Forest Ecology and Management 505 (2022) 119768

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Prescribed fire reduces insect infestation in Karuk and Yurok acorn resource systems

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ARTICLE INFO

Keywords:
Traditional Ecological Knowledge
Prescribed Fire
Curculio
Notholithocarpus
Cydia

ABSTRACT

Prescribed fire is used extensively as a management tool in fire-adapted landscapes of the American West to maintain ecosystem structure and function while reducing wildfire risk. Seasonally specific prescribed fire is used by many Indigenous groups to increase the quality and quantity of cultural resources and promote desired patterns of habitat diversity. Traditionally, the Karuk and Yurok Tribes of California applied fire in tanoak (*Notholithocarpus densiflorus,* Fagaceae) acorn gathering areas during the fall to reduce infestation in acorns by larvae of the filbertworm (*Cydia latiferreana*, Tortricidae) and filbert weevil (*Curculio occidentalis*, Curculionidae). It has become increasingly difficult to select culturally appropriate times in which to apply fire as a resource management tool due to changing environmental conditions and associated political considerations. To assess the effect of non-traditional management on tribal acorn resource systems, we investigated the effects of early summer burning on rates of larval infestation in tanoak acorns. We also studied how competing frugivores affected the availability of edible acorns to human consumers. We found that non-traditional early summer prescribed fire significantly reduced rates of larval infestation during the burn year (36.7%) but no difference between treatments was detected one year-post fire. Selective vertebrate frugivory significantly reduced the density of edible acorns by 39%. Our results highlight the importance of seasonally-specific prescribed fire in managing Karuk and Yurok resource systems and supporting tribal eco-cultural revitalization.

1. Introduction

Fire is an important agent of spatial and temporal disturbance in terrestrial ecosystems of the Pacific Northwest which Native American communities have harnessed to maintain resources essential to livelihood and cultural continuity (Lewis, 1973; Martin and Sapsis, 1992; Kimmerer and Lake, 2001; Storm and Shebitz, 2006; Miller and Davidson-Hunt, 2010; Taylor et al., 2016; Marks-Block et al., 2019). The use of fire in the management of pre-colonial forests by Native Peoples provided sustenance to human and animal populations, shaped local and regional patterns of diversity, and created spatially and temporally heterogeneous terrestrial communities (Lewis, 1973; Martin and Sapsis, 1992; Stephens et al., 2007; Smith, 2011; Lightfoot et al., 2013; Lightfoot and Cuthrell, 2015; Taylor et al., 2016). Acorns produced by trees of the genera *Quercus* and *Notholithocarpus* are used ubiquitously as a food source by Native Californian peoples (Schenck and Gifford, 1952; Hendryx and Davis, 1991; Anderson, 2005, 2007). Acorns are a reliable resource that affords abundant proteins, carbohydrates, and fats (Wolf, 1945; Gould, 1975; Basgall, 1987; Bettinger and Malhi, 1997; Meyers et al., 2007). Within the wild resource systems developed in Indigenous California, the application of prescribed fire was the most important tool for maintaining quantities of edible acorns sufficient to support the nutrition of human and animal populations as well as important ceremonial activities (Driver, 1952; Lewis, 1973; Smith, 2011; Hankins, 2013; Hankins, 2014; Norgaard, 2014a; Rossier and Lake, 2014). The traditional ecological goal of tanoak system-specific prescribed fire is to reduce the incidence of invertebrate larval infestation in acorns increasing in non-infested acorns for 1) human consumption and 2) culturally valuable wildlife consumption (F. Lake, B. Tripp, personal observation, 2010).

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https://doi.org/10.1016/j.foreco.2021.119768
Received 3 April 2021; Received in revised form 3 October 2021; Accepted 5 October 2021

Indigenous burning practices are very precise; their applications vary by season, elevation, habitat type, and desired resource outcome (F. Lake, B. Tripp, personal observation, 2010). Throughout California, understory vegetation and litter in oak-dominated acorn gathering areas is burned in the late summer to late fall to facilitate resource collection and reduce populations of frugivorous insects that infest acorns (Lewis, 1973; Anderson, 2005, 2007). Dendrochronology and fire scar studies conducted in mixed conifer forests in the Klamath Bioregion report that 93% of pre-colonial fires (before 1750) occurred later in the year as secondary growth was slowing or at the annual ring boundary (Taylor and Skinner, 1998, 2003; Fry and Stephens, 2006). These data also document a large increase in fire return interval between pre-colonial and suppression periods (Skinner et al., 2009; Taylor et al., 2016). In modern day forested ecosystems within California, native acorn crop management activities have become increasingly difficult to implement due to high-risk conditions, including higher fuel loading and increasingly dense vegetation of fire-suppressed forests, and limited fire personnel and equipment available to support cultural burning (McCreary, 2004; Anderson, 2007; Hankins, 2014; Long and Lake, 2018; Miller et al., 2020).

In this paper, we investigate the effects of non-traditional early summer fire prescriptions on cultural resource quality, abundance, and consumption pressure from vertebrate and invertebrate consumers. This research contributes a nuanced perspective to modern prescribed fire management practices regarding the importance of considering the seasonality of fire application (Knapp et al., 2009; Ryan et al., 2013). We show that a non-traditional pattern of early summer prescribed burning can reduce infestation of tanoak *(Notholithocarpus densiflorus,* Fagaceae) acorns by larval invertebrate consumers during the fire year but this suppression of insect infestation did not persist into the post-fire year. We also experimentally demonstrate that frugivorous vertebrates significantly reduce the density of harvestable acorns. While our results support the use of seasonally non-traditional fire to tend tribal cultural acorn resources, its effects on co-occurring, tanoak-associated plant species of cultural value are unknown. When investigating traditional ecological management practices, it is important to consider effects on the targeted suite of species rather than a single resource system (Kimmerer and Lake, 2001; Hankins, 2009, 2013, 2014; Marks-Block et al., 2019; Wynecoop et al., 2019; Long et al., 2020; Marks-Block et al., 2021).

