

RESEARCH ARTICLE

RESILIENCE OF CALIFORNIA BLACK OAK EXPERIENCING FREQUENT FIRE: REGENERATION FOLLOWING TWO LARGE WILDFIRES 12 YEARS APART

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ABSTRACT

Historically, oak woodlands in western North America were maintained by frequent fire that killed competing conifers. Today, these woodlands are often in decline as competition from conifers intensifies. Among oak species affected is the ecologically important California black oak (*Quercus kelloggii* Newberry). Within its range, large high-severity wildfires have become more common. We examined responses of black oak to two mixed-severity wildfires 12 years apart (2000 Storrie Fire and 2012 Chips Fire reburn). Regeneration was examined in relation to fire severity as measured by the Relative differenced Normalized Burn Ratio (RdNBR). We found that the RdNBR of the Storrie Fire was a useful predictor of the RdNBR of the Chips Fire reburn, suggesting that effects of the Storrie Fire on vegetation influenced fire behavior in the Chips reburn ($t_{12} = 2.892$, $P = 0.014$, $n = 14$, $r = 0.641$). After experiencing a second top-kill (complete cambium mortality above the root collar) in the Chips reburn, 95% (99 of 104) of black oak sprout clumps resprouted. Twelve years after the Storrie Fire, we found

RESUMEN

Históricamente, los bosques de roble en el oeste de Norte América estuvieron mantenidos por fuegos frecuentes que eliminaban a las coníferas competidoras. Hoy, esos bosques se encuentran en franca declinación al incrementarse la competencia de coníferas. Entre las especies de roble afectadas, está el roble negro de California (*Quercus kelloggii* Newberry). Dentro de su rango de dispersión, grandes fuegos de alta severidad están siendo cada vez más comunes. Nosotros examinamos las respuestas del roble negro a dos fuegos de severidad mixta separados por 12 años de diferencia (el incendio Storrie en el 2000, y el incendio Chips en el 2012). La regeneración fue examinada en relación a la severidad del fuego medida mediante el índice relativo normalizado de tasa de quema (RdNBR). Encontramos que el RdNBR del incendio Storrie fue un predictor útil del RdNBR del incendio Chips, lo que sugiere que los efectos del incendio Storrie influenciaron el comportamiento del fuego del incendio Chips ($t_{12} = 2.892$, $P = 0.014$, $n = 14$, $r = 0.641$). Después de experimentar una segunda muerte de su parte aérea (muerte completa del cambium por encima de la corona de la raíz) en el incendio Chips, el 95% (99 de 104) de los tocones del roble negro rebrotaron. Doce años después del Fuego Storrie, encontramos que una proporción menor de las

lower proportions of sprout clumps produced acorns in places where more overstory trees survived the fire ($t_5 = -3.023$, $P = 0.029$, $n = 7$, $r = 0.804$). After both fires, the crown volume of entire sprout clumps was lower in areas of higher live overstory tree basal area (Storrie Fire: $t_5 = 2.527$, $P = 0.053$, $n = 7$, $r = 0.749$; Chips reburn: $t_5 = -3.597$, $P = 0.016$, $n = 7$, $r = 0.849$). Our finding that most black oak survived successive top-kill from repeat fire suggested that repeated high-severity or mixed-severity fire is not an immediate threat to black oak presence on the landscape. Our findings also suggest that, if high-severity fire is followed by historically normal fire return intervals, rapidly regenerating black oak may be favored over conifers and recover from decline.

matas de roble negro produjeron bellotas en lugares donde más árboles del estrato superior sobrevivieron al fuego ($t_5 = -3.023$, $P = 0.029$, $n = 7$, $r = 0.804$). Luego de ambos fuegos, el volumen de la corona de los rebrotes de todas las matas fue menor en áreas que tenían mayores coberturas de área basal de árboles del estrato superior (Fuego Storrie: $t_5 = 2.527$, $P = 0.053$, $n = 7$, $r = 0.749$; Fuego Chips: $t_5 = -3.597$, $P = 0.016$, $n = 7$, $r = 0.849$). Nuestro descubrimiento de que la mayoría del roble negro sobrevivió a la muerte sucesiva de su parte aérea sugiere que fuegos repetidos de severidad alta o mixta no es una amenaza inmediata para la presencia del roble negro en el paisaje. Nuestros resultados también sugieren que, si un fuego de alta severidad es seguido por fuegos con intervalos de retorno históricos, la rápida regeneración del roble negro puede ser favorecida por sobre la de las coníferas y recuperarse de su declinación.

