KNOBCONE PINE RESPONSE TO SHADING FROM COMPETING CHAPARRAL SHRUBS FOLLOWING STAND-REPLACING WILDFIRE

By

Sean Lindley

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Committee Membership

Dr. David Greene, Committee Co-Chair

Dr. Buddhika Madurapperuma, Committee Co-Chair

Dr. Jeffrey Kane, Committee Member

Dr. Andrew Stubblefield, Program Graduate Coordinator

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ABSTRACT

KNOBCONE PINE RESPONSE TO SHADING FROM COMPETING CHAPARRAL SHRUBS FOLLOWING STAND-REPLACING WILDFIRE

Sean Lindley

In northern California, fire regimes are shifting towards more frequent and larger severe wildfire. There is growing concern that this shift poses a threat to biodiversity in the form of cover type change at the landscape scale, resulting in the extirpation of some species in favor of well-adapted ones. In northern California, mature serotinous conifers, such as knobcone pine (*Pinus attenuata*), and resprouting shrub species easily regenerate in severe patches of any size. There is no general consensus regarding the effects of shrub competition on conifer recruitment; conifer response varies with shade tolerance and other abiotic factors. Knobcone pine and chaparral shrubs are universally shade intolerant, and we expect shading to be the main driver of inter-species competition.

We examined knobcone pine regeneration on lower slopes within the 2018 Carr and Delta fires at the third and fourth post-fire years, as well as the 2008 Motion Fire at the 14th post-fire year, focusing on two measurements of shrub shading: inter-shrub porosity (% shrub cover) and intra-shrub porosity (species-specific crown density). Our response variables included recruitment success (recruits per ovulate cone) and growth (height). We found (1) there were few pine recruits under shrubs, with the bulk of the shrub-induced morality of knobcone pine occurring before the third growing season; (2)

knobcone pine averaged about 6 established recruits per burned parent tree; and (3) the recruits were expected to persist despite limited growth and reach the shrub canopy by about the seventh year after fire. We conclude that competition with shrubs on lower slopes in northern California does not sufficiently impede the post-fire increase in serotinous pine density to limit subtle expansion into chaparral.

ACKNOWLEDGEMENTS

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INTRODUCTION

In many areas of western North America, fire regimes are shifting towards more frequent and larger severe wildfire (Cattau et al., 2020; Parks and Abatzoglou, 2020; Hagmann et al., 2021). Many have speculated that this shift results in the decline of species not historically exposed to large or frequent severe wildfire and favors expansion of more resilient species (Buma et al., 2013; Collins and Roller, 2013; Stevens-Rumann et al., 2019; Tepley et al., 2017; Walker et al., 2018; Boag et al., 2020). In northern California, an area experiencing a notable increase in the area burned at high severity in recent years (Reilly et al., 2017; Parks and Abatzoglou, 2020), species well-adapted to severe fire include serotinous conifers and chaparral shrubs. Both species rely on fire-dependent regeneration mechanisms, rather than structural fire resistance, to persist in landscapes dominated by severe wildfire.

Serotinous conifers require the extreme heat associated with high-severity flame fronts to melt the resin that keeps cones sealed in the aerial seedank. Following a severe wildfire, serotinous conifers release the majority of viable seed within the first post-fire year (Begley, 2010; McNamara et al., 2019; Marlin, 2021), though some viable seed can remain in cones for up to three years (Vogl, 1973; Greene et al., 2013). As a result, seeding from serotinous conifers can occur deep within burn patches beyond the dispersal constraints of their non-serotinous counterparts (Greene and Johnson, 2000). Growth characteristics are broadly similar among serotinous conifer species (Keeley, 2012), where recruits are shade-intolerant, prioritize rapid vertical growth over lateral crown expansion, and develop aerial seedbanks within a short time following fire compared to non-serotinous conifer species (Schopmeyer, 1974; Vogl, 1973; McCune, 1988; Keeley, 2012). Often, serotinous species are drought tolerant (Ilisson and Chen, 2009; Harvey et al., 2016). As testament to the mixed-severity fire regime that typified much of California prior to the 19th century (Perry et al., 2011), serotinous conifer species in three genera (*Pinus, Hesperocyparis,* and *Sequoiadendron*) are found infrequently in mixed-conifer forests throughout the state. Of these species, only knobcone pine *(Pinus attenuata*) has an appreciable range, which stretches from southwestern Oregon to southern California and includes coastal mixed-conifer ranges and inland single-aged stands interspersed among chaparral (USGS, 1999; Fry et al., 2012; Reilly et al., 2019).

Nearly 63% of knobcone pine's range burned between 1925 and 2015 (and considerably more since then) with the most recent return intervals ranging from 10 to 50 years (Reilly et al., 2017; Reilly et al., 2019). Knobcone pine exhibits exceptionally rapid juvenile growth and reaches reproductive maturity at just 5 to 15 years (Keeley et al., 1999; Marlin, 2021; Agne et al., 2022a.). While the pine shows substantial vigor within its early years, it is relatively short-lived, reaching senescence at 75-100 years (Zedler, 1983; Keeley, et al., 1999; Reilly et al., 2019). Given its short lifespan and rapid seedbank development, knobcone pine is well-adapted to (and reliant upon) moderate frequency severe wildfire.

Chaparral shrubs have long been exposed to severe wildfire at somewhat longer return intervals averaging ~32 to 75 years in northern California (Keeley et al., 2005; Perry et al., 2011; Van de Water and Safford, 2011; Lauvaux et al., 2016). In response to high-severity fire, shrubs reliably regenerate via resprouting and/or obligate seeding (Tepley and Anderson-Teixeira, 2017; Sánchez-Pinillos et al., 2018). Like serotinous conifers, the shrubs do not have a dispersal constraint as they utilize in-situ sources for regeneration. Structurally and compositionally, chaparral species facilitate the high-intensity fire required for regeneration, with high canopy bulk densities, continuity of canopy fuels, and production of volatile, highly flammable chemical compounds in conjunction with hot and dry climates conducive to high levels of fuel consumption (Rothermel and Philpot, 1973; Cowan and Ackerly, 2010). These shade-intolerant shrubs prioritize vertical crown expansion early in the regeneration period to obtain canopy dominance. Asexually recruiting (resprouting) shrubs grow faster than sexually derived stems (obligate seeders) because they possess an intact woody root system as well as stored carbohydrates and can initiate regrowth immediately following crown removal via fire (Keeley and Keeley, 1981; Greene et al., 1999; Ritchie and Hamaan, 2006). Resprouting species restore their starch reserves once mature. Obligate seeders and some resprouters have been known to face extirpation when fire intervals are extremely frequent (<12 years) (Zedler et al., 1983; Keeley et al., 2005); though, in a spatial context, the probability of burning this frequently is quite low in chaparral stands (Keeley and Brennan, 2012; Enright et al., 2015; Park et al., 2018; Paudel et al., 2022).

Across the forested portion of its range, knobcone pine has been found to be expanding at twice the rate of extirpation (FIA, date;Reilly et al., 2019); however, much of the pine’s range is classified as chaparral and shrubland (USGS, 1999; LANDFIRE, 2022), and there is little data to suggest whether expansion also occurs in severely burnt chaparral patches. Knobcone pine and chaparral are both found on lower montane slopes of the southeastern Klamath Mountains (and similar landscapes as one moves south) and have been for centuries (Vogl, 1973; Fry et al., 2012; Golightly et al., 2012). Currently, such landscapes host knobcone pine and chaparral in two types of spatial arrangements: 1. forested mixed-conifer stands with few shrubs in the understory bordered by chaparral patches, and 2. small, disjunct islands or single stems within chaparral patches (Howard et al., 1992; Keeley et al., 1999; Fry et al., 2012; Reilly et al., 2019). Given that both knobcone pine and chaparral regenerate well under moderate-frequency severe fire regimes, there is increased potential for interspecies competition between the two under the projected regime shift in northern California.