2. Study system

2.1. Tanoak ecology and Indigenous use

Tanoaks are endemic to the California Floristic Province (including southern Oregon) and are the sole species within the genus *Notholithocarpus* (Manos et al., 2008; Burge et al., 2016). Within the Klamath Bioregion they are found at low and mid-elevations in the coastal and slightly inland portions of the Klamath Mountains between the Yurok coastal village of Requa at the mouth of the Klamath River to Sâmay (Seiad Valley) in Siskiyou County (Bright, 1957; Niemiec et al., 1995; Sawyer, 2007; Bowcutt, 2013). Tanoak acorns are considered ‘two year’ growing acorns as their maturation occurs during the year following flowering and pollination. As with other members of the family Fagaceae including the genus *Quercus*, tanoaks exhibit periodic variable, synchronous seed production or masting behavior (Bowcutt, 2013; Koenig et al., 2015).

Tanoak acorns are an important food source in the cultural diet of the Karuk, Yurok, and other tribes within the species range, and are used in the preparation of acorn soup, bread, and as a ceremonial foodstuff (Harrington, 1932; Wolf, 1945; Hendryx and Davis, 1991; Thompson, 1992; Anderson, 2005; Kroeber et al., 2021). The procurement and processing of tanoak acorns engages cultural and ecological knowledge on many levels including timing of resource procurement, management of familial gathering areas, the weaving of baskets associated with acorns, ceremonial activities utilizing tanoak products, and tanoak responses to fire effects (Gould 1975; Anderson, 2005, 2007). Tanoaks will abscise infested or abnormally developing acorns earlier in the fall while retaining viable acorns in the canopy until kernel filling is completed in the late fall resulting in a bimodal acorn abscission pattern (Niemiec et al., 1995; Rohlfs, 1999; Vander Wall and van Wagner, 2001).

2.2. Frugivorous insect consumers

Tanoak acorn embryos are consumed by larvae of the filbert weevil (*Curculio occidentalis*. Curculionidae) and the filbertworm (*Cydia latiferreana*, Tortricidae) (Tappeiner et al., 1990; Vander Wall and van Wagner, 2001). From late spring through early fall, adult filbert weevils deposit eggs into the developing embryo through an oviposition hole; adult filbertworms lay eggs on the exterior seed coat close to the acorn cupule or on the bark of adjacent twigs of the tree (Rohlfs, 1999; Swiecki and Bernhardt, 2006). After the eggs hatch, filbertworm larvae will burrow into the acorn through the micropile (Rohlfs, 1999). Consumption of acorn tissue by larvae of both insects begins during the summer months (Michelbacher and Ortega, 1958; Rohlfs, 1999). Infestation can occur in the canopy or on the ground once the developing larvae exit the recently dropped acorn in search of additional food sources (Michelbacher and Ortega, 1958; Rohlfs, 1999; Vander Wall and van Wagner, 2001). During the late fall and winter months larvae will overwinter in the litter/duff layer or in fallen acorns and re-emerge as adults the following spring (Danks, 1991; Rohlfs, 1999; Swiecki and Bernhardt, 2006). While not as conspicuous as members of the sister taxon *Quercus*, tanoaks can generate synchronous production of abundant seeds at regular intervals (Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002; Koenig, 2002; Bowcutt, 2013; Koenig et al., 2015). Nut bearing trees exhibit traits to reduce the impact of consumption including the abortion and early dropping of infected nuts and masting (Janzen, 1971; Silvertown, 1980; Sork, 1993; Kelly, 1994; Vander Wall and van Wagner, 2001; Espelta et al., 2008). Evolutionary explanations of masting behavior include predator satiation by which semi-regular, synchronous, large-scale seed production is sufficient to both sate predator populations and allow for seed survival (Janzen, 1971; Silvertown, 1980; Sork, 1993; Bonal and Muñoz, 2007). Masting behaviors are governed by climate, pollen availability, and environmental cues all of which contribute to complex relationships between seed producer and consumer populations (Koenig and Knops, 2005; Pesendorfer et al., 2016; Espelta et al., 2017; Koenig et al., 2017; Greenberg and Zarnoch, 2018). In addition, invertebrate consumers exhibit the capacity to undergo prolonged diapause, which may counteract the defensive effect of variable resource production in masting tree species (Janzen, 1971; Hanski, 1988; Maeto and Ozaki, 2003; Bel-Venner et al., 2009).

2.3. Prescribed fire management of acorns

Throughout California, Indigenous cultural practitioners set fires in the late summer and fall specifically to tend acorn gathering areas (Barrett and Gifford, 1933; Schenck and Gifford, 1952; Lewis, 1973; Gould, 1975; Anderson, 2005, 2007). The application of resource-specific prescribed fire was the primary method used by the Karuk and Yurok Tribes to reduce the incidence of larval infestation in tanoak acorn resource systems (Schenck and Gifford, 1952; Lewis, 1973; Anderson, 2005, 2007). Fall prescribed fires targeted vulnerable phases in the life cycle of frugivorous insects when recently emerged larvae are beginning to consume cotyledon material and night-time ignitions increased the chances of reducing nocturnally active adult filbert worm populations (F. Lake, B. Tripp, personal observation, 2010). Low severity surface fires set in tanoak orchards likely caused large reductions in larval populations living in the litter/duff and in recently abscised acorns (Kimmerer and Lake, 2001; Wikars and Schimmel, 2001; Anderson, 2005, 2007). Field observations suggest that even minimal scorching of the acorn pericarp was sufficient to kill enclosed larvae (F. Lake, A. Halpern, personal observation 2013).

Variable annual acorn production, seed size, elevation, and alteration of the post-dispersal environment affect spatial and temporal seed predation (Baker, 1972; Phillips, 1992; Bonal et al., 2006; Kellner et al., 2014; Puerta-Piñero et al., 2010). Traditional ecological knowledge shared by Karuk and Yurok tribal community members states that fall prescribed fire will reduce larval predation in acorns in both the year of the fire and the subsequent year; however, the effect will be larger in the subsequent year (F. Lake, B. Tripp, personal observation, 2010). The reduction in predation intensity during the year of the fire is hypothesized to occur due to heat-caused mortality of larval predator populations in abscised acorns and the duff layer in the immediate vicinity of tanoak trees (Anderson, 2005, 2007; Ortiz, 2008). Some Karuk practitioners note that burning of fuels that generate localized smoke (within orchard, under trees) serves as a fumigant reducing pests (Bill Tripp, personal observation, 2010). The enhanced post-fire year effect is thought to result from the previous year's treatment fires reducing the number of living larvae that reach reproductive maturity; this reduces the number of eggs and larvae present in the post-fire year to consume the acorn crop thus increasing acorn availability for vertebrate consumers.

