POST-FIRE REGENERATION AND FUEL SUCCESSION PATTERNS IN *HESPEROCYPARIS BAKERI* FORESTS

By

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ABSTRACT

POST-FIRE REGENERATION AND FUEL SUCCESSION PATTERNS IN *HESPEROCYPARIS BAKERI* FORESTS

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Climate change is predicted to cause widespread redistribution of suitable tree habitats, as well as increase the size and frequency of wildfires in the western United States during the forthcoming century. Rare serotinous conifers may have heightened sensitivity to the impacts of both fire regime and climate shifts for multiple reasons. First, the rapid spatial rearrangement of suitable habitat will disproportionately affect trees with constrained seed dispersal capabilities, and limited dispersal is a trait associated with some genera of serotinous trees. Second, a number of serotinous conifers depend on fire disturbances for regeneration, though with the expected increase in annual area burned, immature forests may risk re-burning prior to producing sufficient seed banks. In such a case, high post-fire tree mortality without regeneration would result in population loss or substantial reductions in population size. Baker cypress (*Hesperocyparis bakeri*) is a rare, serotinous conifer with 11 extant populations, and could be adversely impacted by changes in climate and fire regimes. Some remaining populations recently burned in wildfires, which caused extensive overstory mortality and dense post-fire seedling establishment. However, these young cohorts could re-burn before producing viable seed. Further, dispersal capacity has not been quantified in this species. In two separate chapters, the present study examined both 1) the regeneration patterns and dispersal capacity and 2) the fuel succession patterns and associated potential surface fire behavior across a time-since-fire chronosequence in Baker cypress forests.

Specifically, the first chapter investigated the dispersal capabilities of Baker cypress using both empirical observation of post-fire seedling establishment and mechanistic seed dispersal modeling. Post-fire recruitment was dense, averaging 11 recruits/m^2, and occurred primarily in the first two years after fire. However, recruitment was markedly constrained spatially. Most seedlings (~81 percent) established within 5 m of the parent tree, and maximum distance of established seedlings from stand edges averaged 19.2 m. A two-sample Kolmogorov-Smirnov test indicated that the distributions of modeled seeds and observed seedlings were not significantly different, suggesting secondary and long distance dispersal (that would increase dispersal capacity and blur the distinction between a model of primary anemochory and subsequent recruitment) was not a common event. These results aid in explaining why appreciable range expansions in Baker cypress are unlikely and have not been observed. Poor dispersal capacity of this species may hinder its response to rapid climate change.

Chapter 2 examined the fuel succession patterns across a time-since-fire chronosequence of Baker cypress forests, including surface fuel loading by type and tree foliar moisture content. Stand characteristics such as density, composition, and tree-level metrics were also quantified, and stands examined were 3, 10, 40, 107, and 147 years post-fire. A 26 y old planted stand was included for foliar moisture measurements. Fine fuel loading was highest in the 10 y and 147 y stands, while coarse woody fuels peaked in the 10 y stand and thereafter generally decreased with time since fire. Duff loading generally increased with time since fire, though litter loading followed a pattern more similar to the fine woody fuels. Baker cypress foliar moisture content was significantly lower in older foliage, and inversely correlated with stand age. Modeled fire behavior peaked in the 10 y and 147 y stands in accordance with the fine fuel accumulations, and cones were not yet present on the 3 y or 10 y old trees. This indicates that early successional stages of Baker cypress forests contain a narrow temporal window wherein stands could burn prior to seed production. Replicating this research in other *Hesperocyparis* species will provide a better understanding of the ecological processes in rare serotinous conifers, and inform management actions that reduce the chance of population losses.

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PREFACE

This document is formatted pursuant to the Humboldt State University (HSU) Thesis and Project Format Guidelines, and contains two related chapters. Each chapter is intended for separate publication in peer-reviewed journals, so the term “we” is used to account for other authors of the publications in preparation. Some redundancy exists between chapters and headings, due to their similarities.

INTRODUCTION

Fire as a disturbance drives the presence of serotinous conifers on the landscape by prompting regeneration (Agee 1993, Sugihara *et al*. 2006). Some genera of closed-cone trees exhibit a fire-embracing suite of traits, including thin bark, short height, and branch retention (Schwilk & Ackerly 2001), and some may have constrained seed dispersal (Barbour *et al*. 2007). However, timing of fire disturbance events is also pertinent to the survival of serotinous species (Zedler *et al*. 1983, Haidinger & Keeley 1993, Keeley *et al*. 1999). With too frequent of fires, they face burning prior to producing a sufficient crop of seed cones, conceptualized as “immaturity risk”, and in the prolonged absence of fire, they face being outcompeted by later seral-stage or more fire-sensitive species, which is termed “senescence risk” (Keeley & Fotheringham 2000).

Currently, a number of challenges confront the management of rare closed-cone species. Rapid climatic changes have been forecasted to globally redistribute ranges of suitable habitat for tree species in the coming century (Shafer *et al*. 2001, Hamann & Wang 2006, Aitken *et al*. 2008, Iverson *et al*. 2008, Keith *et al.* 2008, Gray & Hamann 2013, IPCC 2014). Additionally, wildfire activity in most forest types of the western United States is expected to increase simultaneously as habitat suitability changes (Fried *et al*. 2004, Westerling *et al*. 2006, Dennison *et al*. 2014, IPCC 2014, Westerling 2016). For tree species with life history processes that are inextricably dependent on fire as a natural disturbance, such as serotinous conifers, the combination of changing climates and fire regimes could have severe impacts on forest health and cause range reductions.

However, informed management strategies can help to curtail the adverse effects of changing climates and fire regimes on rare serotinous species (Noss *et al*. 2006, Millar *et al*. 2007, Flannigan *et al*. 2009, Stephens *et al*. 2013, Loehman *et al*. 2018).

Baker cypress (*Hesperocyparis bakeri*) is an example of a rare serotinous conifer that could be adversely impacted by climate change. Having 11 remaining populations and about 30 distinct stands, it exists only in northern California and southern Oregon (Merriam & Rentz 2010). Some of these populations recently burned in wildfires, which resulted in high percentages of overstory tree mortality and dense post-fire regeneration. The likelihood of reburn in these stands before they reach maturity could be rather low, but the probability of immaturity risk may increase if the trend of increasing wildfire frequency and size continues (Enright *et al*. 2015). Further, the dispersal capacity of this species has not been previously studied; therefore, a critical knowledge gap exists in evaluating its ability to respond to rapid global climate shifts and expand its range after fire.

In two separate chapters, the foci of this study were on the dispersal capacity and the fuel succession patterns of Baker cypress forests. Chapter 1 clarifies the capacity for stand expansion in Baker cypress forests, utilizing both empirical observation of post-fire seedling distribution and a model of seed dispersal parameterized to fire-killed trees. The results of this chapter imply Baker cypress may have a hindered response to rapid climate change. In the second chapter, surface fuel loading and foliar moisture content changes were quantified across a chronosequence of Baker cypress stand ages spanning the vast majority of the age range that currently exists in the species, and surface fire behavior models were parameterized using the fuel profiles at each stand. These results increase our understanding of fuel succession and potential fire behavior patterns in this fire-dependent forest type, and could aid in understanding similar *Hesperocyparis* forest types for which there is limited information.

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CHAPTER 1: POST-FIRE SEEDLING ESTABLISHMENT PATTERNS IN A *HESPEROCYPARIS BAKERI* FOREST

Abstract

Dispersal capacity primarily determines the spatial establishment patterns that drive range expansions and contractions in tree species. For Baker cypress (*Hesperocyparis bakeri*), natural seedling establishment relies predominantly on fire due to cone serotiny, shade intolerance, and small seeds. The wingless and marginally winged seeds of this species constrain its dispersal potential by wind compared to conifers with winged propagules. This study quantified the density and distribution of seedlings following the 2014 Eiler fire in northern California and applied a mechanistic seed dispersal model to fire-killed trees at the site. Post-fire recruitment was dense, averaging 11/m^2, and occurred primarily in the first year after fire. However, recruitment was markedly constrained. On 20 m transects, most seedlings (~81 percent) established within 5 m of the parent tree, and 94 percent established within 10 m. On 50 m transects, maximum dispersal distance from stand edges averaged 19.2 m (±2.7 SE; ranging from 2.3 m to 48.5 m), and scaled linearly with canopy height at the stand edge ($R^2 = 0.57$, $p = 0.0001$). A two-sample Kolmogorov-Smirnov test indicated that the distributions of modeled seeds and observed seedlings were not significantly different (D = 0.3, $p = 0.3291$), suggesting secondary dispersal was probably minimal at the site. Hypothetically, a supplemental dispersal vector (besides wind) would increase dispersal capacity, and

distinguish a model of primary anemochory from subsequent recruitment patterns. Limited seed dispersal may impede migratory potential and response to rapid climate change. These results aid in explaining why appreciable range expansions in Baker cypress are unlikely and have not been recorded.