Competitive dynamics between sexually recruiting conifers and chaparral shrubs are well-documented, though there is no universal consensus on the outcome due to variation in conifer species' shade tolerance and environmental factors such as elevation, climate, and soil. Studies typically focused on two measures of (primarily non-serotinous) conifer responses to shrub competition: recruitment density and growth. In many cases, conifer recruitment in chaparral patches adjacent to forests was found to be limited by shrub cover (Ne'eman et al., 1999; Castro et al., 2002; Erickson and Harrington, 2006; Collins and Roller, 2013). Other studies found no effect on conifer recruitment density, but conifer recruit growth was negatively correlated with shrub cover (Erickson and Harrington, 2006; Downing et al., 2016; Ursell and Safford, 2022). In turn, chaparral species are invariably shade-intolerant and die within a few decades if overtopped by trees (Maestre et al., 2003).

Most studies simply use shrub cover as the primary measure of interspecies competition, though few explore the mechanisms by which competition can limit conifer recruitment or growth. Most inter-species competition is driven by the disproportionate allocation of finite resources (soil-based nutrients, water, and sunlight). The distinction between resources is important for interspecies competition studies due to the range of conifer shade tolerance which can be negatively impacted by shrub cover. For example, there are cases in which both competing (regenerating) species each receive the resources necessary for establishment and growth, at least initially, despite significant shading: in the Mediterranean Basin, chaparral shrubs were found to facilitate conifer recruitment and growth via positive microclimate effects associated with shading, such as soil moisture retention (Castro et al, 2002; Gomez-Aparicio et al, 2005; Rodríguez-Garcia et al, 2011; Ménard et al, 2019). Dickey et al. (1982) found that the shade-intolerant *Pinus ponderosa* establishment patterns were dictated by microclimate variables separate from several shrub species.

The variety of conifer species' responses to shrub competition in the literature, especially in low-elevation Mediterranean stands, warrants a closer look at knobcone pine response to chaparral competition should one wish to accurately predict species cover on a local basis following severe wildfire. In our study, we focus on shading as the dominant limiting factor associated with interspecies competition due to both study species' shade intolerance, prioritization of rapid vertical growth, and resistance to drought. In order to predict whether subtle expansion of knobcone pine stands can occur within chaparral patches, we visited the 2018 Carr Fire (with an inclusion of the 2008 Motion Fire) and the 2018 Delta Fire where knobcone pine and chaparral shrubs are actively regenerating following severe burns. We asked whether shading from regenerating shrubs significantly limits knobcone pine recruitment, growth, and colonization of chaparral. We hypothesized that while knobcone pine recruitment and growth would be limited with respect to increased shrub competition, nonetheless recruit densities and vertical growth rates would be sufficient for subtle knobcone pine expansion to occur within chaparral patches.

METHODS

Study Site

The bulk of our study took place at Whiskeytown National Recreation Area in northern California where the 2018 Carr Fire burned 94,580 hectares, 34% of them severely and 35% moderately (MTBS, 2022). The 2008 Motion Fire burned 11,879 hectares, 20% at high severity and 35% at moderate severity (MTBS, 2022); the majority of the Motion Fire footprint reburned ten years later in the Carr Fire. The fires overlap along the northeastern shore of Whiskeytown Lake (*Figure 1*).

Prior to the Carr Fire, the landscape on these lower slopes was covered by a mix of chaparral and forest, with the trees primarily knobcone pine, gray pine (*Pinus sabiniana*), or oaks (such as *Quercus chrysolepis, Q. douglasii,* and *Q. kelloggii*). The shrub stands seldom formed closed-canopy communities on these dry lower slopes prior to the Carr Fire. Common shrubs were yerba santa (*Eriodictyon californicum*), toyon (*Heteromeles arbutifolia),* greasewood/chamise (*Adenostoma fasciculatum*), bush poppy (*Dendromecon rigida*), poison oak (*Toxicodendron diversilobum*), and obligate seeders ceanothus (*Ceanothus lemmonnii and C. integerimus*) and whiteleaf manzanita (*Arctostaphylos viscida*). In our study of interspecies competition, we were most concerned with larger, rapidly growing shrubs— primarily those derived asexually following fire; the seed-sponsored stems were often and predictably too short to cast shade over the established knobcone pine recruits, and thus were compositionally less relevant to our study. Knobcone pine stands were primarily single-aged, as the landscape is historically exposed to stand-replacing fire which is required for seed release and establishment (Marlin et al., in press). Regionally, summers are hot and dry with temperatures often reaching 35°C and rainfall rarely totals more than 0.7 cm in July, all from rare thunderstorm activity; in the winter months, temperatures average 12°C while average January precipitation typically totals 30 cm (Skinner et al., 2006).

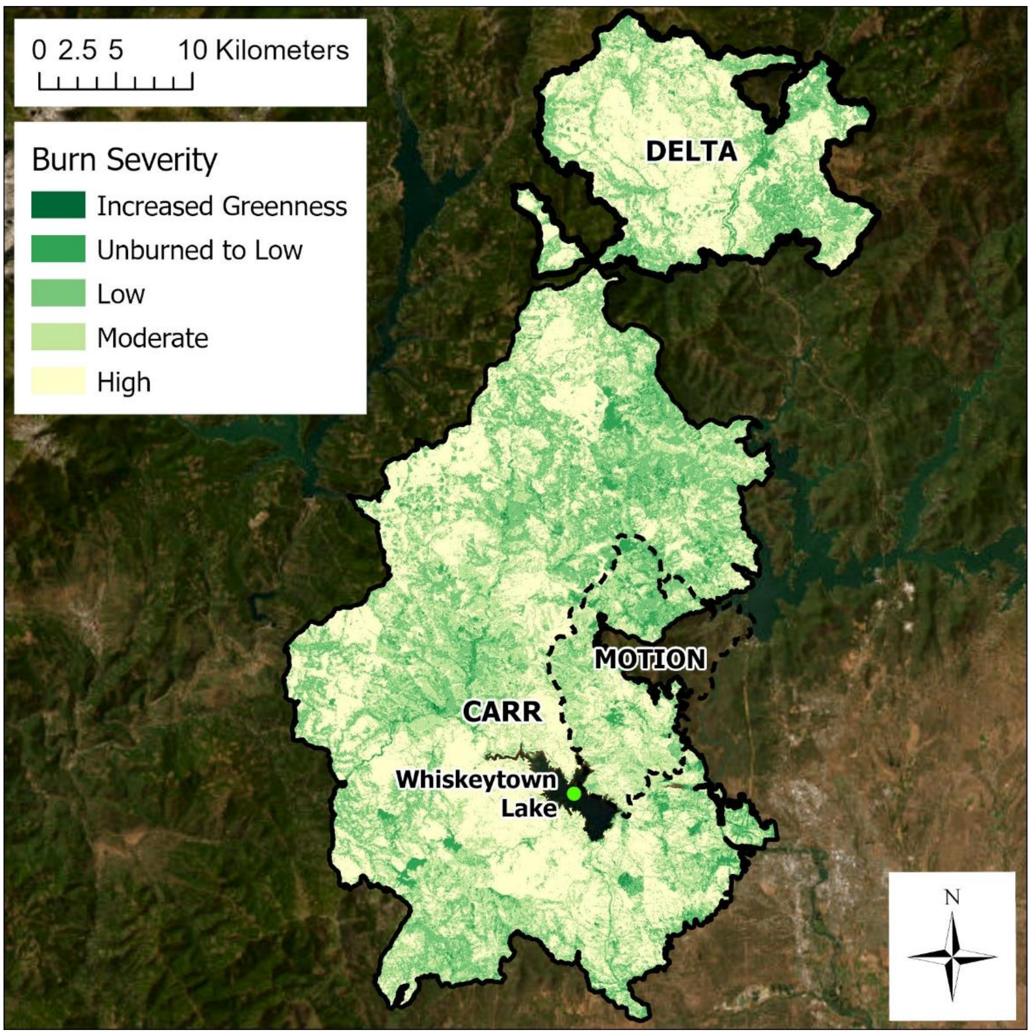

Figure 1. Carr, Motion, and Delta fire perimeters and most recent burn severity (MTBS, 2022). The Motion Fire perimeter is shown as a dashed line.