In addition to frugivorous insects, vertebrates, including deer, rodents, birds, and black bears, visit recently burned orchards to forage on acorns (Koenig and Faeth, 1998; McShea, 2000; Kellner et al., 2014). Cultural practitioners report evidence of vertebrates preferentially consuming sound acorns and leaving infested or otherwise inedible acorns (F. Lake, personal observation, 2011). Types of vertebrate consumers (deer/bear, rodents, and birds) can be identified by the entry marks left on the acorn pericarp (F. Lake, personal observation, 2011).

2.4. Hypotheses addressed by the study

The following hypotheses concerning the independent and interacting effects of fire and seed predators (invertebrate and vertebrates) on acorn condition were tested in our study:

A. Rates of acorn infestation by insect larvae under baseline (unburned) conditions will be similar across research sites and between years.
B. Prescribed fire will reduce incidence of insect infested acorns. Rates of insect infestation will be reduced the year of the fire, and more strongly suppressed in the subsequent post-fire year.
C. By selectively consuming non-infested acorns, non-human vertebrate seed consumers reduce the proportion of fallen edible acorns that are available for tribal uses.

3. Methods

3.1. Study site selection

The study was conducted in 2013 and 2014 within the ancestral territories of the Karuk and Yurok Tribes of California in the mid-Klamath River watershed between Somes Bar and Morek, CA (41°22′34″N 123°28′34″W and 41.3439° N, 123.8539° W). Research sites within Tribal ancestral territories were selected based on the following criteria:

1) Presence of acorn-producing tanoak stand (including former or current tribal family gathering activities).
2) Evidence of historical management according to tribal practitioners as indicated by the presence of acorn processing artifacts (K. McCovey, personal communication, 2011).
3) Contained within private property or reservation land
4) Property steward supportive of the application of prescribed fire, and prescribed fire treatments already planned, permitted, and funded by the landowner.

A site is defined as the area intended for burning within the boundary of private or reservation property. Five research sites were identified and developed (Table 1). Three of the five selected sites (A, B, C) were exposed to two treatments, fire (early summer burn) and no fire (control). Two sites were unable to be burned due to a constrained number of available burn days and existing state fire restrictions (D, E). Data from these two sites were used in the tests of hypotheses A.

3.2. Sample trees and exclosures

Once a site had been identified, all suitable sample trees (>30 cm dbh) were identified within the site; these were distinguished by the presence of acorn remains from the previous year's crop within the dripline of the canopy. The number of sample trees selected within a site (range of 13–30) depended on the size of the site itself and the number of mature tanoaks present. A total of 106 trees were sampled across five sites. A single plot measuring 2 m × 1 m was established under the densest part of the canopy of each sample tree, as judged visually. Our initial study design focused exclusively on insect impacts, so vertebrates were excluded from all plots by installing exclusion cages over each of the study plots. These exclusion cages measured 2 m long × 1 m side × 30 cm tall and constructed of reinforcing bar at the plot corners, ¼" hardware cloth siding, and 2″ hex mesh roofing. This design allowed acorns to fall into the excluded plot through the 2″ hex mesh roof where they were inaccessible to larger vertebrates (e.g., jays, squirrels, black tail deer, black bears). The ¼" mesh siding was large enough to allow fire and frugivorous insects to pass through unimpeded but small enough to exclude vertebrate consumers. Reinforcing bar provided structural support. The exclusion cage was subdivided into two contiguous 1x1 meter subplots. Acorns used for this analysis were collected from one of the subplots (all acorns in the subplot were removed) while those in the adjacent subplot were left undisturbed as a treatment for an associated experiment on the combined effects of fire treatment and seed removal on cultural plant species diversity (results to be reported elsewhere). All exclusion plots were constructed between 2011 and 2013 before treatment fires were applied. Additional non-contiguous, 1x1 meter uncaged plots were installed adjacent (1–3 m away) to each caged plot in 2014 (post-fire treatment) to quantify annual rates of acorn consumption by vertebrate consumers and to assess whether selective vertebrate balanophagy affects the quantity of edible acorns available for human gatherers following prescribed fire. The locations of the uncaged plots were selected so that they matched the burned or unburned condition of the caged plots with which they were paired. A total of 57 additional uncaged plots were installed (Table 1). Extant acorns and understory vegetation were left undisturbed after the establishment of the plots.

3.3. Treatment fires

Fire treatments were applied to the three sites (A, B, C) during the last two weeks of June in 2013. Once ignitions commenced within burn units, broadcast burns were allowed to move unimpeded. As a result, some plots within treated areas burned while others did not, creating a haphazard spatial distribution of burned and unburned exclusion cage plots within burned research sites. A total of 45 trees and associated plots at three treatment sites were exposed to fire (Table 1). Fire line intensity was calculated to assess homogeneity of fire treatments among treated research sites. Presence/absence of stem-bark char and char height were assessed where visible for each tree within the treatment perimeter to estimate fire line intensity using the following equation assuming stem-bark char height to be roughly equal to flame height (Alexander and Cruz, 2017).

$$I_B = 259.833\ x\ L^{2.174}$$

Table 1
Mean values for descriptive site characteristics and treatment specifics for all research sites. Control = Unburned, Treatment = Burned. One plot was constructed per tree. * control plots were constructed in 2014.