Introduction

Climate change is predicted to cause extensive spatial shifts in forest habitats within the next century (Shafer *et al*. 2001, Iverson & Prasad 2002, Iverson *et al*. 2008, Gray & Hamann 2013), but there is indication that the dispersal capacity of many tree species is incommensurate with the rate of change (Aitken *et al*. 2008, Keith *et al.* 2008, IPCC 2014). Life history processes such as seed dispersal and seedling establishment are key factors in determining a species' distribution, migration potential, and metapopulational persistence on the landscape (Primack & Miao 1992, Bakker *et al*. 1996, Tilman & Kareiva 1997, Nathan & Muller-Landau 2000). Therefore, quantifying dispersal capabilities of a plant species is essential to understanding its population dynamics (Willson & Traveset 2000), especially during rapid periods of climate change. Both empirical observation (Mair 1973, Platt & Weiss 1977, Augspurger & Hogan 1983, Lamont 1985, Auspurger & Franson 1987, Nathan *et al*. 1999, Greene *et al*. 2004) and seed dispersal modeling (Andersen 1991, Greene & Johnson 1989, Nathan & Casagrandi 2004) are practical methods of reckoning a tree's means and capacity for transporting propagules.

Factors affecting dispersal and establishment of diaspores vary among tree life history strategies, and often relate to seed morphology (Howe & Smallwood 1982). For some genera of serotinous trees, a fire-embracing suite of traits is typical, including thin bark, short height, and branch retention (Schwilk & Ackerly 2001), and some may have constrained seed dispersal (Barbour *et al*. 2007). While the requisite conditions for opening serotinous cones range from dry weather to fire, some species are more strongly serotinous than others, and are therefore essentially dependent on fire for regeneration (Lotan 1967, Bartel 1980, Tinker *et al*. 1994, Nathan *et al*. 1999, Barbour *et al*. 2007). In these species, dispersal events resulting in successful germination are virtually restricted to early post-fire temporal windows.

Baker cypress (*Hesperocyparis bakeri*) is one such species, a strongly serotinous conifer (Milich *et al*. 2012) in the Cupressaceae that is understood to primarily depend on fire for natural regeneration (Barbour *et al*. 2007, Merriam & Rentz 2010). Baker cypress is also rare, with 11 extant populations in southern Oregon and northern California (Figure 1.1). It is classified as “vulnerable” by the International Union for Conservation of Nature (Farjon 2013). Fire exclusion practices have led to decreased stand health, competitive exclusion (overtopping by shade-tolerant species), and limited regeneration on older, undisturbed sites (Merriam & Rentz 2010). The small seeds of Baker cypress have either no wing or a small fringe of thin tissue around part of the seed coat. Thus, the terminal velocity is expected to be high, and dispersal by wind correspondingly limited (Greene & Johnson 1989).

Figure 1.1. The 11 extant Baker cypress population locations in southern Oregon and northern California, which occupy approximately 34.9 km^2 combined total area.

This study combines empirical observation of post-fire seedling establishment and seed dispersal modeling in a Baker cypress forest. We utilized a mechanistic model of seed dispersal by wind from Greene and Johnson (1989) to predict seed dispersal from a source, and subsequently generate probability density functions (hereafter, dispersal curves) for Baker cypress seeds. The modeled dispersal curves were informed by seed descent velocity tests and parameterized using data from a recently fire-killed Baker cypress forest. We also compared model predictions to the empirical observations of seedling establishment densities per distance from a tree (hereafter, seedling shadows). Cumulative density functions (CDFs) were then derived from the dispersal curves and seedling shadows, and compared statistically using two-sample Kolmogorov-Smirnov (K-S) tests. Specifically, the objectives of this study were to i) characterize the density and distribution of regeneration in a post-fire Baker cypress stand through empirical observation, ii) utilize a mechanistic seed dispersal model to further understand dispersal capabilities under different circumstances, and iii) compare the dispersal curves of seeds and seedling shadows of recruits.

Methods

Site location

The study area was located in Shasta County of northern California, USA. We collected data in a small Baker cypress stand at approximately 1560 m elevation in Lassen National Forest, north of the Thousand Lakes Wilderness. Much of this stand was originally treated during forest operations in 1936, when the area was intentionally burned and stripped in the establishment of a pine plantation (Merriam & Rentz 2010), though Baker cypress and montane chaparral persisted in areas. Initial site preparation included piling of slash and soil in windrows approximately 10 m wide, 0.5 km in length, and about 60 m apart (but ranging from roughly 35 m to 95 m), which still remain at the site. Subsequent operations such as harvesting and replanting of pines also occurred (Merriam & Rentz 2010). During the mid-summer of 2014, the Eiler fire burned a vast majority of this site. Ignition occurred July 31st, and containment was achieved by mid-August (CAL FIRE 2014), though a total area of 13,118 hectares burned. In the immediate vicinity of the Baker cypress stand, there was heavy post-fire mortality and dense subsequent regeneration (Figure 1.2).

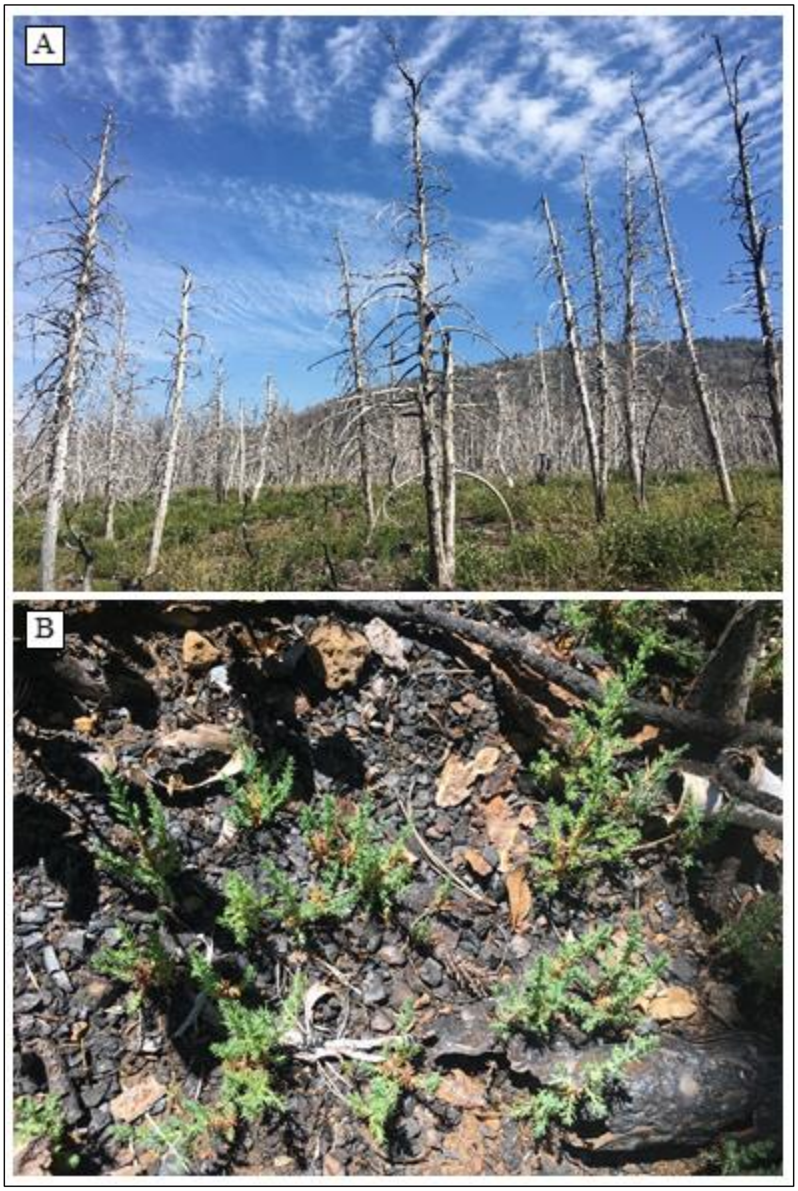


Figure 1.2. Example of high mortality following the 2014 Eiler Fire observed in the Baker cypress forest (A) and dense seedling establishment also observed at the same site (B).

At the time of our study, surrounding forest vegetation included Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*Pinus ponderosa*), and white fir (*Abies concolor*) with an understory predominantly comprised of tobacco brush (*Ceanothus velutinous*) and greenleaf manzanita (*Arctostaphylos patula*). Soil at the site is described as volcanic (Merriam & Rentz 2010). Monthly precipitation in the area for the year of the Eiler fire ranged from 4.8 mm to 105.7 mm with an average of 35.9 mm (WRCC 2017). Mean monthly temperature in the area for that year ranged from 2.8 ℃ to 22.8 ℃, and the average annual temperature was 10.7 ℃ (WRCC 2017).