For our study, we chose severely burned chaparral patches that appeared, from a distance, to have experienced full mortality and contained few, mature knobcone pine stems prior to the fire (*Figure 2*). While these stands were chosen subjectively, we avoided selection bias in that we could not observe the absolute density of knobcone pine regeneration from such a distance.

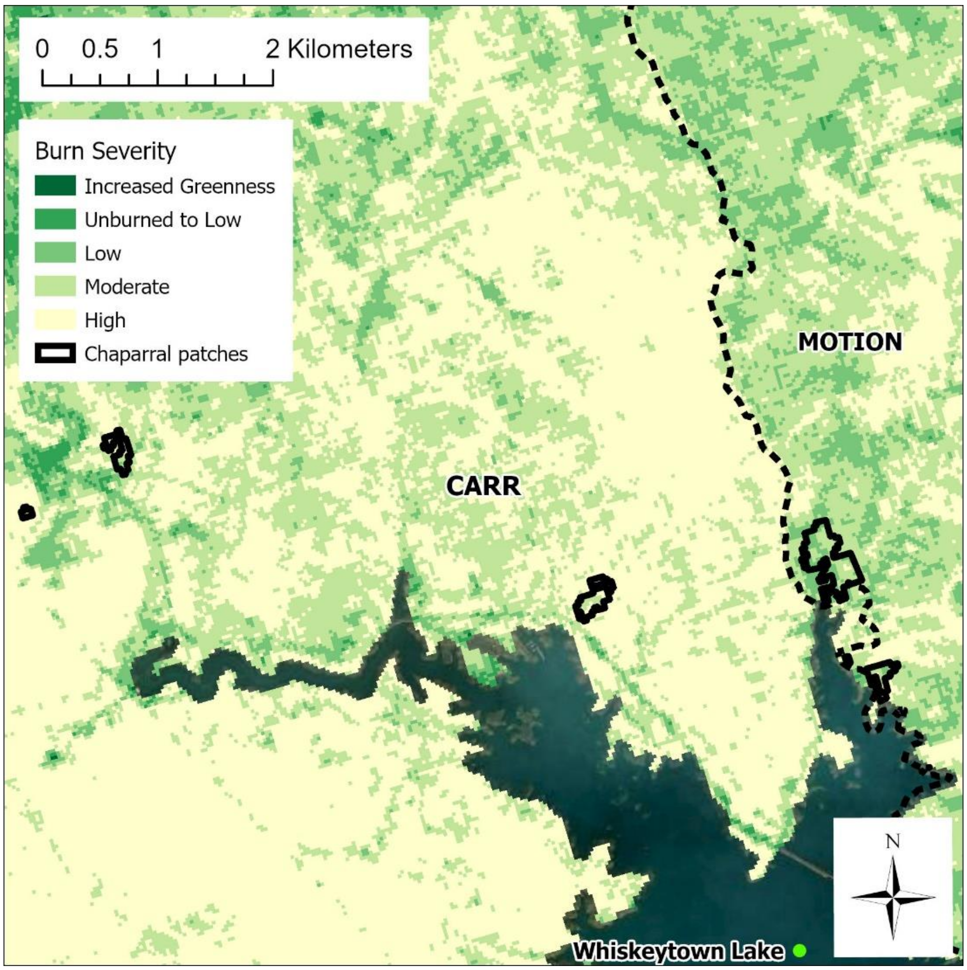

Figure 2: Map of chaparral patches chosen as study sites at the 2018 Carr Fire and estimated burn severity (MTBS, 2022). The southwestern boundary of the 2008 Motion Fire is shown as a dashed line.

For the second portion of our study, we visited the Delta Fire, which burned two months after the Carr Fire (in September 2018) just north of the Carr Fire. Nearly half of the 25,789 hectares were severely burned (MTBS, 2022). The pre-fire landscape there was more heavily dominated by knobcone pine forest compared to our Carr Fire sites, but small chaparral patches were scattered throughout.

Field Sampling

At the Carr Fire, a total of 18 circular plots with radii of 40 m were placed within selected chaparral patches, centered at the stems of dead, mature knobcone trees or in the middle of dead, small knobcone clusters. We recorded the diameter at breast height (DBH) for individual stems and an average DBH for each cluster for all trees within 140 m of the plot center (i.e. well beyond our plot boundaries). GPS coordinates were taken for each individual stem or cluster.

Within each plot, we counted the number of knobcone pine recruits and measured (a) recruit height, and (b) distance to the edge of the nearest shrub crown from the recruit's stem. Nearly all these recruits were 3 years old as the serotinous cones had emptied shortly after disturbance in the autumn of 2018 (Marlin et al., in press). We counted all cones on the ground as well as those still appended to aerial branches within each plot.

Porosity (canopy openness) was used as a measure of light reception by knobcone recruits. We measured this at two levels: inter-shrub (among shrubs at the plot level) and intra-shrub (within a shrub canopy). We measured the former as the percentage of open ground not visibly obstructed by a shrub canopy i.e., 1 minus shrub canopy cover (a percentage). At each plot, shrub canopy cover (%) was visually estimated by each of three researchers for each shrub species thought to be making up 5% or more of the plot's total growing space. The researchers' estimates were then averaged for the plot.

Intra-shrub porosity was defined as the amount of light received underneath each individual shrub crown, measured in lux (lumens per m^2). For shrub species estimated to make up 5% or more of the plot's total ground space, we used a light meter to estimate a lux reading underneath the crowns of three individuals. These readings were averaged for each species in each plot. Three plot "open space" light readings were also taken above the shrub crown for comparison. Maximum crown height (measured from the base of the shrub to the highest point of the shrub crown) and maximum crown width (diameter as measured from above) were recorded for three individuals per species per plot, and then averaged for the plot. Plot-level intra-shrub porosity was calculated as the sum of each species' (and open space) average light reading multiplied by the species' average cover estimate. The result was an estimate of the total amount of light (lux) reaching the soil in each plot as a function of the plot's species composition. Similarly, average plot shrub canopy height was calculated as the sum of each shrub species' average height (m) multiplied by the species' respective cover estimate.