Keywords: 2000 Storrie Fire, 2012 Chips Fire, forest regeneration, post-fire response, *Quercus kelloggii*, RdNBR, reburn, resilience

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INTRODUCTION

There is interest in management and restoration of California black oak (*Quercus kelloggii* Newberry) due to its important ecological role in California's forests (Standiford and Purcell 2015). Black oak mast provides an important food source for a variety of mammalian and avian species (Bowyer and Bleich 1980, McDonald 1990, Koenig *et al.* 2008, Purcell and Drynan 2008). In addition, mature black oak trees have the potential to develop cavities that provide cover, rest, and nest sites for two important western species: fishers (*Martes pennant* Erxleben) and great grey owls (*Strix nebulosa* Foster) (Zielinski *et al.* 2004, Wu *et al.* 2015).

Black oak is widespread in California (Plumb and McDonald 1981). It is found growing as single trees or in groves and is a component of 11 different forest types (McDonald 1990). Mature black oak can yield high-value timber products, but California lacks a well-developed hardwood processing infrastructure and market (McDonald and Huber 1994).

Wildfire influences forest vegetation structure and composition (Scholl and Taylor 2010). This influence is described by three ecologic effects of fire disturbance: fire return interval (FRI), fire severity, and fire extent, collectively described as the fire regime (Agee 1989). The mixed-conifer forests and oak woodlands of western North America histori-

cally were associated with a low-severity fire regime with a FRI of less than 25 years (Agee 1989, Barnhart *et al.* 1996). The fire suppression era, which intensified around 1910, has increased FRIs in western North America, causing forest densification and the decline of oak woodlands (Barnhart *et al.* 1996). Large high-severity fires have become more frequent, causing changes to vegetation structure and composition (Westerling *et al.* 2006, Scholl and Taylor 2010). Longer FRIs have adversely affected black oak by giving young conifers that establish beneath oak trees the time to grow large enough to accumulate thick fire resistant bark. Over time, these conifers are able to pierce the oak crowns, overtopping them and weakening or killing them (Devine and Harrington 2006, Engber *et al.* 2011, Cocking *et al.* 2015). This process is commonly referred to as conifer encroachment, or succession to conifer (Cocking *et al.* 2012, Crotteau *et al.* 2015). While high-severity fires can have negative ecological effects, they may also give a competitive advantage to species such as black oak that have the ability to regenerate quickly by sprouting following top-kill (complete cambium mortality above the root collar). Cocking *et al.* (2014) found that fire severity acted as a catalyst for species compositional changes on the landscape, with low-severity fire favoring encroaching conifers and high-severity fire favoring black oak when present.

Black oak trees and seedlings can resprout vigorously from dormant buds in their root crown after being top-killed by fire (McDonald and Tappeiner 2002). Although sprouting is the primary mode of reproduction for black oak, seed regeneration allows black oak to migrate and adapt to changes in conditions through sexual reproduction (McDonald 1990). Black oak migration is facilitated by animals such as western grey squirrels (*Sciurus griseus* Ord), California scrub jays (*Aphelocoma californica* Vigors), and acorn woodpeckers (*Melanerpes formicivorus* Swainson),

which can move black oak acorns farther from their parent tree than can wind dispersal (McDonald 1990, Koenig *et al.* 2008).

Understanding fire-induced sprouting responses of California black oak could help land managers assist in recovery of black oak ecosystems in California. While there have been studies of the response of top-killed black oak trees following fire (Cocking *et al.* 2012, 2014; Crotteau *et al.* 2015), we are not aware of research examining the response of black oak sprout clumps to top-kill after a short FRI. Therefore, our objectives for this study were to: (1) compare burn severities in the Storrie Fire and Chips reburn, (2) examine black oak's ability to survive successive fire-induced top-kill, and (3) examine the effect of live residual overstory tree basal area (BA) on sprout clump vigor (i.e., in terms of crown volume development) and acorn production after the Storrie Fire and the Chips reburn.

METHODS

Study Area

On 17 August 2000, the Storrie Fire ignited, burning ~23 000 ha of land within Lassen National Forest and Plumas National Forest, California, USA. Twelve years later, on 29 July 2012, the Chips Fire started within the Storrie Fire footprint, reburning ~10 000 ha before moving northeast out of the Storrie Fire footprint to burn a total of ~31 000 ha. Our study area covered 1960 ha of overlapping footprints of the 2012 Chips Fire and 2000 Storrie Fire on the Lassen National Forest (40° 04' 32.7" N, 121° 16' 08.3" W). We restricted our study area to an elevation range from 1158 m to 1734 m, above which California black oak was not found (Crotteau *et al.* 2015).