Data collection

During the summer of 2016, regeneration was examined on 20 belt transects originating from fire-killed Baker cypress (subject trees) with sufficient still-appended cone crops. We recorded subject tree characteristics using standard mensuration methods, as well as seedling distances from subject trees and seedling age (the distinction between new germination and second-year recruits was apparent because of size differences). Tree characteristics recorded included tree height, diameter at breast height (DBH), number of appended cones, and average cone height. Transects were 20 m long, 2 m in width along the proximal half, and 4 m in width along the distal half (to reduce null values with distance; a total area of 60 m^2 per transect). These transect azimuths were selected by determining the direction that led away from interfering seed sources, so that the subject tree or source was ostensibly the source of any regeneration on the transect. Two observers separately counted the number of appended cones per tree, using binoculars if needed, and the average number between the two counts was assumed to be the number of appended cones per tree. Fallen cones, recruit density, and seedbed characteristics were measured in 25 m^2 circular plots centered on subject trees at the origin of each transect. During the summer of 2017, 20 more transects which were 50 m in length and 4 m in width were extended from stand edges with subjectively sufficient still-appended cone crops. Furthest established seedlings from the stand edges were recorded on these transects, and non-systematically searched for ~ 20 – 40 m beyond the transect length in cases when seedlings were established on the further reaches of the transects.

Seed dispersal modeling & statistical analysis

We employed a mechanistic seed dispersal model developed by Greene and Johnson (1989) to predict post-fire seed dispersal by wind (Equation 1.1) and to compare generated dispersal curves with observed post-fire seedling shadows in Baker cypress.

Equation 1.1: $$\frac{dQ}{dx} = \frac{Q}{x\sigma_u\sqrt{2\pi}} exp\left\{-\left(\frac{\ln\left(\frac{x\bar{F}}{H\bar{u}_g}\right)}{\sqrt{2}\sigma_u}\right)^2\right\}$$

Given, x signifies the distance from a seed source and Q represents the number of viable seeds on a tree. H is the seed abscission height, $\bar{F}$ is the seed velocity, and $\bar{u}_g$ is the average horizontal wind velocity linking H and the forest floor. Finally, σ_u is the standard deviation of the logarithms of the horizontal wind speeds. While Equation 1 is a function characterizing the dispersal curve of seeds deposited per distance, it is dimensionless until modified by dividing $\frac{dQ}{dx}$ by $\pi * (r_1^2 - r_2^2)$, where r_1 is the radius of an annulus and r_2 is the radius of the next smallest annulus centered on a tree.

Model variables were assigned values using either field and lab measurements, values from the literature, or a combination. First, Q was assigned using the number of appended cones plus the number of recently fallen cones on the ground in the 25 m^2 plots centered on subject trees. For modeling purposes, we generalized single trees (or in some cases, small assemblages of tightly grouped trees on a windrow) as point sources due to the relative lack of spatial variation in the appended cone crop. Point sources are commonly used in modeling for this purpose, and conceptualized as a single point in three-dimensional space (Lamont 1985, Augspurger & Franson 1987, Greene & Johnson 1989). The sum of all cones associated with the seed source was multiplied by the amount of viable seeds per cone (3.75; Table 1.1), which was a mean average across four populations of Baker cypress for which data is available. Three of the viability estimates were made by Merriam & Rentz (2010); the other estimate was based on a previous study conducted at Humboldt State University (Harris *et al*. unpubl.).

Table 1.1. A synthesis of data used to estimate the number of viable Baker cypress seeds per cone.

Population	**Seeds / Cone**	**Proportion Viable**	**Source**
Lassen	35	0.033	Harris *et al*. unpubl.
Seiad	54	0.060	Merriam & Rentz 2010
Hamburg	57	0.150	Merriam & Rentz 2010
Flounce Rock	34	0.090	Merriam & Rentz 2010
Average (± SE)	45 (± 5.280)	0.083 (± 0.022)	

Mean seed release height (H) was assigned via visual estimate of the average cone height on subject trees as measured by a laser rangefinder/hypsometer. Mean seed descent velocity was measured by collecting Baker cypress seed from living trees near the site: 10 seeds were weighed and then dropped from heights of 2 m, 3 m, 4 m, 5 m, 7.5 m, 10 m, and 12.5 m in a stairwell. The descent of each seed was timed as they were dropped incrementally from each height. Due to small seed size and mass, dropping and tracking seeds was facilitated by covering the seed landing-zone with bright butcher paper. To minimize human error in timing, we also placed an audio recorder near the butcher paper to detect the exact time of the audio signature of each seed's impact. A logarithmic model was fit to the data for the various fall heights (Equation 1.2; $R^2 = 0.96$), which was in turn used to estimate the mean descent velocity (V) for the burnt trees based on abscission height.

Equation 1.2: $V\ (m/s) = 0.7173\ ln\big(Height\ (m)\big) + 2.4438$

We assigned $\bar{u}_g$ following the process described by Greene and Johnson (1996). Median wind speed at 10 m above the ground was based on data from North American airports (4.3 m/s; Luna & Church 1974), which was multiplied by 1.83 to account for the bias introduced by the dependence of seed release on the square of the wind speed (i.e. drag; Greene & Johnson 1992). Using a modified power-law function, the standard value at 10 m was then related to the speed at twice the canopy height (u_{2zh}; when z_h signifies canopy height), where the drag introduced by a forest is null. Using u_{2zh}, we derive the expected wind speed at canopy height using a supracanopy flow model for neutral stability, in which we employed a displacement height value of 0.57 * z_h and a roughness length value of 0.1 * z_h for a leafless canopy (Allen 1968). The within-canopy horizontal wind speed profile (at various heights) was calculated via Dumbauld & Cionco (1985), while accounting for underestimated wind speeds in the lower half of the canopy (Greene & Johnson 1996), where flow is effectively independent of height (Landsberg & James 1971). From the wind vertical profile, we estimated $\bar{u}_g$ given H. For the standard deviation of the logarithms of the horizontal speed (σ_u) we also assumed the North American airport average σ_u of 0.55 (Greene & Johnson 1996). Note that the model presented here ignores the contribution of vertical winds; it is assumed that the distances are so short and the vertical speeds of the falling seeds so large, that vertical turbulence will play an unimportant role in the dispersal of cypress, as opposed to other conifers with winged propagules.

Generated dispersal curves from the mechanistic model of seed dispersal were then compared with the seedling shadows in the Baker cypress forest. We assigned model parameters for dispersal curves using values observed for each individual subject tree in the field, as well as mean values for data from all 20 subject trees (in order to represent the average tree conditions). Resulting dispersal curves from the models were compared to the seedling shadows by deriving CDFs from the dispersal curves and seedling shadows, and then performing two-sample K-S tests where the test statistic (D) indicates the maximum distance between the two CDFs being compared. The null hypothesis of the two-sample K-S test is that both samples are derived from the same distribution

(Gotelli & Ellison 2012). In this experiment, we tested significance at $\alpha = 0.05$, and rejected the null hypothesis for any K-S test results with $p < 0.05$ (Gotelli & Ellison 2012). We also compared the dispersal curve from the model parameterized using average tree conditions to the seedling shadow of average seedling density per distance from the subject trees using a K-S test. Further, we generally examined hypothetical dispersal possibilities using upper and lower ranges of observed tree characteristics we used to parameterize models. We also analyzed relationships between tree characteristics and post-fire recruitment density and dispersal using general linear models. Analyses were computed within the R environment (R Core Team 2018).

Results

Post-fire regeneration and distribution of seedlings

Seedling density observed in the 25 m^2 plots centered on subject trees was high following the wildfire; an average of 11 seedlings/m^2 and as many as 34 seedlings/m^2 were recorded in this immediate vicinity of seed sources. However, seed density was lower when averaged within the area of the 60 m^2 transects originating at the subject trees and progressing distally from the seed source, with a mean of 2.5 seedlings/m^2. Thus, seedling establishment was mainly concentrated near the subject trees. As measured on the 20 m transects, a majority of seedlings (81 percent) established within 5 m of the seed sources, while 94 percent established within 10 m (Figure 1.3). Regeneration occurred primarily within the first year after fire, although 41 percent of recorded seedlings established the second year. We observed very little regeneration in 2017 (dating from the third year after fire). The maximum seedling distance on the 50 m transects averaged 19.2 m (±2.7 SE), and the furthest seedling observed from a seed source was 48.5 m. For the transects where seedlings were found more than 25 m away from the stand edge, we also looked beyond 50 m in a non-systematic manner but found no recruits.