In late July 2022 we resampled 6 of the 18 original Carr Fire plots to measure knobcone recruits' response to shading by shrubs. Within each of the six circular plots, we installed a transect 24 m long and 2 m wide. This time, transects were placed in parts of the plot observed to contain the most open space, in the hope that having a sufficiently large gradient in light receipt to detect an effect on pine recruits due to proximity to a shrub. Using sampling methods from Greene et al. (2007), we held a meter stick at a right angle to either side of the transect centerline at every meter along the transect, referred to hereafter as *uniform sample points*. We then measured the distance from the uniform sample point to the crown edge of the nearest shrub. If the measurement began *within* the shrub, i.e. if the shrub was located on the transect line, then the measurement was written as a *negative value*. Additionally, for every knobcone recruit within 1 perpendicular m of the transect centerline, we measured its distance to the edge of the nearest shrub crown. If the recruit was within a shrub's crown, the distance was again recorded as a negative distance from the crown edge. Altogether, we sampled 300 uniform points and 170 recruits at the Carr Fire. For additional data points in a similar post-fire landscape, we used these same field procedures at the 2018 Delta Fire, approximately 40 km northeast of our Carr Fire study site, in five additional plots totaling 250 uniform points and 202 recruits.

Under the assumption that growth rates can be indicators of shade tolerance or intolerance, as well as useful predictors of recruit height relative to shrub canopy height, we visited several unburned knobcone pine stands within overlapping areas of the 2008 Motion Fire and the 2018 Carr Fire in the Fall of 2022. In two inclusions on nearby slopes, we established one 20 × 20 m plot and cut every knobcone pine recruit > 1.8 m tall, collected a disk every 0.5 m along the stem, and then recorded the ages after sanding. We also measured the height of every shrub within the plot, additionally noting if the shrub was dead, showed significant live crown loss, or appeared healthy. Altogether, we sectioned 21 trees > 3 m tall, and five of them were dead.

Finally, in order to understand mortality rates in local recruit cohorts, we re-censused nearby permanent plots containing knobcone pine recruits established by Marlin (2021). Recruits within each plot were aged using bud scale scars, and recruit counts for each cohort were used to estimate age-specific survivorship relative to previous years' recruit densities.

Data Analysis

The three main response variables of interest in the Carr Fire plot portion of our study were plot recruitment success (knobcone pine recruits per cone), plot recruit density (knobcone pine recruits/m^2) and plot average recruit height (m). Independent variables were either shrub competition predictors or pre-fire pine stand predictors. Two of our eighteen original plots were excluded from analysis as they were extreme outliers in terms of two response variable values (recruit density and recruits per cone).

Using the R programming language (R Core Team, 2022), we developed best-fit univariate or multivariate linear models for each of the response variables versus shrub and pre-fire knobcone pine stand predictors. Prior to developing best-fit models, we used a variance inflation factor (VIF) function from the *car* package (Fox and Weisberg, 2019) to detect multicollinearity between predictors. Predictors which had VIF values > 6 were considered as showing a high degree of multicollinearity, and colinear parameters were removed from analysis until each remaining parameter had a VIF value < 6. Shrub competition predictors included in the modeling process were plot intra-shrub porosity (lux), average distance to the nearest shrub crown (cm), shrub cover (%) and shrub volume (cm^3). Pre-fire stand predictors included the total number of knobcone pine cones within the plot, pre-fire knobcone pine stand basal area (cm^2) and pre-fire knobcone pine stand density (stems/ha).

Models were generated using exhaustive search methods via a regression subsets function from the *leaps* package (Lumley, 2020). Outputs were summarized and the best possible number of variables was chosen using the maximum adjusted R-squared value, then best possible parameters were identified and linear models were generated. Best-fit linear models were summarized to ensure that the model met statistical assumptions necessary to be deemed significant ($p < 0.05$) and predictors were relevant to the response variable.

A one-way analysis-of-variance (ANOVA) test was performed to determine interspecies variation in intra-shrub porosity using individual light readings from all 18 plots. The Tukey HSD (honestly significant difference) test was performed in R (R Core Team, 2022) to identify any significant variation between two species' (or one species versus open space) mean lux readings. For the transect methods at the Carr Fire and Delta Fire, difference of proportions tests were used to compare the frequency distributions of distance to the nearest shrub crown from uniform sample points and recruits. This method allows us to test whether a uniform sample point and a recruit are equally likely to be found within a given distance of a shrub, or if spatial distributions of recruits are statistically non-random.

RESULTS

Carr Fire Plots

Within the 18 Carr Fire plots, the mean density of recruits was 377 stems/ha while the mean density of burnt trees was 62 stems/ha. That is, on average, the knobcone pine stands in these plots from before the fire were more than replacing themselves, with about six recruits per burned adult by the end of the third post-fire summer. Only one plot had fewer recruits than burnt trees. There was no significant relationship between plot recruit density and pre-fire knobcone pine density (p = 0.572; R^2 = 0.022) or pre-fire basal area (p = 0.641; R^2 = 0.016). Similarly, basal area did not predict recruitment success (p = 0.9285; R^2 < 0.001), nor did pre-fire knobcone pine density (p = 0.247; R^2 = 0.094). Pre-fire cone density within the plots was not a significant determinant of recruit density (p = 0.555; R^2 = 0.024) or recruitment success (p = 0.128; R^2 = 0.147). The same was true of plot recruit density (p = 0.346; R^2 = 0.059) and recruitment success (p = 0.136; R^2 = 0.142) when all cones within 140 m of the plot center were included in recruitment success calculations.

While post-fire knobcone pine recruit densities were significantly greater than pre-fire stand densities in nearly every case, the minimum density required to *fully convert* a chaparral patch to forest was not met. For reference, Marlin (2021) reported that the average pre-fire knobcone pine density in mature forested stands at Whiskeytown was ~700 trees per hectare on low-productivity slopes such as the ones we studied. Three of our plots surpassed 375 stems per hectare, just over half of this typical forest density, while an additional five reached about 25% in the third post-fire year. Most plots achieved about one eighth of the Whiskeytown stocking standard (88 stems/ha).

In all but two of the 18 plots, the resprouting shrubs had an average canopy height greater than the average recruit height. Average recruit height showed a general decline as the height of the shrub canopy increased in many cases, but across all plots this relationship was weak and not quite significant (p = 0.069; R^2 = 0.204). As of the third summer following the Carr Fire, the shrubs averaged 1.50 m in height while the young trees averaged 0.56 m. Additionally, the shrubs had by year 3 grown laterally as much as they had vertically; the mean ratio of height to shrub crown diameter was 0.98.

Recruitment success (defined as recruits per cone) was nearly negatively correlated with shrub cover (*Figure 3*, p = 0.056; R^2 = 0.222), while mean recruit height had no apparent correlation with shrub cover (p = 0.983; $R^2 < 0.01$). Overall recruit density had a weakly negative and significant relationship with shrub cover (p = 0.040; R^2 = 0.27) (*Table 1*). Neither recruit height (p = 0.131; R^2 = 0.145) nor recruitment success (p = 0.575; R^2 = 0.021) showed a significant relationship with the distance to the nearest shrub crown across all plots.