Climate in the study area was characterized by warm dry summers (mean maximum temperature from 1909 to 2016, June to September: 24°C to 29°C; WRCC 2016) and cool wet winters (mean maximum temperature

from 1909 to 2016, December to March: 5°C to 10°C; WRCC 2016). Mean annual precipitation was 849 mm (from 1948 to 2010), with average snowfall of 330 cm (from 1948 to 2010, WRCC 2016). Soils in the area were variable with primarily basalt and some andesite parent materials, with textures ranging from loams to gravelly sandy loams. Rocky outcroppings occurred on some slopes. Slopes ranged from alluvial areas with 0% to 35% slopes, to hilly and steep mountain slopes of 35% to 100% (NRCS 2016).

Dominant forest type was Sierra Nevada Mixed Conifer, which includes the dominant species Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), sugar pine (*P. lambertiana* Douglas), incense-cedar (*Calocedrus decurrens* [Torr.] Florin), and white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) (Eyre 1980). The most commonly associated shrubs were pinemat manzanita (*Arctostaphylos nevadensis* A. Gray), greenleaf manzanita (*Arctostaphylos patula* Greene), whitethorn ceanothus (*Ceanothus cordulatus* Kellogg), deerbrush (*C. integerrimus* Hook. & Arn.), snowbrush (*C. velutinus* Douglas ex Hook.), bush chinquapin (*Chrysolepis semper-virens* [Kellogg] Hjelmqvist), and huckleberry oak (*Quercus vacciniifolia* Kellogg).

Sampling Methods

We used previously established experimental units from the Crotteau *et al.* (2013) study of regeneration following the Storrie Fire in which areas were stratified by forest community types occupying three elevation ranges: mixed conifer (elevation 0 m to 1463 m), low elevation fir (elevation 1463 m to 1774 m), and high elevation fir (elevation 1774 m to 2188 m) (Eyre 1980). Each forest community type was then further stratified by four fire severity levels: unchanged, low, moderate, and high. Sixty experimental units were randomly selected from the population of

polygons representing the 12 “forest-type × fire-severity” combinations (i.e., five units per stratum). Each experimental unit was represented by a cluster of 19 to 22 fixed radius 0.004 ha regeneration plots laid out in an elongated diamond pattern and spaced 20.1 m apart. Overstory trees were sampled using variable radius plots centered on seven of the regeneration sample plots spaced 40.2 m apart using a 4.592 m² ha⁻¹ basal area factor prism. These plot clusters were measured over a two-year period, 11 and 12 years following the Storrie Fire (Crotteau *et al.* 2013).

Of the 60 plot clusters (units) established by Crotteau *et al.* (2013), 14 were within our study area. The remainder were either not re-burned or not remeasured. We used the previously collected data from the years 2011 and 2012 prior to the Chips Fire reburn (Chips reburn). We also collected data from these 14 units in the summer of 2015, three years after the Chips reburn, to assess regeneration response of black oak sprout clumps and seedlings observed in the original study (Crotteau *et al.* 2015). For each sprout clump within the regeneration plots, we collected: stem count, two perpendicular crown widths (to nearest 1 cm), diameter at breast height (DBH, to nearest 1 cm), and height (to the nearest 0.1 m). Dead remnant stems of the Storrie-Fire-origin sprouts were visually inspected for presence of attached acorn caps as evidence of acorn production prior to the Chips reburn. We tallied black oak seedlings (DBH <10 cm) within each regeneration plot. To examine the effect of live residual overstory BA on sprout clump vigor, we re-evaluated all overstory trees (live and dead with DBH >10 cm) in variable radius plots by recording species, DBH (to nearest 1 cm), and mortality.

Due to the complicated nature of two successive mixed-severity fires, black oak individuals were affected differently throughout the study area. There were three types of sprout clumps that we observed in 2015 following the reburn: (type 1) those originating

from a parent tree that was top-killed by the Storrie Fire but not top-killed by the Chips re-burn, (type 2) those originating from a parent tree top-killed by the Chips re-burn, and (type 3) those originating from a sprout clump that was top-killed in the Chips re-burn (i.e., black oaks experiencing top-kill in both fires). For this study, black oak trees (DBH >10 cm) that were not top-killed but experienced fire damage that resulted in a sprouting response were not considered sprout clumps and were treated as a black oak tree. For crown volume analysis after the re-burn at age three years, we were only interested in the response of the type 3 sprout clumps that experienced a second fire-induced top-kill. We excluded type 2 sprout clumps from the crown volume analysis because their volume growth response may be different than type 3 sprout clumps. We included all sprouts clump types in the sprout clump density estimate after the Chips re-burn.