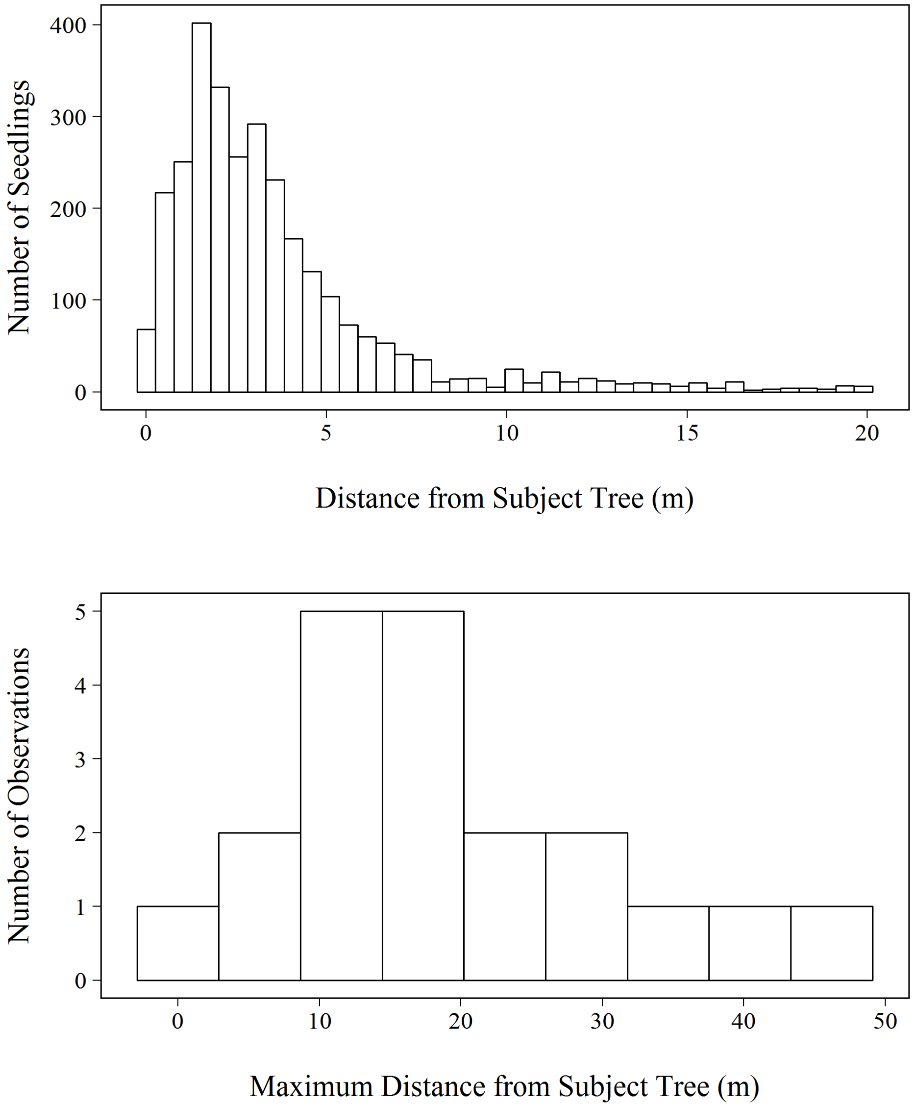


Figure 1.3. Frequency distributions of established seedling distances from Baker cypress subject trees along all 20 m transects (2,941 total observations; top) and maximum distances of established seedlings from Baker cypress stand edges along all 50 m transects, 4 m wide (bottom).

As expected, cone density (cones/m^2) on burnt subject trees was positively correlated with post-fire seedling density ($R^2 = 0.47$, $p = 0.0007$). Likewise, maximum seedling establishment distance from subject trees positively correlated with canopy height ($R^2 = 0.57$, $p = 0.0001$). The number of still-appended cones on subject trees was variable, ranging from approximately 60 to 3,600, averaging 1,200. Notably, no correlation was observed between DBH and number of appended cones ($R^2 = 0.02$, $p = 0.5716$), nor between DBH and the number of cones associated with the seed source (including those on the ground immediately beneath the tree; $R^2 = 0.02$, $p = 0.5243$).

Seed dispersal models

By comparing the dispersal curve parameterized using average values observed at the stand level to a seedling shadow which represented the average density of seedlings per distance at the stand, we found that the distributions were not significantly different (D = 0.3, $p = 0.3291$), suggesting they were from the same distribution (Figure 1.4). Similarly, 11 out of the 20 transects modeled individually for each subject tree matched the observed CDFs for seedling distributions when compared using a K-S test (Table 1.2). Notably, 7 of 9 non-matching transects had recruitment densities ≤0.5 recruits/m^2 when averaged on the transect area while all matching transects had recruitment densities >0.5 recruits/m^2, meaning there may not have been enough recruitment data in most non-matching individual transects to discern a precise seedling shadow for comparison.

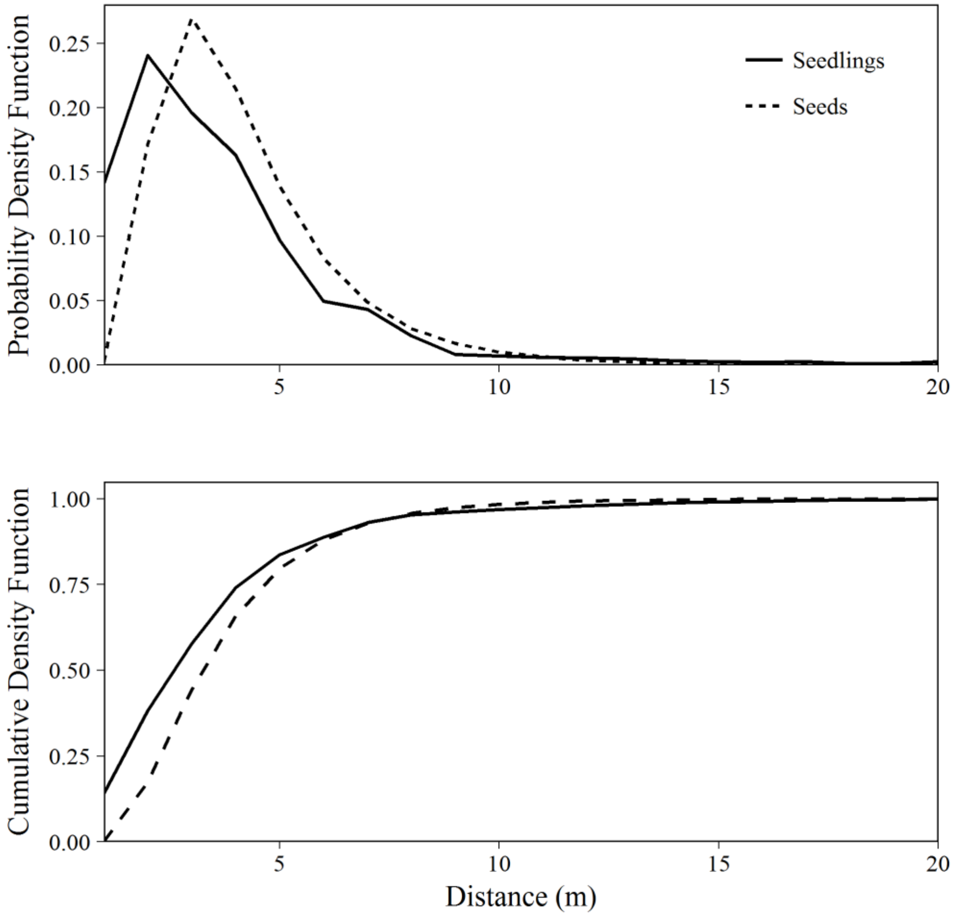
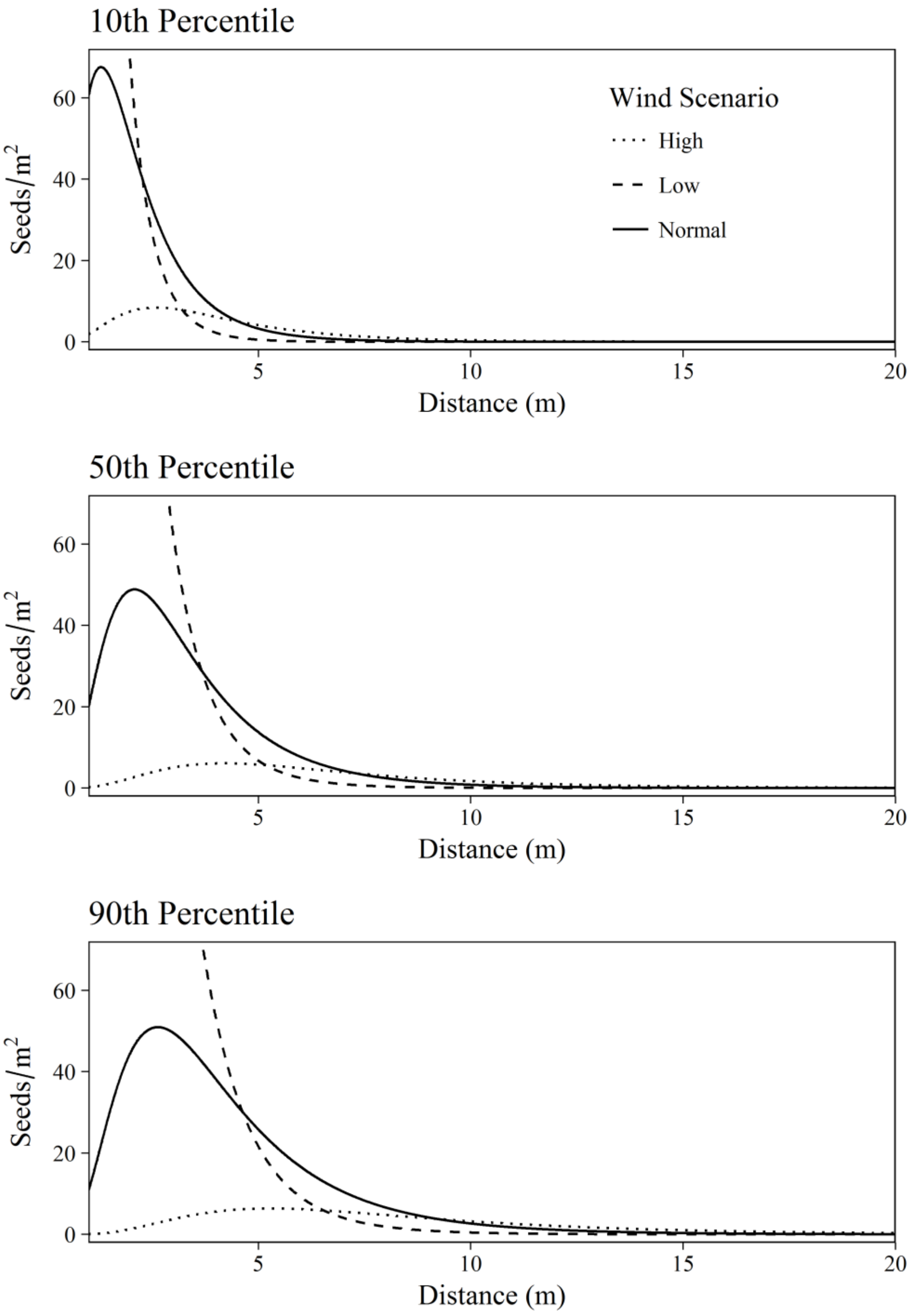