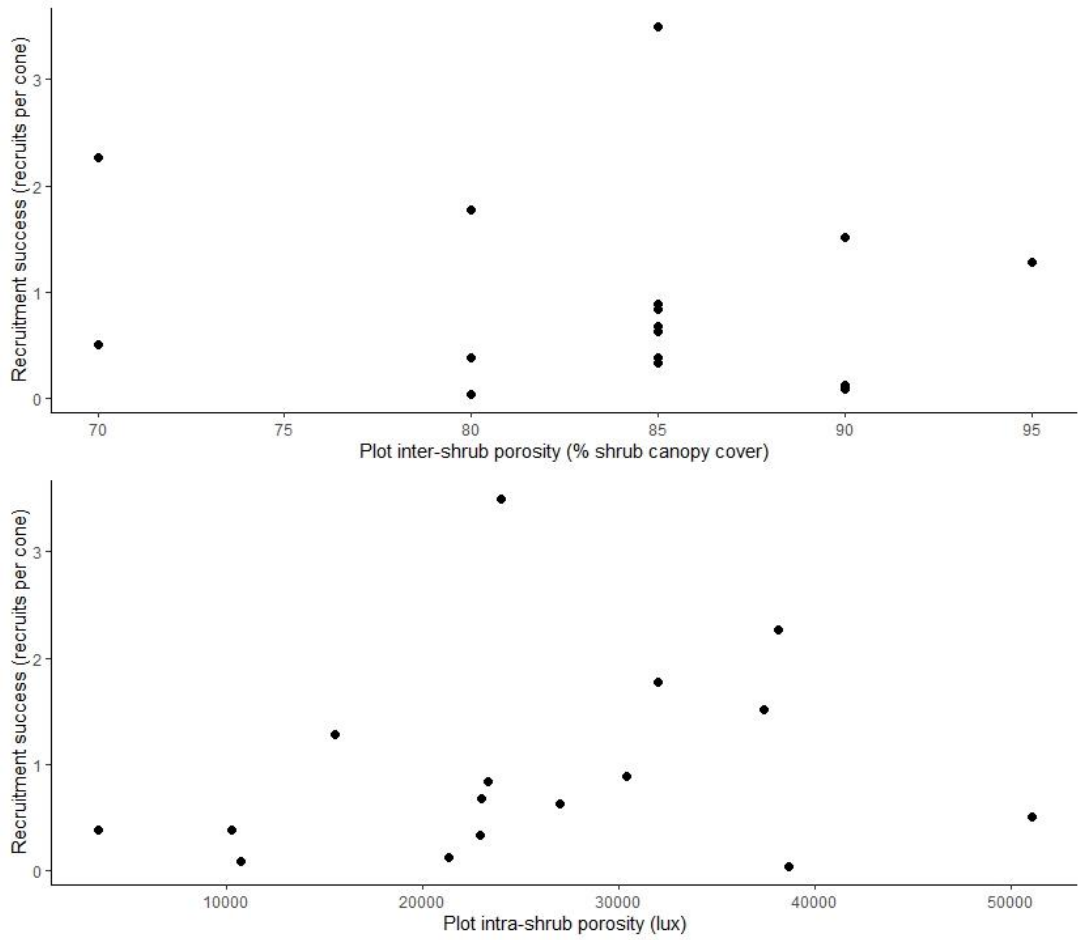

Figure 3. Recruitment success (recruits per cone) versus plot inter-shrub porosity (% shrub canopy cover) and plot intra-shrub porosity (lux, lumens/m^2). Two extreme outliers were omitted. Recruitment success was calculated using only cones found within the plots.

Table 1. Generalized linear model and predictor coefficients for recruit density as a function of shrub cover (Recruit density (recruits/m^2) ~ Shrub cover (%)). The predictive model meets the assumptions necessary to be considered significant ($p < 0.05$, all covariate variance inflation factors < 6).

Predictor	**Coefficient**	**Standard error**	***p***
Intercept	0.410	0.166	0.027
Shrub cover	-0.005	0.002	0.040
Summary	**R^2 = 0.268**	**Adjusted R^2 = 0.216**	**p = 0.040**

Intra-shrub crown porosity did not significantly vary between any two shrub species ($p > 0.05$); there was substantial overlap between most species (**Error! Reference source not found.**); thus, we did not consider dominant species in regression analyses. All shrub species lux values were significantly lower than the open space values ($p<0.001$). The resprouting shrubs were not providing dense shade; the lowest light values recorded (*Quercus* spp., **Error! Reference source not found.**) received more sunlight than would the floor of a dense forest (cf. Chazdon and Pearcy, 1991; Messier et al, 1998). Oak species and toyon had the densest canopies, while yerba santa displayed a wide range of intra-shrub porosity among all plots. The calculated plot-level intra-shrub porosity had no significant relationship with recruitment success (*Figure 3*, $p = 0.293$; $R^2 = 0.050$) or recruit height ($p = 0.293$; $R^2 = 0.073$) at the plot level.

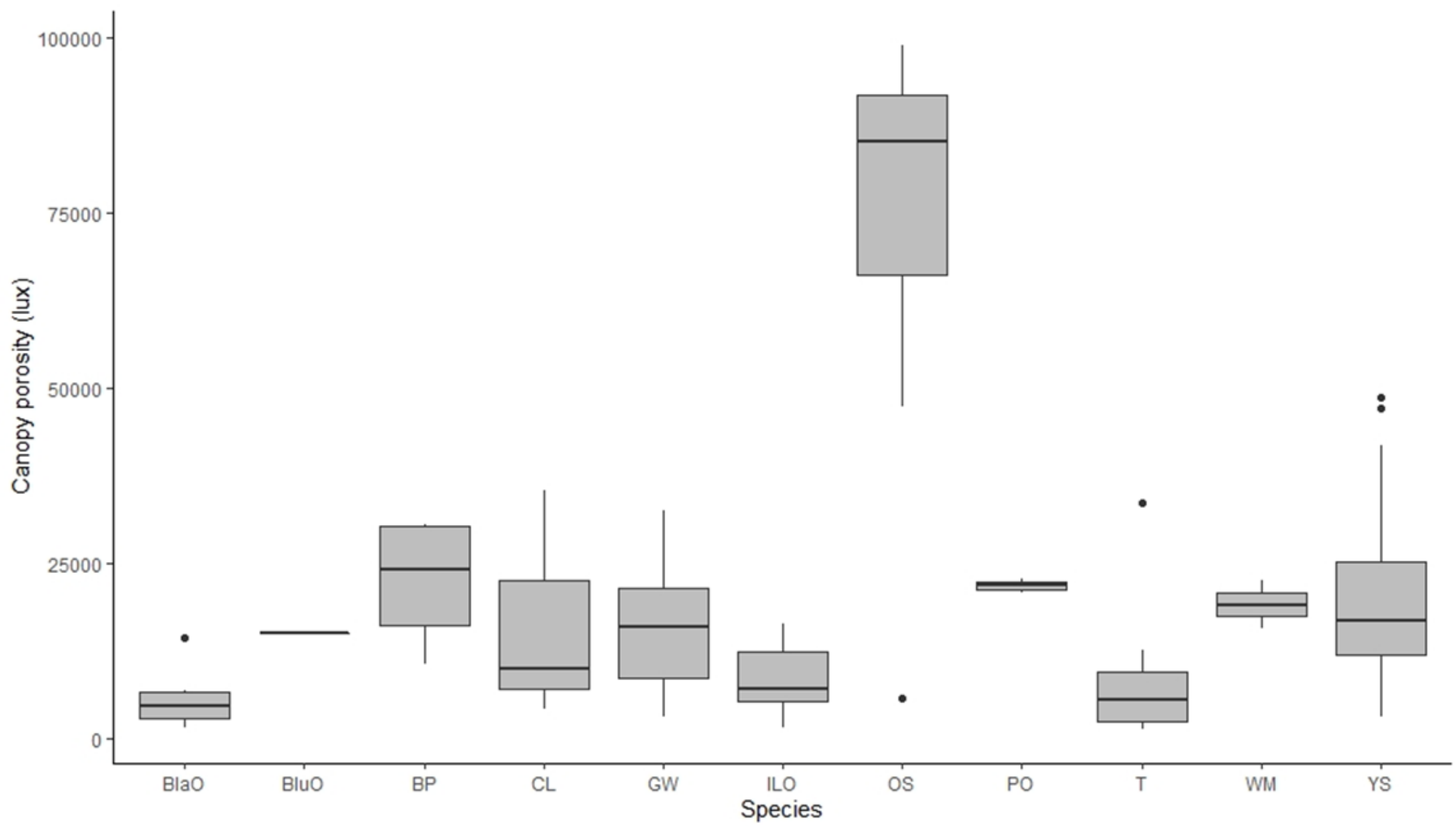

Figure 4. Intra-shrub canopy porosity (lux; lumens/m^2) by species compared to the open space (OS) light reading. BlaO = black oak, Q. kelloggii; BluO = blue oak, Q. douglasii; BP = bush poppy, D. rigida; CL = Ceanothus, C. lemmonnii and C. integerimus.; GW = greasewood/chamise, A. fasciculatum; ILO = interior live oak, Q. chrysolepis; PO = poison oak, T, diversilobum; T = toyon, H. arbutifolia; WM = whiteleaf manzanita, A. viscida; YS = yerba santa, E. californicum.