Fire severity throughout the Storrie Fire and Chips Fire re-burn was categorized using the Composite Burn Index (CBI). The CBI was derived from Relative differenced Normalized Burn Ratio values (RdNBR; Miller *et al.* 2008) provided by the Remote Sensing Application Center, Salt Lake City, Utah, USA. The RdNBR is a metric derived from a comparison of pre-fire and one year post-fire reflectance imagery captured by Landsat (30 m × 30 m spatial resolution). The RdNBR is used as an indicator of vegetation change due to fire in forested ecosystems (Miller *et al.* 2008).

Data Analysis

For all regression analysis, we used simple linear regression. We checked each regression for normality using the Q-Q test; we checked residuals by plotting residuals versus fitted values; and we checked leverage using Cook's distance.

To meet our first objective, we calculated an average RdNBR value of the Storrie Fire

and the Chips re-burn for each unit. We achieved this by first clipping RdNBR raster data by unit area, then we calculated an area-weighted mean RdNBR using the number of hectares represented by each RdNBR value. We used regression analysis to examine the relationship between Chips re-burn RdNBR and Storrie Fire RdNBR. To meet our second objective, we calculated percent survival of sprout clumps for each unit by dividing the number of Storrie Fire sprout clumps that were top-killed by the Chips re-burn and resprouted, by the total number of Storrie Fire sprout clumps. We then took the mean survival percent among units to report percent survival for the re-burn area. To meet our third objective, we assumed that a paraboloid function,

$$volume = \left(\frac{\pi}{2}\right) \times height \times radius^2, \quad (1)$$

best described the crown shape of each multi-stemmed sprout clump, and we used average crown *radius* (m) and *height* (m) data to estimate individual sprout clump crown *volume* (m³). We used regression analysis to examine the effect of live overstory BA on sprout clump crown volume 11 and 12 years after the Storrie Fire and three years after the Chips re-burn. We used simple linear regression to examine the proportion of sprout clumps that produced acorns 12 years after the Storrie Fire as a response to live overstory BA.

RESULTS

The Chips re-burn RdNBR was positively correlated with the Storrie Fire RdNBR ($t_{12} = 2.892$, $P = 0.014$, $n = 14$, $r = 0.641$; Figure 1). The slight negative relationship between live overstory BA loss and Chips re-burn RdNBR ($t_{12} = -1.373$, $P = 0.195$, $n = 14$, $r = 0.368$; Figure 2) was driven by one high leverage outlier.

In the original Crotteau *et al.* (2015) study 11 and 12 years after the Storrie Fire, there were 57 black oak seedlings counted in 34 of

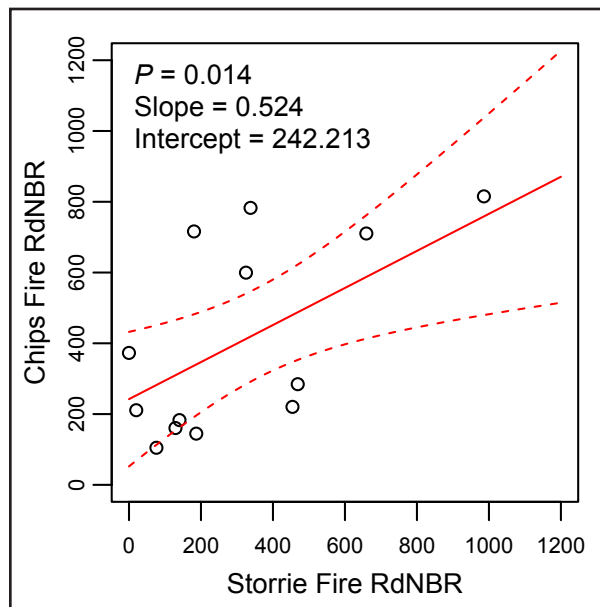


Figure 1. Fire severity of two successive fires as measured by RdNBR. The Storrie Fire ignited on 17 August 2000, burning ~23 000 ha of land within Lassen National Forest and Plumas National Forest, California, USA. Twelve years later, on 29 July 2012, the Chips Fire started within the Storrie Fire footprint, reburning ~10 000 ha. The red line represents the results of a simple linear regression model with 95% confidence interval (red dashed line) of the relationship between Storrie Fire severity and Chips Fire reburn severity.

