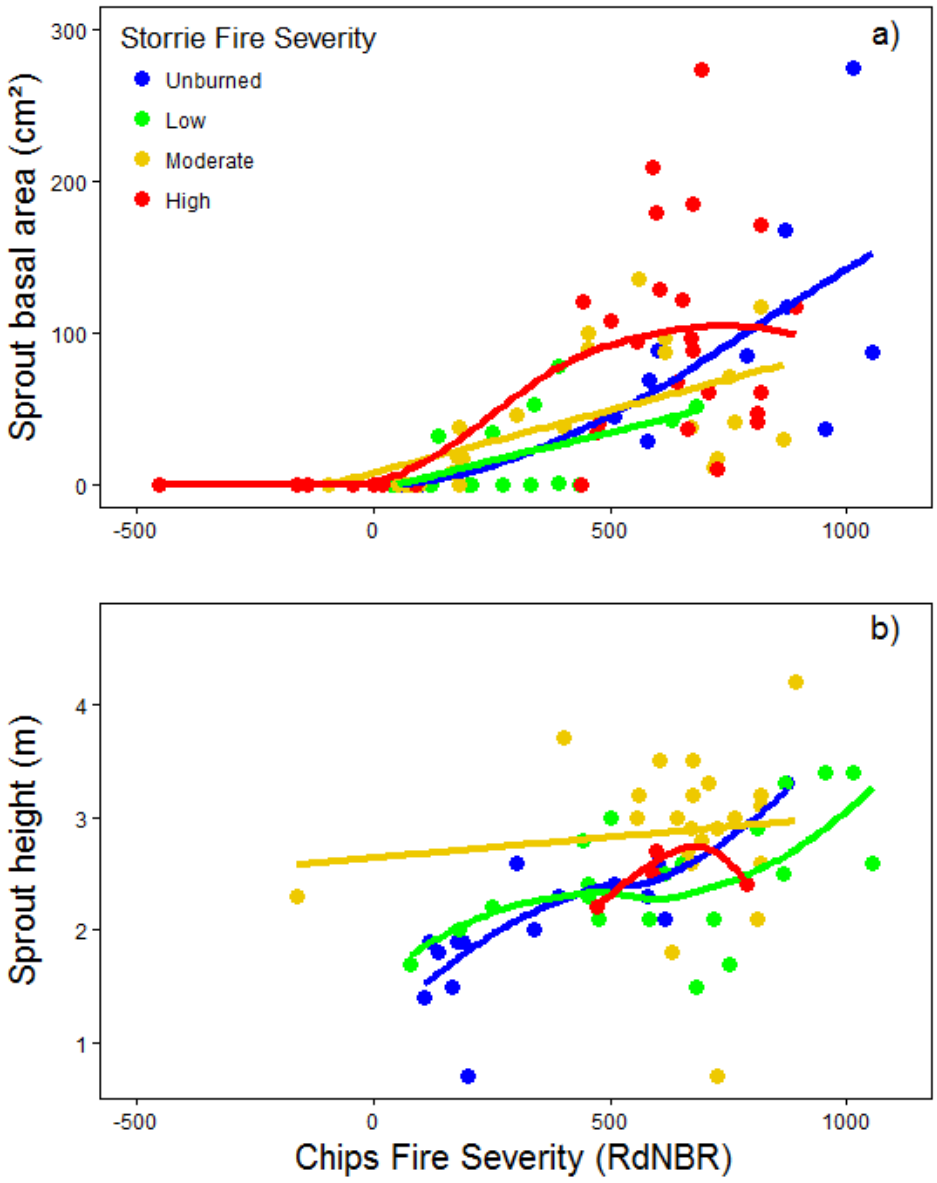

Figure A: Post-Chips Fire oak sprout response classified by Storrie Fire severity class. No discernable relationship exists between prior burn severity and response to a second fire.

Figure B: Heat map showing variability in mean duff consumption across three oak woodland burns units, Joint Base Lewis-McChord, Washington.