In nearly every case, relationships between response variables and individual factors related to shrub shading (inter-shrub or intra-shrub porosity) and pre-fire knobcone pine stand conditions were neither strong enough nor significant to predict any effects on knobcone recruitment or growth. Best-fit analysis generated only one significant multivariate model, which gives average recruit height (m) as a function of plot intra-shrub porosity (lux), average distance to the nearest shrub (m), and average shrub volume (p = 0.049; R^2 = 0.551); per the function, recruit height was positively correlated with plot intra-shrub porosity and average distance to the nearest shrub, and negatively with average shrub volume, though none of these relationships alone were statistically significant (*Table 2*).

*Table 2. Generalized linear model and outputs for recruit height as a function of plot intra-shrub porosity, average distance to the nearest shrub crown, and shrub volume (Average recruit height (m) ~ Plot intra-shrub porosity*Average distance to the nearest shrub crown (m)+ Average shrub volume (m^3)). The predictive model meets the assumptions necessary to be considered significant ($p < 0.05$, all covariate variance inflation factors < 6).*

Predictor	**Coefficient**	**Standard error**	***p***
Intercept	3.580×10^{-1}	2.080×10^{1}	0.113
Plot intra-shrub porosity	4.545×10^{-1}	7.535×10^{-4}	0.559
Average distance to nearest shrub crown	1.579	7.696×10^{-1}	0.065
Shrub volume	-6.746×10^{-6}	3.515×10^{-6}	0.081
Plot intra-shrub porosity*Average distance to nearest shrub crown	-3.907×10^{-5}	2.863×10^{-5}	0.200
Summary	**R^2 = 0.551**	**Adjusted R^2 = 0.388**	***p* = 0.049**

Carr Fire and Delta Fire Transects

The re-survey of 6 of the original 18 Carr Fire plots (first surveyed in 2021) one year later (recruits now four years old) and 5 new plots (2022) at the Delta Fire showed an evident lack of 4-year-old knobcone pine recruits underneath shrub crowns, compared to a substantial proportion of uniform sample points found beneath a shrub crown (*Figure 5*). The average distance from a knobcone pine recruit to the nearest shrub crown (17.3 cm at Carr, 29.29 cm at Delta) was clearly greater than the distance from uniform sample points to the nearest shrub crown at both fires (8.13 cm at Carr, 4.43 cm at Delta). Difference of proportions tests for distances of 4-year-old knobcone recruits < -5 cm vs >-5 cm were $p < 0.00001$ at both fires. Where knobcone pine recruits were found within shrub crowns, it was clear that the bulk of the recruits were near the crown edge; over one half, nearly two thirds of the recruits that established *beneath shrubs* were found within 10 cm of the edge of the shrub crown (0 to -10 cm) (*Figure 5*). At the other extreme (open spaces; >65 cm beyond a shrub crown edge), there was little difference in recruitment at either fire using a difference of proportions test ($p = 0.47$ at Carr and 0.16 at Delta). Delta Fire recruit densities averaged 0.84 recruits/m^2 compared to 0.59 recruits/m^2 at the Carr Fire.

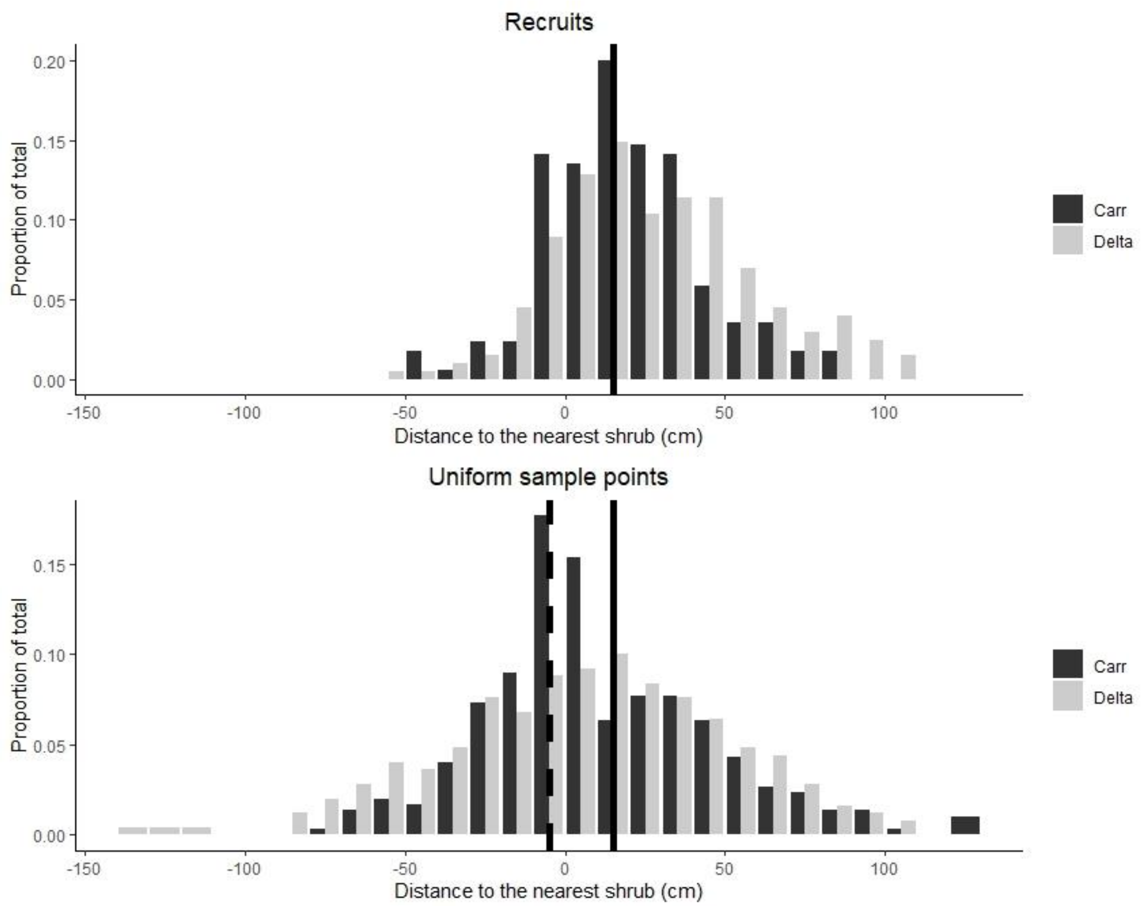

Figure 5. The proportion of the total 4-year-old Carr Fire or total 4-year-old Delta Fire recruits and uniform sample points at distances from the nearest shrub crown. Negative distances indicate that the pine recruit or the uniform sample point lies within a shrub crown, -x cm from the edge of the crown. The distribution centerlines are shown for the Carr Fire (dashed) and Delta Fire (solid).