270 regeneration plots. Three years after the Chips reburn, we counted 30 black oak seedlings on 19 of these same 270 regeneration plots. We did not inspect the seedlings to determine if they were seedlings that survived the Chips reburn, seedling sprouts, or seedlings established post Chips reburn. This amounted to an average density of 54 seedlings ha^{-1} and 28 seedlings ha^{-1} among units for the Storrie Fire and Chips Fire, respectively (Table 1). The presence or absence of oak seedlings in sample plots varied widely following the Storrie Fire and the Chips reburn, and was not related to any metric that we observed.

In seven of the 14 units, there were 104 California black oak sprout clumps observed in 2011 and 2012 (Table 2). These sprout clumps had all originated from top-killed

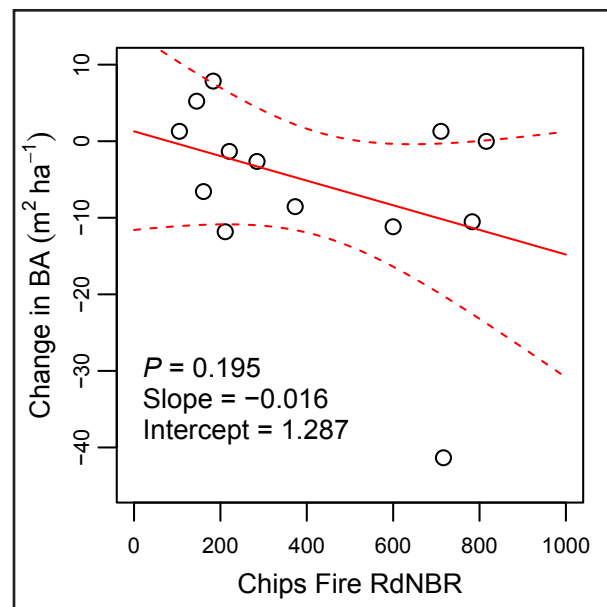


Figure 2. Change in live overstory basal area (BA) as a response to Chips Fire severity, in terms of RdNBR. Change was calculated by taking the difference between pre-fire BA measured in 2011 and 2012 and post-fire BA measured in 2015. The red line represents the results of a simple linear regression model with a 95% confidence interval (red dashed line). Twelve years after the Storrie Fire, on 29 July 2012, the Chips Fire started within the Storrie Fire footprint, reburning ~10 000 ha.

black oak trees after the Storrie Fire. Three years after the Chips reburn, we observed 103 live sprout clumps in the same units (Table 2). Of these 103 sprout clumps, 99 originated from top-killed sprout clumps and four from top-killed black oak trees. In the 2012 Chips reburn, all 104 Storrie-Fire-origin sprout clumps were top-killed; of these top-killed sprout clumps, 99 (95%) resprouted after the Chips reburn (Figure 3). Mean black oak sprout clump survival rate among units was 96% with a standard deviation of 4%, and with a range of 90% to 100%. Sprout clump density following the Storrie Fire and Chips reburn was 96 sprout clumps ha^{-1} and 95 sprout clumps ha^{-1} , respectively.

After 11 and 12 years, black oak sprout clump crown volume was lower beneath a denser live overstory BA ($t_5 = -2.527$, $P =$

Table 1. California black oak (BO) seedling and sprout clump density after 2000 Storrie Fire and 2012 Chips Fire reburn. Count data collected in 0.004 ha plots ($n = 270$) expanded to hectare level. Live overstory basal area (BA) summary data for 98 samples taken in conjunction with regeneration counts.

	Statistic	Seedlings (ha ⁻¹)	Sprout clumps (ha ⁻¹)	Overstory BO BA (m ² ha ⁻¹)	Overstory conifer BA (m ² ha ⁻¹)
Storrie Fire (11 and 12 yr post fire)	mean	53	96	0.4	26.9
	SD	75.7	137.3	1.2	20.2
	minimum	0	0	0	0
	maximum	247	429	4.6	60.4
Chips Fire reburn (3 yr post fire)	mean	28	95	0.1	21.6
	SD	53.5	133.4	0.5	21.7
	minimum	0	0	0	0
	maximum	195	403	2.0	61.7

Table 2. Unit forest community types (mixed conifer = elevation 0 m to 1463 m, and low elevation fir = elevation 1463 m to 1774 m) and summary statistics for fire severity in terms of composite burn index (1 = unchanged, 2 = low severity, 3 = moderate severity, 4 = high severity). California black oak (BO) sprout clump counts pre 2012 Chips Fire in 2011 and 2012 and post Chips Fire sprout clump counts in 2015.