Site	Elevation (meters)	Slope	Aspect	Site Area (hectare)	Total Sample Trees	Treatment	Treatment Date	Burned Plots	Control Plots	Uncaged Plots (2014)	Average diameter breast height (DBH)	Average Canopy Cover (%)	Average Canopy Area (m^2)	Average Fireline Intensity (kW/m^{-1})
A	368	13°	S	1.12	26	Burned	6/11/2013	21	5	26	70.81	88.79	81.27	7245.82
B	423	16°	SE	0.45	18	Burned	6/23/2013	14	4	18	77.14	86.00	91.62	47918.84
C	514	10°	NE	0.36	13	Burned	6/17/2013	10	3*	13	85.31	92.02	110.51	3314.48
D	315	11°	NE	1.45	19	Unburned	N/A	N/A	19	N/A	62.13	80.99	77.11	N/A
E	742	7°	SE	3.26	30	Unburned	N/A	N/A	30	N/A	103.53	78.60	135.74	N/A

3.4. Site characteristics

Sample tree diameter was measured at breast height (1.3 m) for each tree under which a plot had been placed, percent canopy cover over each plot was estimated using a concave densitometer, and canopy area was determined by taking canopy radius measurements at the cardinal directions and calculating the elliptical area of the tree canopy. Average nearest neighbor distance was calculated using measurements from sample trees at breast height to the four closest neighbors (Table 1). Annual precipitation data were assessed for the hydrologic years of treatment at Somes Bar, CA (Western Regional Climate Center, 2021).

3.5. Acorn collection

Laboratory dissections were performed on acorns collected from the experimental plots in 2013 and 2014. For both years, collection of acorns from all cages was conducted at three time points: early (late September-early October), mid (mid-late October) and late acorn production season (early-mid November). In 2014, in addition to the three collections from the exclusion cages, acorns were collected from each uncaged plot to measure the impact of acorn consumption by vertebrate consumers on acorn infestation rates and to assess the impact of frugivory on the quantity of edible acorns at each site.

Paper sacks containing acorns from each plot were stored in canvas bags, labelled by sampled site and time point. The use of paper and canvas, as opposed to plastic bags, minimized mildew infestation, enhanced airflow, and shortened drying time. Acorns were allowed to dry for 3–4 months at room temperature to mimic indigenous acorn storage protocols. Acorns were cracked using a hammer and picked apart by hand. The cotyledon was examined for frass, the presence of larvae, or cotyledon discoloration resulting from insect consumption. An acorn was counted as having been attacked if a larva was present within the acorn, the cotyledon was partially or completely consumed, or frass was present within the pericarp (Fig. 1). Edible acorns were considered those with undamaged cotyledons that had completed maturation.

3.6. Statistical tests

All analyses were performed in R using the lme4 and dplyr packages (Bates et al., 2015; Team and Core, 2021; Wickham et al., 2021). Figures were created using ggplot2 and corrplot packages in R and in JMP (Wickham, 2016; Inc., 2021; Wei and Simko, 2021). Acorn count data from all collection timepoints at each caged or uncaged plot were summed within year prior to analysis yielding a total count of acorns per cage by year. The proportion of acorns attacked by insects and the proportion considered edible were calculated by dividing the number of insect-infested or edible acorns recovered from a plot by the cumulative annual acorn yield per plot. To model the proportion of infested acorns as a function of the covariates, design-based, binomial generalized linear mixed models (GLMM) with logit link functions were developed for each hypothesis (Barr et al., 2013; Zuur et al., 2016). Logit links are used for observations with only two possible outcomes and binomial distributions are useful for modeling proportion or binary data. Baseline acorn infestation, effect of fire treatment on infestation rates, and the effect of frugivore exclusion on edible acorn availability were modeled separately using appropriate data subsets. Treatment (categorical, two levels), year (categorical, two levels), and exclusion category (categorical, two levels) were modeled as fixed effects. To incorporate dependency among observations from the same sites and trees, models considered these as random effects with a hierarchy of trees nested within sites. Proportion data were weighted by the total number of acorns produced per plot in a given year. Data exploration followed Zuur (2010) and model development, diagnostics, and reporting suggestions for GLMMs follow Zuur (2016) (Zuur et al., 2010, 2016). Odds ratios (OR) were used to quantify comparisons of proportions related to fixed effects (Rita and Komonen, 2008; Sowerwine et al., 2019). Odds ratios are represented as the relationship between fixed factors and the proportions of edible or infested acorns. OR > 1 indicates an increase in the proportion of infested or edible acorns in response to a unit increase in fixed categorical variables, OR < 1 indicates a decrease in the proportion of infested or edible acorns in response to a unit increase in fixed factors. Relationships are considered significant if the 95% confidence intervals do not include an OR = 1 (Persoskie and Ferrer, 2017)

The following analyses were conducted:

A) Pearson's correlation matrix to assess the relationship between site characteristics (dbh, canopy area, canopy cover, average distance to nearest neighbor) and the proportion of infested acorns. Results were used to determine site characteristic variable inclusion in subsequent generalized linear mixed models.
B) Generalized linear mixed effect models:

Fig. 1. Filbert weevil (*Curculio occidentalis*, Curculionidae) larva in an incompletely filled/infested tanoak acorn with frass. Filbert weevil larvae are distinguishable by the lack of prolegs, milkier color, and a grub-like body shape (Walton et al., 2007). Photo: Frank K. Lake (USFS) and Karuk Tribe.

1. Comparing baseline (untreated) rates of insect infestation in acorns collected from exclusion cages in unburned areas of five research sites during the 2013 and 2014 sampling years.
2. Assessing the effect of summer fire treatment on the proportion of infested acorns during the treatment year (2013) and the year following treatment (2014) in exclusion cages at the three treated sites.
3. Investigating the effect of frugivore exclusion and fire treatment on the proportion of edible acorns at the three treated sites in 2014.

4. Results

4.1. Comparison of site characteristics

Site characteristics were similar with the exception of canopy area and aspect (Table 1). Sites spanned elevations from 368 to 742 m and slopes were modest (10–16°). There was some variation in aspect (south to northeast), in average tree canopy area (83–131 m^2), canopy cover (76.60–92.02%), and d.b.h. (70–100 cm). Fire line intensity showed significant variation between sites (3314.48–47918.84 kW/m^{-1}). The grand average forest floor density of acorns across all sites was 16.96 $acorns/m^2$ in 2013 and 7.23 $acorns/m^2$ in 2014. A total of 3,499 acorns were assessed across treatments, sites, and years.