Figure 1.4. Mean probability density functions (top) and cumulative density functions (bottom) for seeds and seedlings per distance from subject Baker cypress trees. Given, average seedling density per distance observed two years following the 2014 Eiler fire was compared to a model of seed dispersal parameterized using average conditions.

Table 1.2. Two-sample Kolmogorov-Smirnov test results comparing differences in the cumulative density functions of modeled viable seeds/m^2 against the cumulative density functions of established Baker cypress seedlings/m^2 on 20 transects following the 2014 Eiler Fire. The test statistic (D) denotes the maximum distance between the cumulative density functions being compared. Note that α is tested at a 0.05 level: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Subject tree	**D =**	**Total recruits on transect**	**Total density (m^2) on transect**
1	0.45*	15	0.25
2	0.20	56	0.93
3	0.30	51	0.85
4	0.35	192	3.20
5	0.35	552	9.20
6	0.40	99	1.65
7	0.25	196	3.27
8	0.50*	30	0.50
9	0.35	595	9.92
10	0.55**	22	0.37
11	0.75***	17	0.28
12	0.30	322	5.37
13	0.60**	3	0.05
14	0.70***	19	0.32
15	0.50*	222	3.70
16	0.45*	56	0.93
17	0.45*	18	0.30
18	0.35	32	0.53
19	0.30	142	2.37
20	0.10	302	5.03

When model parameters were assigned using average values observed at the stand, the predicted modal dispersal distance was 3 m, while the modal distance of established seedlings from subject trees was 2 m (Figure 1.4). This suggests the mechanistic model predictions of dispersal were slightly further than recorded seedling distances from subject trees. However, the model parameterized using average values also indicated that 99.3 percent of all viable seed would, at least initially, be distributed within 20 m of the parent tree. Under average conditions, less than 0.001 percent of seeds were expected to be transported past 60 m by wind alone. Independent of changes in individual model covariates, the vast majority of primary dispersion was still predicted to be within 20 m of the subject tree. For hypothetical dispersal situations, we manipulated individual model covariates to be the 10th, 50th, and 90th percentile values for tree characteristics in the stand and applied three wind speed scenarios to each: 50 percent of the expected value for wind speed (Low), 100 percent of expected (Normal), and 200 percent of expected (High) (Figure 1.5). Anticipated dispersal is slightly lengthened by assuming the more extreme conditions. Yet, increases in abscission height that would normally substantially increase expected dispersal in other species with winged seeds are not as pronounced in Baker cypress, as the terminal velocity of seeds is so high. In the scenario of 90th percentile values for observed tree characteristics and 200 percent of the expected wind speed, we expect 76 percent of seeds land within 20 m, and 97.6 percent land within 40 m (Figure 1.5). Under these conditions, the model predicts about 0.003 percent of seeds would fall beyond 60 m of the parent tree, and 0.0007 percent of seeds would fall beyond 80 m. On the 20 repetitions of the 50 m transects, we observed only one seedling established beyond 40 m from a seed source.


10th Percentile

50th Percentile

90th Percentile

Figure 1.5. Dispersal scenarios showing model parameters at 10th, 50th, and 90th percentile values for seed velocity, seed quantity, and abscission height. Values for wind speed are shown at 50 percent (Low), 100 percent (Normal), and 200 percent (High) of the expected value.

Discussion

Ecological considerations

Baker cypress seed dispersal and seedling establishment distances were markedly constrained, with only a meager portion of seedlings establishing further than 15 m from a parent tree. In agreement with the observed phenomenon of very limited seedling distances from parent trees, the modeled seed dispersal predictions suggest most seeds would be deposited within 20 m of the parent tree, even under a variety of scenarios (Figure 1.5). This finding is consistent with thought that the bulk of seed crops are deposited close to the parent plant (Levin & Kerster 1974, Verkaar *et al*. 1983) while long-distance dispersal usually accounts for only a small amount of propagules (Harper 1977). This constraint for Baker cypress is partially a product of the lack of a wing for a seed this size, which does not allow it to utilize the wind as effectively as other species with winged seeds (Sheldon & Burrows 1973) and travel long distances as efficiently (Nathan & Ne'eman 2000). We observed Baker cypress seed velocities averaging 4.11 m/s when dropped from 10 m in a stairwell, indicating the potential descent rates are much faster than demonstrated velocities of winged seeds (Green 1980, Guries & Nordheim 1984, Augspurger 1986, Nathan & Ne'eman 2000).

Given its strict shade intolerance and presumed limited seed dormancy once outside the cone (Barbour *et al*. 2007), we expect the species persists only when it colonizes soon after a disturbance. In this vein, the present study detected dense regeneration mainly within a 2-year post-fire window, after which new germination was scarce. Our results were consistent with previous records of high post-fire regeneration in the species despite the very low viability (Merriam & Rentz 2010), suggesting the fundamental constraint for this species is dispersal rather than seed production or juvenile survivorship.

At present, this cypress species is rare (Griffin & Critchfield 1972), declining (Farjon 2013) and found in what is considered to be 11 small populations in northern California and southern Oregon (Merriam & Rentz 2010), but about 30 discrete stands. Thus, as a metapopulation, it requires that the loss of habitat be balanced by the creation of new habitat at distances not exceeding the dispersal capacity of the species (Hanski & Gilpin 1991). Habitat is lost or substantially reduced for this species at sites where shade-tolerant species are competitive and can eventually overtop the cypress. Merriam & Rentz (2010) noted cone production increased with stand age, but observed almost no cypress recruits on the deep, well-shaded organic layer in older stands. Consequently, extensive overtopping by shade-tolerants could lead to the death of the canopy-forming initial post-fire cohort, resulting in the loss of a stand if competing allospecifics are not removed (Farjon 2013).