Unit	Forest community type	2000 Storrie Fire severity	2012 Chips Fire severity	BO sprout clump count 2011 to 2012	BO sprout clump count 2015
23	Low elevation fir	1	2	0	0
32	Low elevation fir	4	4	18	17
35	Low elevation fir	2	2	0	0
46	Mixed conifer	2	4	0	0
48	Mixed conifer	2	2	0	0
49	Mixed conifer	1	3	0	0
52	Mixed conifer	3	2	15	17
53	Mixed conifer	4	4	33	31
54	Mixed conifer	2	2	6	6
55	Mixed conifer	3	4	1	1
56	Mixed conifer	2	2	0	0
57	Mixed conifer	3	3	9	9
59	Low elevation fir	3	2	0	0
60	Low elevation fir	4	4	22	22
Sum				104	103
Average		2.57	2.86	7.43	7.36
SD		1.02	0.95	10.62	10.32
Minimum		1	2	0	0
Maximum		4	4	33	31

0.053, $n = 7$, $r = 0.749$). The model estimated sprout clump crown volume of 26.7 m³ with no live overstory BA, but only 7.2 m³ with 30 m² ha⁻¹ live overstory BA (Figure 4). Crown size among three-year-old reburn clumps was also smaller in areas with higher live overstory

BA ($t_5 = -3.597$, $P = 0.016$, $n = 7$, $r = 0.849$). The model estimated crown volume of 7.8 m³ for sprout clumps with no live overstory BA, but only 3.9 m³ with 30 m² ha⁻¹ live overstory BA (Figure 5). The proportion of sprout clumps that produced acorns 12 years after re-



Figure 3. California black oak (*Quercus kelloggii* Newberry) sprout clump three years after experiencing a second fire-induced top-kill (complete cambial mortality above root collar) 12 years after the first fire-induced top-kill, in Lassen National Forest. Present in the image is the original tree stem that experienced the first top-kill, center. We also see the shorter and abundant dead stems that are the remnants of the sprout clump that experienced the second top-kill. Lastly, we see the current sprout clump at age three years in the middle of the growing season. Image captured 17 May 2015.

sprouting was lower in areas with greater live overstory BA ($t_5 = -3.023$, $P = 0.029$, $n = 7$, $r = 0.804$). In areas with no live overstory BA, our model estimated 45% of sprout clumps produced acorns 12 years after fire-induced re-sprouting, compared to 0% in areas with 30 $\text{m}^2 \text{ha}^{-1}$ live overstory BA (Figure 6).

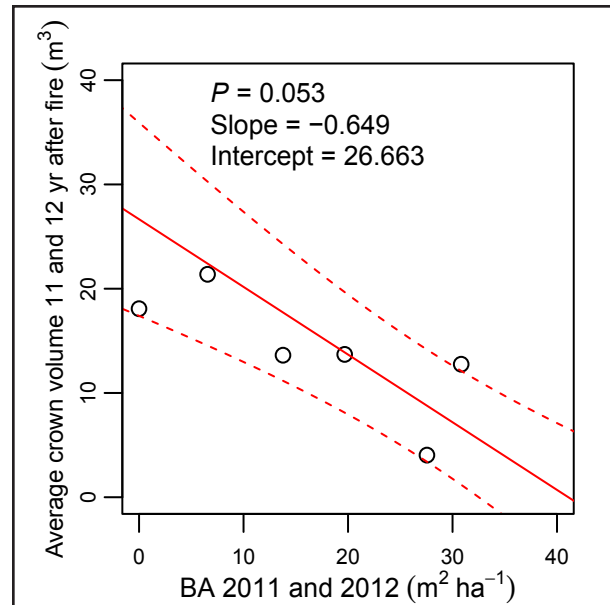


Figure 4. California black oak sprout clump volume following fire-induced top-kill (complete cambial mortality above root collar) as a response to live overstory basal area (BA) 11 and 12 years after the Storrie Fire. The red line represents the results of a simple linear regression model with a 95% confidence interval (red dashed line).