Pearson's correlation matrix indicated a significant correlation between canopy area and diameter breast height (d.b.h) (Table 2, Fig. 2); however, there were no significant correlations between site variables and the proportion of infested acorns (Table 2, Fig. 2). As a result, site variables were omitted from subsequent models.

Average annual precipitation is 1356 mm per hydrologic year for the study area. Annual precipitation (Oct. 1-Sep. 30) at Somes Bar, CA (Lat: 41.390069°N, Long: 123.492672°W, Elev: 915ft.) was 1232 mm for the treatment year (2012–2013) and 1064 mm for the post-fire year (2013–2014) (Western Regional Climate Center, 2021).

4.2. Variation in baseline infestation rates

Acorn production varied between treatment years with a ~ 43% mean reduction in 2014 (mean: 7.23, SD: 6.68) compared to 2013 (mean: 16.96, SD: 13.40). There was a significant difference in baseline rates of insect infestation in acorns within unburned caged plots across the two treatment years: Baseline infestation rates were significantly lower in 2014 than in 2013 (OR: 0.34, 95% CI:0.24 – 0.49, $p = 0.001$, Table 3). Between subject variance for the nested random effects site and tree was minimal and 15% of the stochastic variance within the model was accounted for by the random variable (ICC = 0.15, $\tau_{00} = 0.60$, Table 3).

4.3. Effect of burning on infestation rates

Fire treatment significantly reduced insect infestation in collected acorns (OR:2.14, 95% CI: 1.07–4.28, $p = 0.031$, Fig. 3, Table 4). Infestation rates were significantly lower in 2014 than in 2013 (OR: 0.54, 95% CI: 0.38–0.76, $p = 0.001$, Fig. 3, Table 4). Treatment effects did vary by year: While fire treatment reduced the proportion of infested acorns in the fire year (2013) by 36.7%, no difference between the treatments was evident in the year following fire (2014) (OR:0.33, 95% CI: 0.14 – 0.79, $p = 0.012$, Fig. 3, Table 4). Between subject variance for the nested random effects site and tree was minimal and 14% of the stochastic variance within the model was accounted for by the random variable (ICC = 0.14, $\tau_{00} = 0.54$, Table 4).

4.4. Effect of mammalian acorn consumption and prescribed fire on edible acorn availability

Selective acorn consumption by vertebrates reduced the proportion of edible acorns in uncaged plots by ~ 39% (OR:0.49, 95% CI: 0.33 – 0.73, $p = 0.001$, Fig. 4, Table 5). Neither fire alone (OR: 0.77, 95% CI: 0.24 – 2.50, $p = 0.67$, Fig. 4, Table 5) nor the effect of early summer fire in the two exclusion categories (OR:0.51, 95% CI: 0.12–2.25, $p = 0.37$, Fig. 4, Table 5) significantly affected the proportion of edible acorns. Between subject variance for the nested random effects site and tree was high and 35% of the stochastic variance within the model was accounted for by the random variable (ICC = 0.35, τ_{00} = 1.79, Table 5).

Table 2
Pearson's correlation matrix describing the relationship between stand level characteristics (d.b.h., canopy cover, canopy area, average tree distance) and the proportion of infested acorns.

Pearson Correlation Matrix - Correlation Coefficients

	DBH	Canopy Cover	Canopy Area	Avg. Tree Dist.	Proportion Infested
DBH	1.00	−0.12	0.69	0.54	0.02
Canopy Cover	−0.12	1.00	−0.14	−0.27	0.05
Canopy Area	0.69	−0.14	1.00	0.51	−0.02
Avg. Tree Dist.	0.54	−0.27	0.51	1.00	−0.13
Proportion Infested	0.02	0.05	−0.02	−0.13	1.00

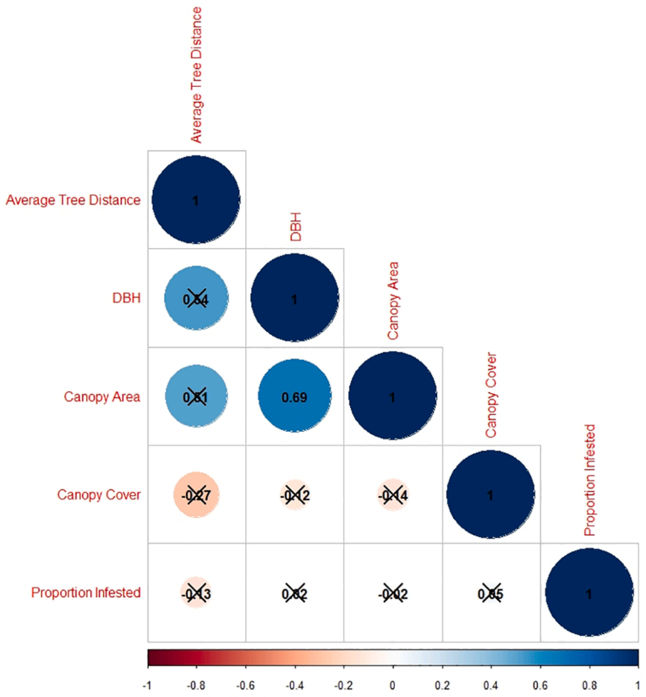

Fig. 2. Pearson's correlation matrix for site variables and the proportion of infested acorns. Correlation is indicated by the number inside the circle, the size of the circle describes the degree of correlation, the color describes a negative or positive relationship between variables (blue = positive, red = negative), and the X's indicate the relationships that are not significant (α = 0.05).

5. Discussion

Overall, acorns were considerably less infested with insects in 2014 than 2013. Non-traditional prescribed fire reduced insect infestation rates by an average of 37% in the year of the fire (2013) but increased the rate of infestation by 9.5% in the year following fire (2014). Vertebrate seed predators were shown to preferentially consume sound acorns regardless of burn treatment thus reducing the proportion of edible acorns in open plots by 38%; this was not affected by fire

Table 3
Outputs for a generalized linear mixed model of the baseline proportion of acorns infested with invertebrate larvae at all sites (n = 5) showing variation explained by both random effects (site and tree), covariate estimates (year), odds ratios for covariates (OR), 95% confidence intervals around the odds ratios, and the p-value for the estimate ($\alpha = 0.05$).