Despite its disjunction between stands, Baker cypress was recently shown to have high genetic diversity (Bower & Hipkins 2017) despite geographic barriers to gene flow among extant populations. This suggests Baker cypress was once more widely and continuously distributed (Barbour *et al*. 2007, Terry *et al*. 2016, Bower & Hipkins 2017). Overall, a severe dispersal constraint in Baker cypress is a problem presumably shared by the other endemic wingless and marginally winged serotinous cypress species in

California. While competitive in fire-prone environments, range expansion events in Baker cypress are spatially limited and restricted to short post-fire windows. Therefore, the species is spatiotemporally hindered compared to species with winged seeds that can establish a new cohort each year.

Model comparison

In 55 percent of individual transects originating from Baker cypress, modeled seed distributions matched that of observed seedling distributions. When only considering transects with average seedling density $>0.5/m^2$, distribution conformance increases to 11 out of 13 transects. This rate of conformance is high, given that the model is designed to predict primary seed dispersal by wind, and we have compared expected seed dispersal curves directly to established seedling shadows. This suggests secondary dispersal, which would increase dispersal capacity and blur the distinction between a model of primary anemochory and subsequent recruitment, was not commonplace after the Eiler fire. Some discrepancies between dispersal curves and seedling shadows can be attributed to the rather low density of recruits on transects that were not in agreement with the model (meaning there was not enough data to discern a curve from the established seedlings on some transects). At the stand level, with far more data points available, the respective distributions were more highly similar, indicating the seed dispersal model was a reasonably accurate method for predicting seedling establishment patterns in at least this species, where secondary dispersal events were seemingly inconsequential.

Despite the statistical similarity of the distribution of dispersal curves and observed seedling shadows, the model of average conditions predicted a modal dispersal 1 m further than the modal distance of observed seedlings from a subject tree (Figure 1.4). While not an extreme difference, we may have marginally overestimated dispersal capacity via wind, or it may be that the microsite conditions closer to parent trees offer some favorable condition for germination. In either case, the statistical similarity of the dispersal curve and the seedling shadow indicate the tail of the distributions would also be similar (Nathan & Muller-Landau 2000) indicating a low probability of long-distance dispersal events resulting from wind. Other obligate-seeders may also present us the opportunity to compare the model of seed dispersal by wind directly to post-fire establishment with reasonable accuracy.

While secondary dispersal does not seem to have been an important event at this site (as suggested by the shape and scale of the seedling shadows), it may still occur to a minor extent in Baker cypress. Hypothetically, seeds deposited on snow could undergo secondary dispersal via wind (Greene & Johnson 1997). Callahan (2013) observed cone caching by rodents in a stand of the related species MacNab cypress (*Hesperocyparis macnabiana*), though studies that have tracked rodent seed caches in the region observed dispersal only over short distances (Fitch 1948, Fiehler 2007), meaning a cone-cache would probably not drastically increase dispersal. Rodent density in post-fire forests has been shown to vary widely depending on forest type, burn size, and burn intensity (Lawrence 1966, Schwilk & Keeley 1998, Lee *et al*. 2008). Though, small seeds are less likely to be cached by animals (Kerley & Erasmus 1991, Vander Wall 1994), presumably because of lower nutritional value.

Implications for management

Due to excellent regenerative response of mature stands to fire, and poor health on sites with interspecific competition, fire reintroduction is an intervention to consider. Wildfires typically burn at high severity in this forest type, and Baker cypress seedling establishment is most dense after high-severity fire (Frame 2011). Prescribed fire is another option that has been used to regenerate live and dead serotinous conifer stands (Sharpe *et al*. 2017), so overtopped cypress in poor health (or which have been recently killed) could yield adequate regeneration if viable seed were present. Unlike the managed wildfire option, though, prescribed fires are typically low-severity (Ryan *et al*. 2013) to facilitate containment. No studies have yet examined whether low-severity fire can induce adequate regeneration in Baker cypress. For this reason, future management could involve managed wildfire for mature stands. A study of Baker cypress' regenerative response to prescribed fire of varying severities would also inform managers whether or not this method is effective.

While fire remains the ideal natural disturbance to generate a new cohort, alternate options could be considered in areas where Baker cypress occurs in a mosaic of land ownership and management objectives do not align with allowing fire. Thinning interspecific competition via careful harvesting would allow the cypress within a stand to persist for far longer (Merriam & Rentz 2010). However, large diameter fir and pine species overtopping some Baker cypress stands may be too large to be effectively removed by fire alone, and should be cut prior to planned burning in any case. Pre-fire thinning treatments have also been shown to increase cone crops per tree and post-fire seedling establishment in other serotinous species (Verkaik & Espelta 2006), and our results link high cone production with successful post-fire regeneration in Baker cypress. For these reasons, silvicultural removal of competing fir and pine species is desirable when applicable.

We observed healthy Baker cypress near the study site which were planted in 1992 as part of a mitigation effort following the construction of a natural gas pipeline. A treatment on the pipeline which masticated cone-bearing branches and disturbed the soil yielded some Baker cypress germination, and intensive forest operations have been shown to yield regeneration of serotinous species (Smith *et al*. 1997, Yorks & Adams 2003). The thinning of interspecific competition which disturbs soil could potentially initiate a new cypress cohort, though this method warrants testing and many Baker cypress stands are quite inaccessible, making managed wildfire a more feasible option in most cases. Overall, the extreme dispersal constraint we observed in Baker cypress, unless otherwise obviated, means the species is unlikely to appreciably expand its range in the near term. Expansion events are also limited spatially, and temporally to the first few years following a fire. With the rapid onset of climate change, this species may be unable to spatially follow suitable habitat.

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CHAPTER 2: POST-FIRE FUEL SUCCESSION PATTERNS IN *HESPEROCYPARIS BAKERI* FORESTS

Abstract

Serotinous conifer regeneration is typically fire-driven, but altered fire regimes may eliminate stands of rare serotinous species. Fire exclusion can allow overstory transition to shade-tolerant species, while increased fire frequency could cause young stands to burn before sufficient cone production. This study characterizes fuel dynamics and potential surface fire behavior across a chronosequence of Baker cypress (*Hesperocyparis bakeri*) stands. Surface fuel loading by type, tree and shrub foliar moisture content, and forest density and composition were quantified in stands aged 3, 10, 40, 107, and 147 years post-fire. A planted stand aged 26 y was included for tree foliar moisture measurements. Litter and 1 h through 100 h time-lag (TL) fuels were highest in 10 y and 147 y stands, while 1000 h TL fuels peaked in the 10 y old stand and subsequently decreased with time since fire. SDI increased with time since fire, with a maximum observed SDI of 491.9. Duff loading also generally increased with time since fire. A multiple regression model indicated foliar moisture content in Baker cypress was inversely correlated with stand age, and older foliage had significantly lower moisture than younger foliage on individual trees ($R^2 = 0.42$, $p < 0.0001$). Modeled fire behavior peaked in 10 y and 147 y stands in accordance with 1 through 100 h TL fuel accumulations. Results from this study indicate early-successional stages of Baker

cypress forests contain a narrow temporal window wherein stands could burn prior to seed production.

Introduction

Fire is an integral ecological process that drives the presence of serotinous conifers on the landscape (Agee 1993, Sugihara *et al*. 2006). However, the timing of fire can have a profound impact on serotinous plant populations (Zedler *et al*. 1983, Haidinger & Keeley 1993, Keeley & Fotheringham 2000). In the prolonged absence of fire, serotinous species face being outcompeted by later seral-stage species, a process that has been termed "senescence risk". In this scenario, invasion of shade-tolerant, fire-sensitive species increases competition, resulting in mortality of the serotinous species without subsequent regeneration. Conversely, if the time between fires is too short, serotinous species may burn prior to producing a sufficient seed crop, a process that has been termed "immaturity risk" (Keeley *et al*. 1999, Keeley & Fotheringham 2000). Immaturity risk has been well documented in obligate-seeder species that decreased in range after increased wildfire frequency, such as knobcone pine (*Pinus attenuata*; Keeley *et al*. 1999), alpine ash (*Eucalyptus delegatensis*; Bowman *et al*. 2014), hairy-leaf ceanothus (*Ceanothus oliganthus*; Zedler *et al*. 1983), and Tecate cypress (*Hesperocyparis forbesii*; Zedler 1977, De Gouvenain & Ansary 2006). Population models of Tecate cypress determined that fire return intervals shorter than 40 years would result in a substantial population reduction in this rare species (Rodríguez-Buriticá & Suding 2013). The likelihood of fires occurring outside the reproductive lifespan of forests may be low in many forest types, but could become more commonplace in the future. Enright *et al.* (2015) note that climate change-driven increases in fire frequency could increase the probability of immaturity risk, and drought-driven increases in time to stand maturity could lengthen the temporal window of opportunity for immaturity risk to occur.