2008 Motion Fire Growth Rates

At the two stands from the 2008 Motion Fire that remained unburnt by the Carr Fire, there were 21 recruits for which we sampled ages. Five of these stems were dead. All 16 living stems recruited the year after the fire. These 14-year-old stems averaged 4.6 m in height while the shrubs averaged 2.2 m. That is, the shrubs no longer formed the upper canopy layer. Following the Motion Fire, the average tree would have been taller than 1.8 m (mean shrub height at the Carr Fire in 2021) at year 6 and taller than 2.2 m (mean shrub height at the Motion Fire in 2022) at year 7 (*Figure 6*). Indeed, 9 of the 16 measured living stems surpassed shrub height by the seventh post-fire year, and 7 outgrew the shrubs prior to year 6; the remaining 7 live stems had less total growth, but growth rates remained nearly linear and therefore are trending towards surpassing the shrub canopy with one to two more years of vertical growth (*Figure 6*).

Dividing all censused Carr Fire recruits into quartiles based on height, we project (assuming near-linear growth rates, like Motion Fire recruits) that the upper quartile will surpass the shrub canopy by year 7, while the third and second quartiles will breach by years 10 and 12, respectively (*Figure 6*). The lowest quartile of Carr Fire recruits we censused is not projected to surpass the shrub canopy within 14 years. The youngest of the five dead stems at the Motion Fire stand was 7 years old, giving a mean annual survivorship rate (all 21 stems; 2015-2022, inclusive) of 0.97 for the subsequent 8 years following the fire. Shrubs found underneath these taller recruits, specifically beneath live crowns of knobcone, were negatively impacted by shading. Both dead shrubs were found directly below live crowns while 6 of the 7 shrubs showing dramatic losses in live crown were directly beneath live tree crowns. Our resampling of the Carr Fire permanent plots from Marlin (2021) showed us that only 2.2% of recruits had died during the preceding year; annual survivorship (2021-2022) was 0.98.

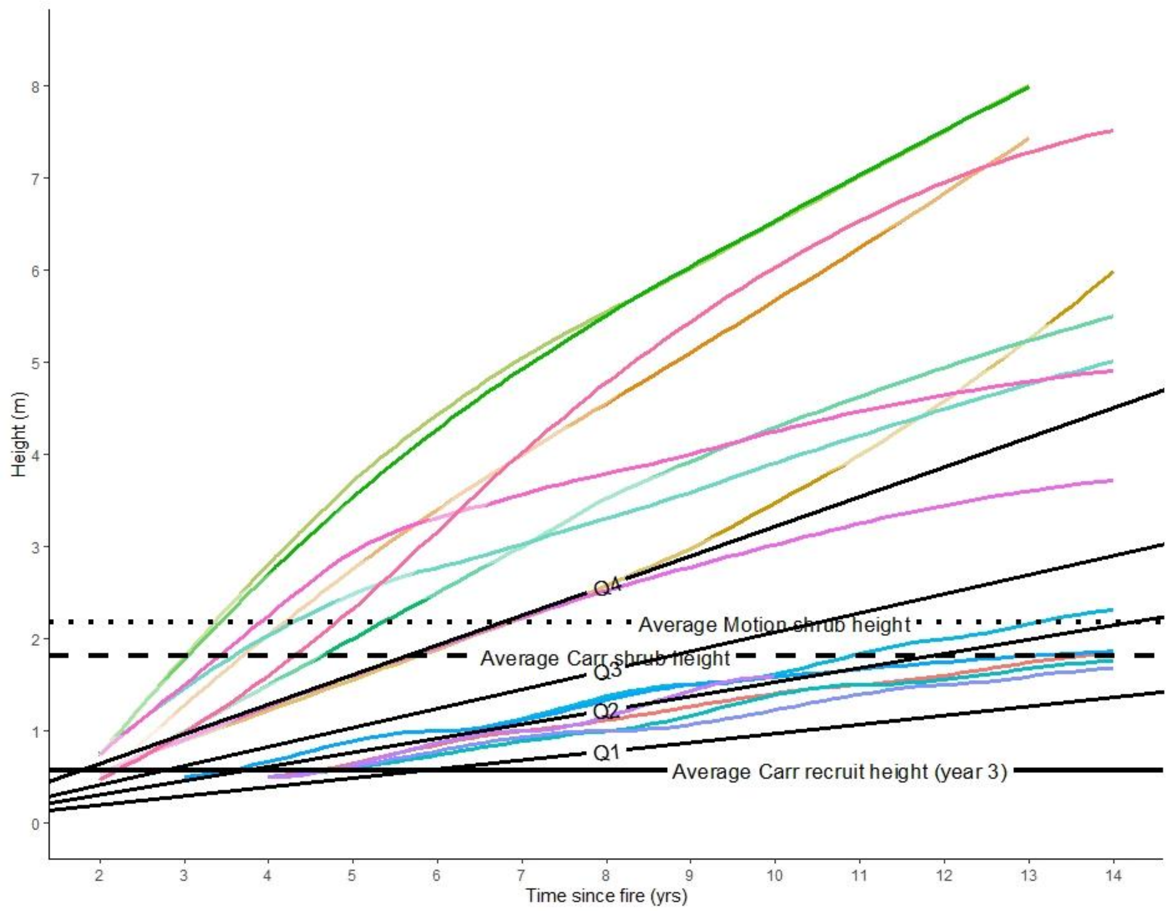

Figure 6. Surviving knobcone pine growth trends through the first 14 growing seasons following the 2008 Motion fire. Mean shrub heights from the Motion and Carr fires, in addition to mean recruit height at the Carr fire, are shown as horizontal lines for reference. The lines labeled Q1 – Q4 represent projected growth rates (assuming near-linear growth over a 14-year period) for each height quartile of censused third-year Carr Fire Recruits found in our 18 survey plots.

DISCUSSION

We visited the 2018 Carr and Delta Fires and an unburnt inclusion of the 2008 Motion Fire to measure the effects of shading via shrub competition on knobcone pine recruitment and growth. By focusing on shading and species growth characteristics, our study provides insights that can allow us to predict whether cover type change can occur via subtle range expansion at the stand scale. First, the Carr Fire and Delta Fire portions of our study allowed us to identify which parameters of shrub competition have meaningful impacts on knobcone pine recruitment and growth. We hypothesized that knobcone pine recruitment would be limited by shrub competition to some degree, though we would observe recruitment beyond the initial stand densities. Our findings support this: in severely burnt chaparral patches containing few burnt knobcone pine seed sources, we observed increased recruit densities in all but two cases, averaging a 600% increase at the Carr Fire and an 850% increase at the Delta Fire by the third and fourth post-fire years, respectively. Within the Carr Fire, we found lower absolute recruit densities in chaparral patches compared to those found in previously forested areas with proportionally higher pre-fire knobcone pine densities (Marlin et al., in press).