Fixed Effects						
Predictors	*Estimate*	*Std. Error*	*z-value*	*Odds Ratios*	*95% CI (OR)*	*p-value*
Intercept	−0.67	0.131	−5.78	0.51	0.39 – 0.66	**<0.001**
Year	−1.08	0.181	−5.95	0.34	0.24 – 0.49	**<0.001**
Random Effects						
σ^2	3.29					
τ_{00} SITE:TREE	0.60					
ICC	0.15					
N SITE	5					
N TREE	56					
Observations	104					

treatment.

Site characteristics were not significantly correlated with the exception of d.b.h and canopy area. Fire line intensity varied between research sites; however, char height was affected by the presence of moss which, according to Alexander and Cruz (2017), decouples direct the relationship between stem-bark char and flame height resulting in the potential overestimation of fire line intensity.

Baseline infestation rates in unburned sites did differ between sampling years, being higher in 2013 than in 2014. Since overall seed production at sites was also higher in 2013 than in 2014, the difference in infestation rates is not explained by the predator satiation hypothesis which posits that, during years of increased seed production, rates of seed predation will be reduced compared to years of low seed production years (Janzen, 1971; Silvertown, 1980; Koenig and Knops, 1997; Kelly and Sork, 2002). Simple predator satiation dynamics might not consider the possibility of prolonged diapause in curculionid weevils and other insect predators, which could generate different correlation patterns (negative, positive, or none) between insect damage and acorn production in alternate years (Janzen, 1971; Hanski, 1988; Maeto and Ozaki, 2003; Bel-Venner et al., 2009). Results from studies both supporting and contradicting the predator satiation hypothesis as it relates specifically to acorns and insect predators have been summarized by Rohlfs (1999).

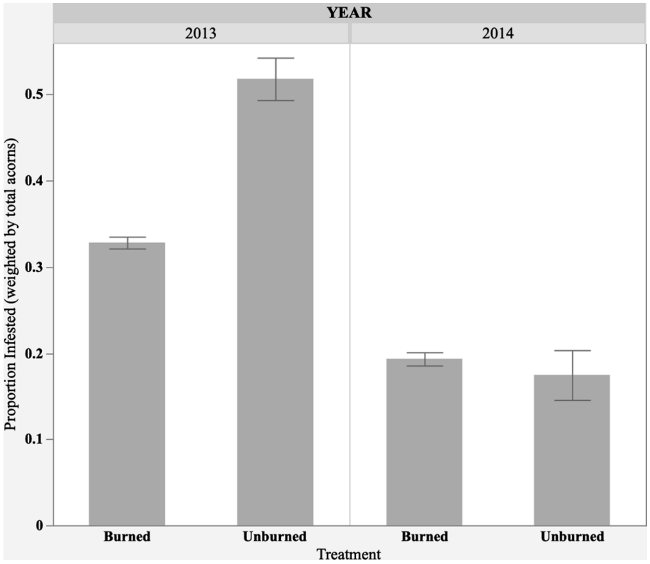

Fig. 3. Mean (+/- 1 SE) proportion of insect-infested acorns weighted by total acorns collected in burned versus unburned plots in the year when fire was applied (2013) and one year post-fire (2014).

In addition to the consumption of tanoak acorns, *Curculio occidentalis* and *Cydia latiferreana* are generalist consumers of nuts from the genus *Corylus* (including *Corylus maxima*, the agriculturally produced filbert) and other species of *Quercus* that grow in proximity to *N. densiflorus* in the Klamath Bioregion including *Q. agrifolia*, *Q. garryana*, *Q. kelloggii* and *Q. sadleriana* (Rohlfs, 1999; Bruck and Walton, 2007; Walton et al., 2007). As different species of *Quercus* exhibit different masting intervals, generalist insect populations living in adjacent areas containing other species of *Quercus* could have migrated into the research sites during the fire year (2013) and increased baseline infestation rates (Sork, 1993).

Moisture-related factors could have contributed to the general reduction in infestation rates during 2014. An inverse relationship between soil moisture and overwintering survival in *Curculio* larvae has been described (Ricca et al., 1996), as well as a correlation between survival and vapor pressure deficit in adult curculionids (Lampasona et al., 2020). While precipitation may directly influence invertebrate survival through its effects on soil moisture or indirectly as vapor pressure, annual precipitation for the hydrological year (Oct. 1-Sep. 30) at nearby Somes Bar, CA was only slightly higher in 2012–2013 (1232 mm) than in 2013–2014 (1064 mm). Both years were moderately lower than average (1356 mm) for the study area (Western Regional Climate Center, 2021).

Dispersal capacity could affect the relative species contribution to infestation rates during treatment years: Species of *Curculio* respond variably to risk emphasizing dormancy or dispersal strategies and traveling up to 10,000 m (Pélisson et al., 2013), mark-recapture studies document related taxa of *Cydia* traveling upwards of 750 m (Keil et al., 2001). While invertebrate frugivores were observed in various stages of dormancy (A. Halpern, personal observation 2013), this study did not account for dispersal as a factor affecting infestation rates.

Elevation can affect rates of infestation (F. Lake, personal observation 2013); however, there was no discernable pattern of variation in baseline infestation rates over the modest range of elevations examined in this study (Table 1). In studies examining patterns of *C. latiffereana* and *C. occidentalis* infestation in blue and valley oak acorns, elevation was found to be the most significant factor: insect attack of acorns was higher at higher elevations (4,200–4,690 ft.) and lower elevations (1,250–2040 ft.) than at intermediate elevations (2,640–3,910) (Phillips, 1992). Interviews with Karuk and Yurok elders noted that higher elevation sites generally had lower levels of insect infestation (Lake, 2007). Research sites for this study varied in elevation between 368 and 742 m (1207 and 2434 ft.) and fall into the low to mid-elevation categories described by Phillips (1992).

While early summer fire treatment was effective in reducing the numbers of infested acorns during the fire year, treatment application did not match the traditional timing of fire application nor did the projected pattern of reduced infestation in the year following fire emerge in burned plots. Cultural practitioners hypothesize that smoke from prescribed fires may act as a site-level fumigant to deter reproducing adults from ovipositing, reduce invertebrate acorn consumer populations the following year, and could confound a plot-specific treatment effect (Tripp, B., personal observation).