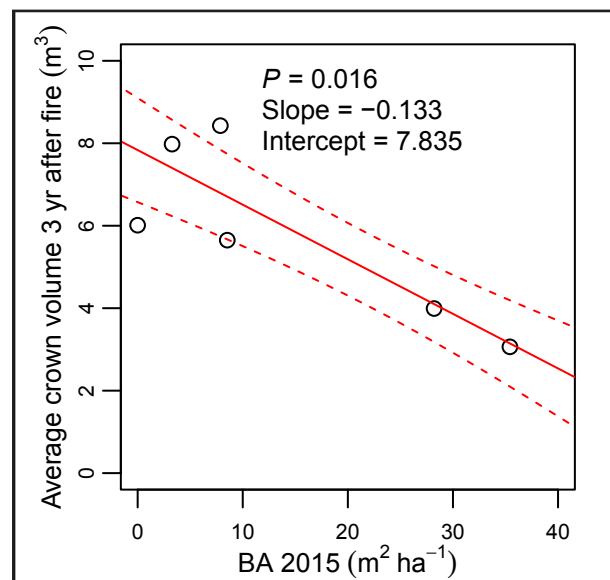


Figure 5. California black oak sprout clump volume following fire-induced top-kill (complete cambial mortality above root collar) as a response to live overstory basal area (BA) three years after the Chips Fire reburn. The red line represents the results of a simple linear regression model with a 95% confidence interval (red dashed line).

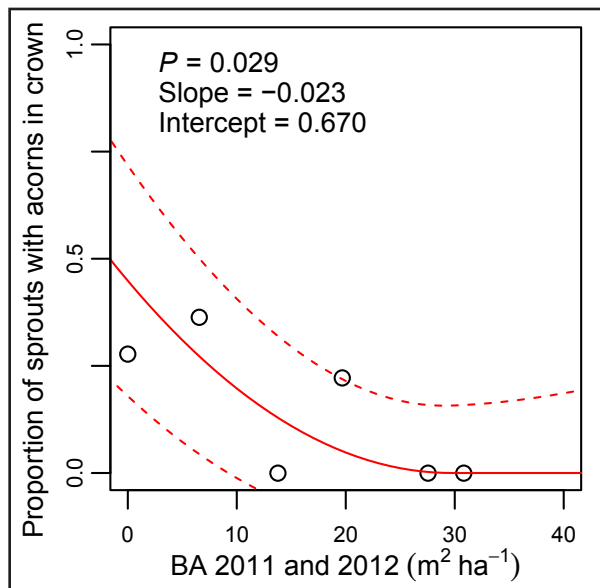


Figure 6. The proportion of California black oak sprout clumps, after a square root transformation (untransformed values shown), that produced acorns after 12 years after fire-induced top-kill (complete cambial mortality above root collar) in relation to live overstory tree BA. The red line represents the results of a simple linear regression model with a 95% confidence interval (red dashed line).

DISCUSSION

Storrie Fire severity, in terms of RdNBR, appeared to be a useful predictor of the Chips reburn severity at a 12 year fire return interval (Figure 1). In the Rogue-Siskiyou National Forest in northwest California, USA, Thompson *et al.* (2007) observed similar results in the Silver Fire and Biscuit Fire reburn at a 15 year FRI. In our study on Lassen National Forest, variation was highest when the Storrie Fire RdNBR ranged from ~200 to ~450 (Figure 1). If we compare these values to a BA loss severity classification by Miller *et al.* (2008), we see that they fall into the upper range of low severity through moderate severity (low <370, moderate = 371 to 574, high >575). Where the Storrie Fire severity was in the ~200 to ~450 range, the Chips reburn RdNBR ranged from low to high (Figure 1). These areas catego-

rized as having moderate RdNBR may have experienced patchy burn severity. Our data indicated that areas experiencing low-severity fire during the Storrie Fire (in terms of RdNBR) generally experienced a low-severity fire during the Chips reburn, while areas experiencing high-severity fire also often experienced high-severity reburn in terms of RdNBR (Figure 1). High RdNBR values from the Storrie Fire probably come from change in the form of tree cover being lost, exposing bare ground, and releasing rapidly resprouting shrubs. In contrast, high RdNBR values from the Chips reburn may represent the loss of dense shrub layers and regenerating trees. Live overstory tree cover remaining in areas of low RdNBR following the Storrie Fire might have also survived the Chips reburn, leaving the landscape relatively unchanged in Landsat satellite imagery.

Data collected from multispectral satellite imagery, and the products derived from them such as RdNBR, have become a common tool used for estimating fire severity on the landscape following a fire (Miller *et al.* 2008). However, following the Chips reburn of the Storrie Fire, the loss of live overstory BA varied with respect to an increase in Chips reburn RdNBR (Figure 2). The slight trend we see in Figure 2 is primarily driven by one unit that experienced a high level of BA loss. This result suggests that RdNBR may be less reliable for predicting BA loss from a recent reburn.