On a fine scale of comparison, i.e. between our chaparral-dominated plots, we focused on specific parameters of shading by shrubs, and found very limited effects on knobcone pine recruitment. We had initially controlled for the suspected influence of seedbank size (number of cones) on absolute knobcone pine recruitment densities by using recruitment success (recruits per cone) as a response variable. Recruitment success did not significantly change in any discernable direction with respect to either inter-shrub porosity (space between shrubs) or intra-shrub porosity (space within shrubs). We also included the influence of seed sources up to 100 m outside the plot boundary (within the known seed dispersal constraint for knobcone pine), which again did not predictably vary with any measure of porosity. The lack of strong a strong relationship between recruitment success and any measure of inter-shrub porosity is due perhaps simply to the fact that shrub cover in the plots did not vary sufficiently to separate the signal from the noise: 5-30% was the range of observed stand porosities using the conventional method for estimating species shrub cover.

Interestingly, however, absolute recruit density at the plot level significantly varied in response to shrub cover and no other measure of shrub competition or pre-fire stand density, age, or seed availability, indicating that the presence of shrubs alone generally limits the availability of adequate growing space for recruits. Agne et al. (2022a) found no significant relationship between early post-fire knobcone pine recruit densities and shrub cover ranging from 10% to 70%, though they observed recruit densities in primarily densely forested pre-fire stands and *did* find significant influences of seedbank size. Their findings, in conjunction with ours and those of Marlin et al. (in press) hint at an absolute density threshold for knobcone pine recruits which is seemingly greater in forested stands than in chaparral. The transects we placed at six of the original Carr Fire plots and at five additional plots at the Delta Fire support the expected decline in recruit density relative to shrub cover. The distribution of uniform sample points relative to nearby shrub crowns (*Figure 5*) implies that knobcone pine recruits found along the same transects are not randomly distributed; that is, the recruits were found disproportionately outside the crowns of shrubs. The relationship implies the opposite of the shrub-seedling facilitation effect observed in several Mediterranean pine species (cf. Castro et al, 2002; Gomez-Aparicio et al, 2005; Rodríguez-Garcia et al, 2011; Ménard et al, 2019).

It is likely that differential mortality had occurred, then, directly beneath the shrub crowns in the early post-fire years prior to our study. We can estimate how many recruits were lost during early competition with shrubs: about half of the area examined in the six Carr Fire and five Delta Fire plots was occupied by shrub crowns between the second and third post-fire year; if the density of seeds under these crowns was the same as in the inter-shrub spaces, then by subtraction we calculate that approximately 25% of the potential germinants were lost to competition with shrubs in the first summer. We point out that this calculation assumes that the intensity of granivory was independent of distance to burnt shrub, but it may well be that rodents forage more frequently in the immediate area of a skeletal burnt shrub crown than away from it as the dead branches would provide more shelter from predators.

The great majority of knobcone pine recruit deaths occurred between seed abscission and the third-year census. Wagner (2000) and Wagner and Robinson (2006) explored trends in conifer recruit mortality, suggesting that there is a “critical period” during which conifers are most vulnerable to shrub cover, usually within the first two years if they are shade-intolerant species (e.g. knobcone pine) and the first four if they are shade-tolerant. *Pinus halepensis,* a comparable European pine occupying a similar landscape and exhibiting the same growth characteristics, shows that the bulk of density-dependent mortality occurs within the first 8 years of growth, after which survivorship nears 1.0 immediately (Schiller, 1978). Keeley et al. (1999) noted major declines in knobcone pine recruit density by the third post-fire year, and attributed seedling mortality to abiotic factors as much as seedling density. Concurrently, we observed the majority of knobcone pine recruit mortality within the first two years at the permanent plots of Marlin et al. (in press) with little mortality in the third year, and survivorship from year 4 onward is projected to remain near 1.0, suggesting that at present, our plots contain tolerable recruit densities. Here, we attribute initial mortality to shrub competition rather than density-dependent or abiotic factors, consistent with Beatty and Taylor (2001), Nagel and Taylor, Lauvaux et al. (2016), and Guiterman et al. (2018).

The recruits that survived the first few post-fire years at the Carr and Delta fires were then those found beyond shrub crowns, and the rapid lateral expansion of shrubs accounts for those found within the outer 5 cm of the shrub crown in the fourth post-fire year (*Figure 5*) (Ritchie and Hamann, 2006). We had hypothesized that shrub competition would limit the pine recruits' growth, but alone would not induce mortality in the long term. Recruit height was not significantly impacted by distance to the nearest shrub alone, though our multivariate linear model tells us that if the shrub in question is large and dense (meaning increased volume and decreased intra-shrub porosity), we will predictably see growth limitations for the pine recruit as one gets closer to the crown (*Table 2*). As the shrub crown expands, and vertical growth slows, we can look to our findings at the 2008 Motion Fire to understand how our older recruits (rather than first-year germinants) will fare beneath the shrub canopy.

We found that the mean recruit height at the Motion Fire exceeded the mean shrub height (as of the 14^{th} growing season) at approximately 6.5 years after fire. This is an overestimate of the required time as the local mean shrub height would have been somewhat shorter at 6.5 years. Assuming linear growth rates, similar to those observed at the Motion Fire, we can project that 50% of our censused Carr Fire recruits will breach the shrub canopy by year 10, and half of these by year 7 (*Figure 6*). The Motion Fire recruits found beneath the shrub canopy at year 14 still exhibit linear (and slower) growth rates with no recent signs of decline, suggesting limited mortality even for the slowest growing Carr Fire recruits within the next few years. Once recruits breach the shrub canopy, the main source of mortality for the knobcone stems is shading by taller conspecifics rather than shrubs. That is, the stand, if sufficiently dense, enters the self-thinning stage at about 7 years (the earliest death of the 5 dead stems—all above the shrub canopy—we sampled in the Motion plots). Begley (2010) examined knobcone pine height growth rates between the 7th and 10th post-fire years and found little shrub- or thinning induced mortality; rather, almost all mortality was either caused by rodent kill over the study period or by surface fire which occurred at year 10. Similarly, by year 7, they found that the upper two quartiles of knobcone pine recruits had breached the average shrub canopy height by year 7, and those in the understory did not show any signs of slowing their lesser growth rates over the study period (Begley, 2010).

While we found that chaparral shrubs indeed limit knobcone pine recruitment and growth to a degree, the latter is expected to persist if shrub competition is the only limiting factor. The scattered distribution of knobcone pine within chaparral is characteristic of our sites at Whiskeytown since at least the mid-to-late 1800s (Golightly et al., 2012), suggesting that other factors, mainly short or extended fire-return intervals, are key to maintaining vegetation composition in the long term. The regimes moderating knobcone pine and chaparral populations, by nature, have potential for overlap (Van de Water and Safford, 2011; Agne, 2022b), and increasingly so under the expected increase in frequency found across western North America (Cattau et al., 2020; Parks and Abatzoglou, 2020; Hamann et al., 2021). The known expansion of knobcone pine's range in forested areas under increasing severe fire frequency (Donato et al., 2009; Reilly et al., 2019) is also expected where the pine is found interspersed with chaparral, though at a slower rate, per our findings. At our study site, the probability of a reburn prior to the stand reaching reproductive maturity is 0.097 (Marlin et al., in press) and increases with time. If subsequent fires occur between years of knobcone pine immaturity (> 8 years) and senescence (< 75 years), we would then expect to see slow conversion of chaparral to forest, though further research is needed to determine the spatial extent of knobcone pine expansion within chaparral patches in order to address concerns of landscape-wide cover type conversion. Our study has implications for predicting cover type at the local scale where there is potential for subtle knobcone pine range expansion. Findings are limited to either serotinous or low-elevation shade-intolerant pines, though our methods could be applied broadly to detect whether conifer stand expansion occurs along forest boundaries and within shrublands at upper elevations.

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