Tanoak orchards are typically burned in the fall months to target adult insect predators and larvae during vulnerable life history stages, and to reduce, but not completely exterminate, populations of reproducing adults which would lay the eggs that infest the following year's acorn crop (Jack, 1916; Anderson, 2005; Swiecki and Bernhardt, 2006; Anderson, 2007; Ortiz, 2008). Karuk cultural practitioners do not use fire as a management tool in the spring when cultural celestial indicators are absent from the sky at certain times of the year (B. Tripp, personal observation, 2013). When these celestial bodies cannot be seen, fire can only be used for heating and cooking (B. Tripp, personal observation, 2013). Our treatment fires did not occur during the assumed optimal season for tanoak management (fall months) but did occur at a time

Table 4

Outputs for a generalized linear mixed model of the proportion of acorns infested with invertebrate larvae at treatment sites (n = 3) showing variation explained by both random effects (site and tree), covariate estimates (year and burning), odds ratios for covariates (OR), 95% confidence intervals around the odds ratios, and the p-value for the estimate (α = 0.05).

Fixed Effects						
Predictors	*Estimate*	*Std. Error*	*z-value*	*Odds Ratios (OR)*	*95% CI (OR)*	*p-value*
Intercept	−0.59	0.150	−3.964	0.55	0.41 – 0.74	**<0.001**
Year	−0.62	0.174	−3.549	0.54	0.38 – 0.76	**<0.001**
Treatment	0.76	0.353	2.161	2.14	1.07 – 4.28	**0.031**
Year * Treatment	−1.1	0.437	−2.508	0.33	0.14 – 0.79	**0.012**
Random Effects						
σ^2	3.29					
$\tau_{00\ \mathrm{SITE:TREE}}$	0.54					
ICC	0.14					
N $_{\mathrm{SITE}}$	3					
N $_{\mathrm{TREE}}$	53					
Observations	102					

Table 5

Outputs for a generalized linear mixed model of the proportion of edible acorns at treatment sites in 2014 (n = 3) showing variation explained by both random effects (site and tree), covariate estimates (burning and exclusion category), odds ratios for covariates (OR), 95% confidence intervals around the odds ratios, and the p-value for the estimate (α = 0.05).

Fixed Effects						
Predictors	*Estimate*	*Std. Error*	*z-value*	*Odds Ratios (OR)*	*95% CI (OR)*	*p-value*
Intercept	−1.64	0.34	−4.87	0.19	0.10 – 0.38	**<0.001**
Treatment	−0.26	0.60	−0.49	0.77	0.24 – 2.50	0.669
Exclusion Category	−0.72	0.21	−3.49	0.49	0.33 – 0.73	**<0.001**
Treatment * Exclusion Category	−0.67	0.76	−0.89	0.51	0.12 – 2.25	0.375
Random Effects						
σ^2	3.29					
$\tau_{00\ \mathrm{SITE:TREE}}$	1.79					
ICC	0.35					
N $_{\mathrm{SITE}}$	3					
N $_{\mathrm{TREE}}$	49					
Observations	91					

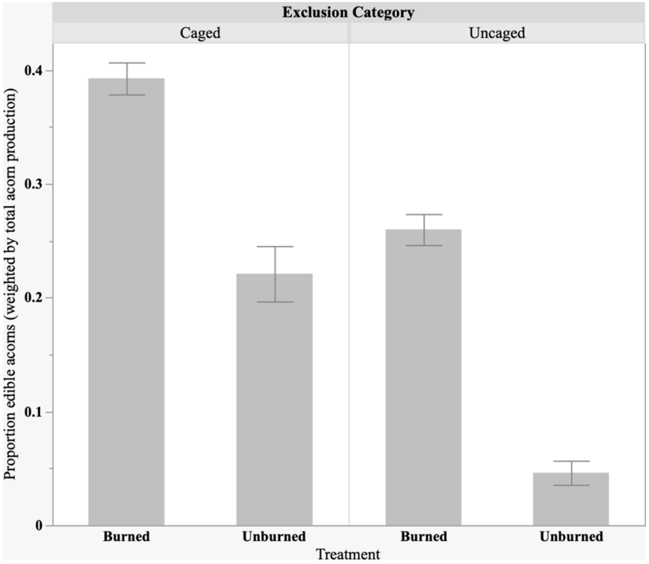

Fig. 4. Mean (+/- 1 SE) proportion of edible acorns weighted by total acorns collected in caged versus uncaged plots under burned and unburned treatment conditions in 2014.

when appropriate celestial indicators were present in the sky. Given that, while burning was done during a non-traditional time of the year for acorns, our treatment fires occurred at a time when fire management activities beyond cooking and heating are not culturally taboo. Therefore, fire management activities at this time, while not optimal, are culturally acceptable. As an extension of the current study, traditional practitioners hypothesize that treatment fires conducted during culturally optimal tanoak management season would reduce rates of insect infestation even more significantly during both the fire and post-fire year than those conducted during other culturally acceptable fire management windows (B. Tripp, personal observation, 2013).

The study results are consistent with published accounts of the application of prescribed fires by Indigenous peoples to reduce predation pressure by insects on *Quercus* acorns in other regions of North America. Wright (1986) provided evidence to support the mitigating effect of prescribed fire on weevil infestation of acorns in red oak (*Quercus rubra*) populations in southeastern Ohio (Wright, 1986). Riccardi (et al. 2004) demonstrated the combined effects of prescribed fire and thinning in reducing predation from *Curculio* and *Conotrachelus* weevils in *Q. vetulina* (black oak) and *Q. prinus* (chestnut oak) (Riccardi et al., 2004). Populations of curculionid weevils were reduced following spring fire in *Q. rubra*, *Q. alba*, and *Q. prinus* dominated forests of West Virginia (McCann et al., 2006). In contrast, other studies have shown little to no effect of spring prescribed fire treatments on insect, specifically weevil, populations in eastern US oak-dominated forests (Lombarde and McCarthy, 2008)