The 12-year FRI was within the range the historic pre-settlement FRI of 2 to 15 years for this region and forest type (Beaty and Taylor 2001). Within our plots, 100% of black oak sprout clumps arising after the 2000 Storrie Fire were top-killed in the 2012 Chips reburn. Outside our sample plots, very few sprout clumps were not top-killed (i.e., only partially consumed crown). During our assessment of Storrie Fire-origin sprout clumps in 2015, we noticed that bark was still present on some of the fire-killed sprout stems; their bark was thin (less than ~6 mm thickness), suggesting that

the cambium was vulnerable to heat damage at this young age. The combination of thin bark, dense crowns (Crotteau *et al.* 2015), and highly volatile foliage (Engber and Varner 2012) likely contributed to the high top-kill rate of sprout clumps in the Chips reburn.

California black oak presence on the landscape was resilient with 95% of the 12-year-old sprout clumps resprouting after a second top-kill in the 2012 Chips reburn. In contrast to the young sprout clumps that we studied, when black oak trees are top-killed by fire, we may expect slightly lower proportions to resprout. Two studies in the Sierra Nevada found 89% and 90% of top-killed black oak trees resprouted following prescribed fire (Regelbrugge and Conard 1993, Stephens and Finney 2002). In the Klamath Mountains of northwest California, 82% of top-killed black oak trees resprouted following wildfire (Cocking *et al.* 2012). In a study conducted 10 years after the 2000 Storrie Fire, 89% of top-killed black oak trees had resprouted (Cocking *et al.* 2014). While the causes of black oaks failure to resprout after fire are not yet well understood, Cocking *et al.* (2014) found that black oak tree complete mortality is closely related to encroaching tree characteristics, which suggests that competition and pre-fire vigor may be more important than age or other factors known to affect resprouting in black oaks (McDonald 1990). These findings suggest that repeated high-severity fire is not an immediate threat to black oak presence on the landscape; however, it does impact the tree form.

Twelve years after the Storrie Fire, while not statistically significant, California black oak sprout clump crowns in areas with no live overstory competition were three times the size of those with high amounts of live overstory competition (Figure 4). After the reburn, at age three years, sprout clump crowns in areas with no live overstory competition were twice the size of those in areas with high live overstory competition (Figure 5). The difference in the effect that live overstory competi-

tion had on sprout vigor (according to crown volume development) between the 12-year-old and 3-year-old sprout clumps may relate to early reliance on energy stored in the resprouting root system before leaf area increases and transitions from a carbon sink to becoming a source of carbon production dependent on light and other resources (O'Hara and Berrill 2010).

The varying proportions of sprout clumps that produced acorns 12 years after the Storrie Fire indicated that acorn production was much less likely in areas where more overstory trees survived the fire (Figure 6). McDonald and Tappeiner (2002) also reported early acorn production following top-kill by mechanical harvest of California black oaks. Wildlife lose this food source in the years immediately after wildfire-induced top-kill in black oak stands. Therefore, management that promotes early production of acorns, such as reducing overstory tree cover near black oak sprout clumps, may provide some benefit to wildlife. It is not known if these young sprout-clump-produced acorns are viable; according to McDonald (1990), black oak trees in natural stands do not produce viable seed until at least age 30 years. Shorter fire return intervals that preclude viable acorn production in resprouting black oak will not immediately favor regenerating conifers over sprouting black oaks, but without seedling regeneration, we expect the extent and representation of black oak to gradually decline according to the attrition rate among top-killed black oaks that do not resprout after fire. If the high top-kill rate of sprout clumps that we observed in the 12-year FRI is repeated over time, it may reduce the recruitment of mature black oak trees. This would also impact wildlife dependent on stem cavities and large limbs that can develop on mature oak trees.

Our sample was small, with only 14 experimental units experiencing reburn, but the sampling covered a large area (1960 ha) and presented a rare opportunity to study how Cal-

ifornia black oak sprout clumps responded to two successive mixed-severity wildfires. While the conclusions we draw from these data are informative, without replication across California black oak's range, we advise caution inferring the behavior of black oak in this specific study area to the black oak range as a whole.

In areas that harbor oaks, some post-fire management practices may support the recovery of oak ecosystems in western North America. For example, refraining from planting conifers near sprouting oaks, and reducing the

density of conifers in areas where there are high densities of oaks may facilitate oak woodland recovery. Wildfire surrogate treatments may also favor oak over conifer (Moghaddas *et al.* 2008). Nevertheless, oak's ability to regenerate sexually and asexually after high-severity fire and mixed-severity repeat burning suggests that reintroduction of fire, preferably coinciding with good seed production (Keeley and Mantgem 2008) and coupled with active post-fire management, will be effective in enhancing the recovery of declining oak ecosystems.

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