Past fire exclusion practices have substantially lengthened fire return intervals in many forests types (Parsons & DeBenedetti 1979), though current trends indicate that large wildfire frequency in the western U.S. is increasing (Westerling *et al*. 2006, Dennison *et al*. 2014, Westerling 2016). These changes can be partially attributed to the effects of climate change and uncharacteristically high fuel loading accumulations resulting from fire exclusion (Gilliam & Platt 1999, Johnson *et al*. 2001, Keane *et al*. 2002, Miller *et al*. 2009). As a result, modern wildfires are becoming more difficult to control (Keane *et al*. 2002, Calkin *et al*. 2005, Savage & Mast 2005), and increased temperatures and earlier snowmelt have been associated with a lengthened fire season (Westerling *et al*. 2006, Westerling & Bryant 2008, Westerling 2016). Further, drought and increasing temperatures are expected to continue contributing to increases in fire frequency (Fried *et al*. 2004, Stephens *et al*. 2013) and tree mortality (van Mantgem *et al*. 2009, Allen *et al*. 2010) over the next century.

Detrimental effects of fire regime alterations such as senescence and immaturity risks are magnified for rare serotinous conifers because of their reliance on timely disturbance cycles. Of the species in the *Hesperocyparis* genus (Adams *et al*. 2009), most are rare and sparsely distributed across the western U.S. (Griffin & Critchfield 1972). So, the need for understanding fire regimes in forests of these fire-embracing (Schwilk & Ackerly 2001) species is compounded by their scarcity. Fuels succession chronosequences (Agee & Huff 1987, Schimmel & Granström 1997, Porto *et al*. 2013) provide insight into forest fuel dynamics over time, and by extension, potential fire behavior patterns (van Wagner 1977). However, the literature is lacking in studies of post-fire fuel succession patterns in serotinous conifers, which rely on fires for regeneration.

Predicting potential surface fire behavior in a given forest is dependent on surface fuel loading measurements, as loading is a critical determinant of fire intensity and spread (Rothermel 1972). Surface rate of spread (ROS) and flame length (FL) are most influenced by fuelbed height, fine woody fuels, and live surface fuels, given that moisture content is low enough to facilitate fire spread (Sugihara *et al*. 2006). Coarser fuels ≥1000 h time-lag (TL) are not major drivers of fire spread, but heavily influence intensity and residence time (Sugihara *et al*. 2006). Predictions of crown fire ignition and spread must also account for crown base height (CBH), crown bulk density (CBD), and live fuel moisture content (FMC) (van Wagner 1977, Keyes 2006; but see Alexander & Cruz 2013). However, live FMC is frequently mischaracterized or inaccurately estimated (Varner & Keyes 2009). Previous research has demonstrated FMC varies seasonally and annually, among different species, and across foliar age (Agee *et al*. 2002, Keyes 2006), but the dynamic between stand age and foliar moisture remains poorly understood.

This study addresses the issue of post-fire fuel succession patterns in Baker cypress (*Hesperocyparis bakeri*) forests, investigating surface fuel loading patterns, potential surface fire behavior, and live FMC patterns across a time-since-fire (TSF) chronosequence. Baker cypress is a rare serotinous conifer (Milich *et al*. 2012) classified as “vulnerable” by the International Union for Conservation of Nature (Farjon 2013). Currently, there are 11 extant populations, the oldest of which was roughly 156 y at the time of this study (Merriam & Rentz 2010, Bower & Hipkins 2017). Senescence due to intraspecific competition and a virtual absence of regeneration has been observed at the older sites (Frame 2011, Farjon 2013), and Baker cypress do not produce cones consistently until between 16 y and 26 y (Merriam & Rentz 2010). Presumably, a reburn within this window would cause substantial population size reductions due to immaturity risk. Successful management and effective timing of fuelbed manipulations could be informed by more detailed information on fuel succession patterns in this rare species. The objectives of this study were to i) characterize surface fuel loading by type across a chronosequence of Baker cypress stands ranging from 3 to 147 years, ii) model changes in predicted fire behavior across the stand age chronosequence, and iii) examine changes in live FMC across the stand age chronosequence.

Methods

Site locations

The study took place in north-central and northeastern California, in Shasta, Siskiyou, and Plumas counties (Figure 2.1). Stands were selected to represent a majority of successional stages in Baker cypress ecosystems, as the maximum existing Baker cypress stand age was approximately 156 y at the time of the study (Merriam & Rentz 2010). We selected stand ages which were 3, 10, 40, 107, and 147 y at the time of sampling. Another 26 y old stand, planted as 1-0 plugs in a mitigation effort following the construction of a natural gas pipeline (Kyle Merriam pers. comm.), was adjacent to the 147 y stand. We sampled the 26 y stand as an additional site for the study of foliar moisture, as it offered us the opportunity to compare the tree foliar moisture content of two different stand ages without site variation. However, we excluded it from stand density and fuel loading measurements since it did not represent natural post-fire stand conditions (Figure 2.2). The youngest stand sampled, at 3 y post-fire, burned during the 2014 Eiler fire in Shasta County, California. The 10 y post-fire stand burned in the 2007 Moonlight fire in Plumas County, California. The 40 y and 107 y stands were within the Timbered Crater Baker cypress population, and formed distinct cohorts after burning in the 1987 Horr’s Corner fire and the 1910 Glass Mountain fire, respectively. The 147 y stand in Shasta County has been subject to fire exclusion, and fire information was not available for this site. In this case, we approximate TSF as the oldest tree cored at the site during a stand inventory we conducted the previous year.

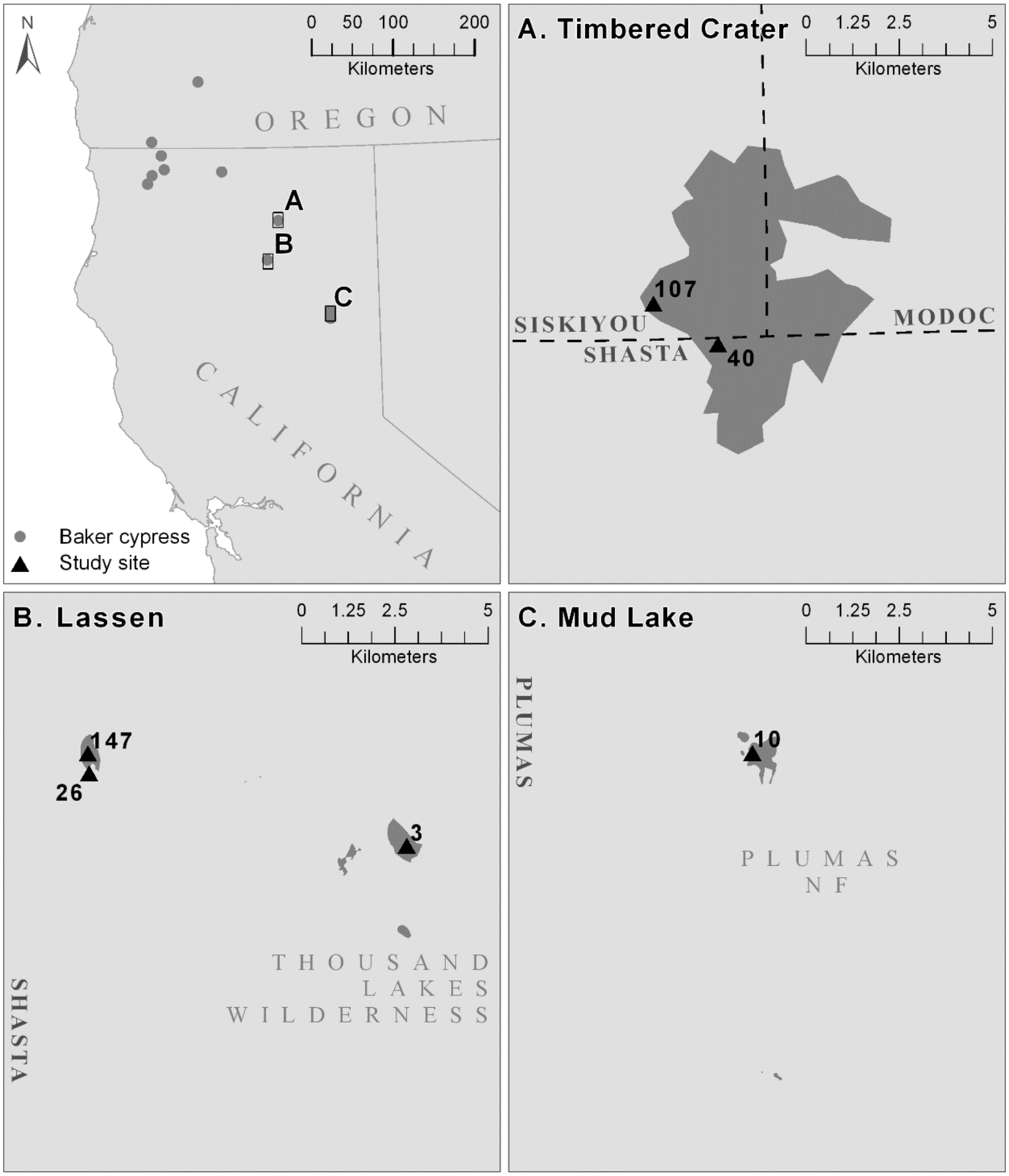

Figure 2.1. The locations of extant Baker cypress populations (locator map; top left panel) and the study sites in California. The 40 y and 107 y stands are located in the Timbered Crater population (A). The 3 y, 26 y, and 147 y stands are located in the Lassen population (B), and the 10 y stand consists of the Mud Lake population (C).