There was a sizable and significant effect of herbivory on the number of edible acorns in uncaged plots compared to caged plots indicating that vertebrate seed predators do feed selectively and focus on sound acorns while leaving the inedible, insect infested acorns untouched. Burning did not affect this behavior; however, individual sites and trees did explain a moderate portion of the observed variance (35%). This is consistent with other studies documenting enhanced predation on acorns in the presence of ungulate frugivores (Bonal and Muñoz, 2007), multi-level population effects on acorn consumer exclusion (McShea, 2000) and species-specific habitat preferences relating to the dispersal of acorns (Perea et al., 2011). In addition to the direct effect of fire on invertebrate seed consumers, habitat structure and composition may indirectly determine patterns of vertebrate seed predation and dispersal: Repeated fire entries, including cultural burning, can change patterns of vegetation flammability, fire severity, canopy architecture, and post-fire assemblage composition (Knapp et al., 2007; Keeley et al., 2011; Hankins, 2013). Acorn dispersers and consumers exhibit preference for foraging and caching in specific environments in which fire may play a structuring role (Bonal et al., 2006; Espelta et al., 2009; Perea et al., 2011). As humans are one of many species that consume acorns, Tribal gathering practices have been designed to ensure the availability of the resource for all species for which acorns are a dietary staple (F. Lake, personal observation, 2013).

While the results of this study suggest that tanoak orchards could be burned annually to achieve a goal of reduced acorn infestation it is important to consider both the seasonally-specific effects of culturally preferred fall fire that may have been lost with non-traditional summer treatments and the availability of sufficient fuels to support annual burning (Anderson, 2007): Treatment fires were set before both the emergence of adult moths and weevils in the summer and oviposition events in the fall (Swiecki and Bernhardt, 2006). Invertebrate overwintering strategies may mitigate the effect of burning on fire-year populations and negate the post-fire year effect anticipated for traditional fall burning by providing insulation and reducing heat-related mortality (Danks, 1991; Wikars and Schimmel, 2001; Swiecki and Bernhardt, 2006; Lombarde and McCarthy, 2008). Surface fuel continuity for desired fire intensity and post-fire effects from Fire Safe Council (FSC) and Prescribed Fire Training Exchange (TREX) cultural treatments in tanoak-dominated stands and orchards indicate a median 5-year fire return interval (FRI) with a range of 3–7 years based on surface fuel accumulation (F. Lake, personal observation, 2021). Research investigating the flammability of mixed-species fuelbeds relating specifically to common tanoak associates describe non-additive or synergistic effects (Varner et al., 2015, 2017). Field observations indicate that sites with a greater black oak component could burn more frequently (3–5 years) than those with a greater madrone component (5–7 years) (F. Lake, personal observation, 2021). Increased flammability and fire behavior are associated with deeper fuel beds in *Quercus* and sister taxa-dominated forests while fire severity influences rates of mortality in overwintering insects (Wikars and Schimmel, 2001; Engber and Varner, 2012). Given these constraints, it is likely that annual early summer burning in tanoak orchards would be constrained by fuel availability and less efficient as a mitigation practice for frugivorous invertebrates.

6. Conclusions

The absence of opportunities to procure, process, and consume traditional foods have adverse effects on the health of Indigenous Californian communities in the Klamath River Basin (Norgaard, 2014b). The act of tending wild resources such as acorns not only increases access to nutritious, culturally relevant foods but also strengthens individual and community relationship with place and ancestral lands, an essential part of Indigenous identity and community well-being (Anderson, 2005). Access to culturally appropriate seasonal fire treatments for acorns in northern California is limited by access to agency permits during appropriate burn windows, limited fire-qualified personnel, and equipment availability to support cultural burning (McCreary, 2004; Anderson, 2007; Hankins, 2014; Long and Lake, 2018; Miller et al., 2020). Our study shows that when fire is applied earlier in the year, it can still be a useful management tool for promoting a viable acorn resource but the effects are not as comprehensive or lasting. This partially addresses the current fire management challenge in western North America and in particular, the socio-cultural and ecological tradeoffs in seasonality of prescribed burning (Ryan et al., 2013). However, the seasonal application of prescribed fire is designed to target multiple resource systems with a single event and the timing of management activities is connected to broader socio-ecological activities. As such, further cross-disciplinary research investigating fire seasonality, tanoak acorn availability, and associated cultural plant assemblage effects is needed to fully address the cultural and management implications for this critical Indigenous resource.

7. Declarations

Author Contributions: K.T. provided background and traditional ecological knowledge supporting the experiment, A.A.H., F.K.L., W.P.S., and T.J.C. conceived of and designed the experiment. A.A.H. performed the experiment. A.A.H., and W.A.P. analyzed the data. A.A.H. wrote the manuscript and W.P.S., F.K.L., K.T., and T.J.C. provided edits; members of the Karuk and Yurok Tribes provided additional editorial advice. The authors declare that they have no conflict of interest. All opinions, findings, and conclusions or recommendations expressed here are those of the authors and do not necessarily reflect the views of the Tribes nor should be construed to represent any official USDA or US government determination or policy.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors gratefully acknowledge the oversight and support of the Yurok Tribe Culture Committee and Yurok tribal community members and cultural practitioners Robert McConnell Sr., Margo Robbins, and Elizabeth Azzuz as well as members of the Karuk Research Advisory Board and Karuk cultural practitioners including Kathy McCovey, Leaf Hillman, and Lisa Hillman. We gratefully acknowledge Hoopa tribal community member/cultural practitioner Clarence Hostler, and Deborah Hostler. This project would not have been possible without the support of Scott Stephens (U.C. Berkeley). Treatment fires and site preparation were achieved with assistance from Will Harling and the Mid-Klamath Watershed Council/Orleans-Somes Bar Fire Safe Council, Ben Riggan, Diana Samuelson, and Josh Myer and Delmar Jordan AKA “Seagull” from the Yurok Tribe.

Funding

This study was funded by the USDA-National Institute of Food and Agriculture-Agriculture and Food Research Initiative Food Security Grant #2012-68004-20018, the Department of Integrative Biology and the Graduate Division at the University of California, Berkeley, the Northern California Botanists, and the USDA Forest Service, Pacific Southwest Research Station.

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