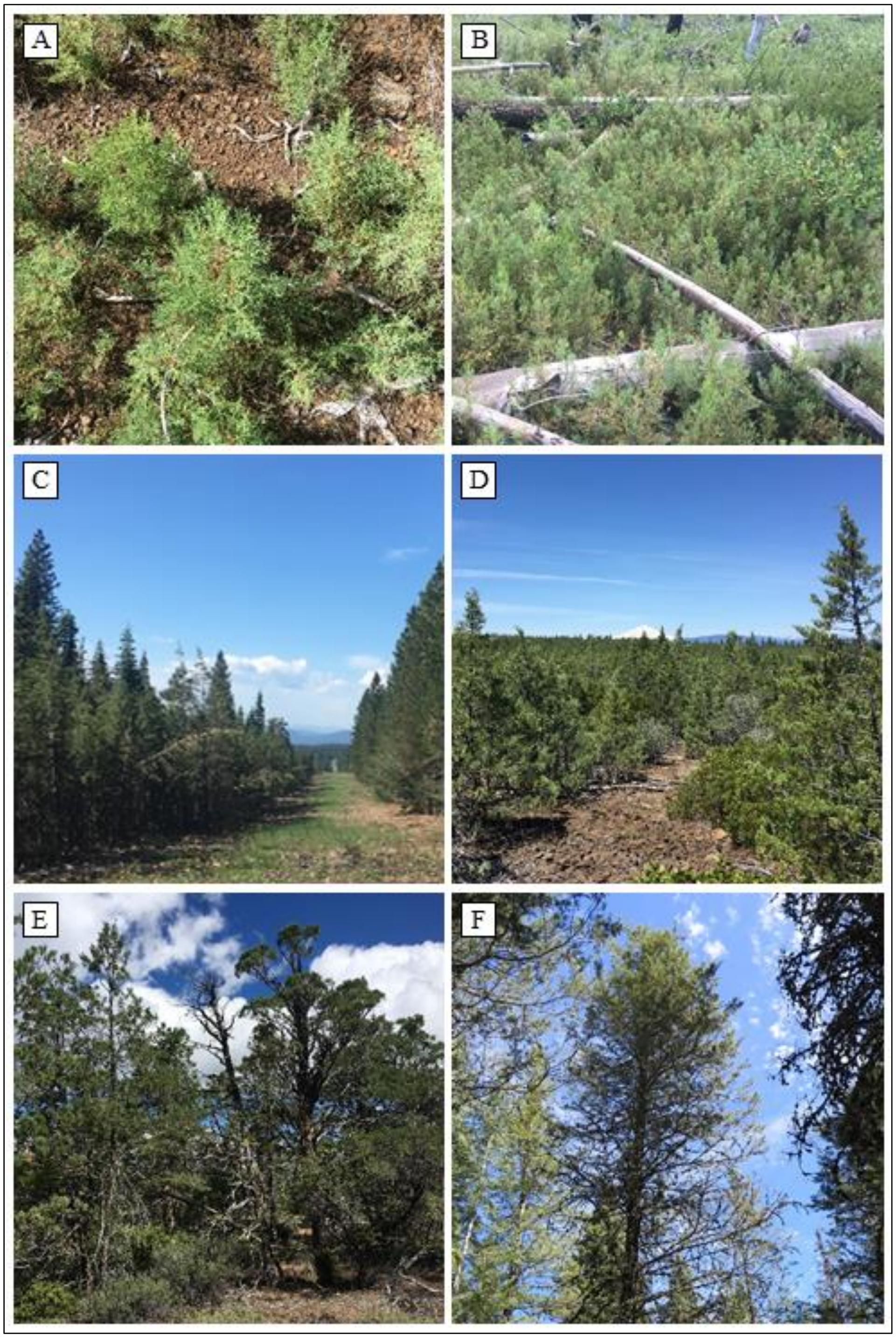

Figure 2.2. Photos representing typical Baker cypress stand conditions in the chronosequence: stand ages include 3 y (A), 10 y (B), 26 y (C), 40 y (D), 107 y (E), and 147 y (F).

We used geographic information systems-based methods to minimize variations in among-site topographical characteristics, while representation of stand ages within the existing age range was maximized. Vector layer data of known fire perimeters from the California Department of Forestry and Fire Protection were overlaid onto the geographical range of Baker cypress forests in northern California (provided by Kyle Merriam, unpubl.) in order to select stand ages. One stand older than available fire records was also used (and TSF was determined to be 147 y using dendrochronological methods). Slope and aspect rasters were derived from United States Geological Survey Digital Elevation Models from the within sites that maximized successional-stage representation, and then raster calculations were used to filter for gentle slopes and generally north-facing aspects. Selected sites exhibited *Arctostaphylos patula* as the dominant or codominant species in the shrub layer, with the exception of the 10 y stand, at which the shrub layer was chiefly *Ceanothus velutinous*.

For comparison, we calculated the stand density index (SDI) of each site via Reineke (1933). The highest SDI of all Baker cypress stands surveyed was 491.9, at the 147 y site in Shasta County (Table 2.1). We observed mortality and declining tree health in this stand, and this SDI is consistent with SDI maximums of other shade-intolerant species (Woodall *et al*. 2005). Therefore, we speculate that this stand was near the maximum possible SDI for Baker cypress.

Table 2.1. Site attributes at each Baker cypress stand measured in the chronosequence.

Fire or Site name	**Age (y)**	**Aspect (Azimuth)**	**Slope (%)**	**Elevation (m)**	**Metric SDI**	**Cones / Tree**
Eiler	3	27	8	1560	0	0
Moonlight	10	5	23	2034	22.3	0
Pipeline[a]	26[b]	336	8	1344	n/a	120
Horr's Corner	40	13	7	1130	93.7	210
Glass Mountain	107	333	1	1098	209.6	240
Burney[a]	147	336	8	1344	491.9	1290

[a] Site name was substituted if a fire name was not available.

[b] Stand was artificially regenerated and therefore excluded from fuel loading and density measurements.

Data collection and calculations

We characterized each site using fixed tree plots and standard mensuration methods. Trees >3 cm DBH were measured for height and diameter at breast height (DBH) in 1/40th ha plots, while trees <3 cm DBH were tallied. In addition to tree measurements, we collected dead downed fuel loading data at all sites using the planar intercept method (Brown 1974). The 147 y site was sampled using a systematic grid design containing 16 tree plots and thirty-two 12 m fuels transects along random azimuths during a stand and fuels inventory conducted at the site in 2016. The remaining sites were sampled in 2017 using 12 tree plots and sixteen 16 m transects per site, which were determined using the "generate random points" tool in ArcMap 10.2 (Esri, Redlands, CA). Transect azimuths were also randomly generated in these surveys. Coarse woody fuels were counted along the full transect lengths, 100 h TL fuels were counted along the first half, and 1 and 10 h TL fuels along the first quarter. Litter and duff depths were measured at the quarter, half, and full mark length of each transect. The highest fuelbed depth was also measured three times per transect on 1 m planes preceding the quarter, half, and full transect length marks. All 1000 h fuels were measured, categorized as rotten or sound, and identified to species. Live surface fuels were collected in 1 m^2 plots at the end of all transects for the Burney site, and at the end of 9 transects for the remaining sites. Collected fuels were separated into woody or herbaceous categories, dried for 72 h at 60°C, and then weighed. Live woody and herbaceous loading was then calculated as the weight of the live fuel type per square meter, and converted to Mg/ha.

We calculated fuel loading (Mg/ha) for 1 h to 100 h TL fuels (Equation 2.1) and 1000 h TL fuels (Equation 2.2) following Brown's (1974) assumptions for particle diameters and specific gravities of conifers. Given that *n* signifies the number of particles intercepted, *d* is the particle diameter, *s* is the particle specific gravity, *a* is the particle angle correction factor, and *Nl* is the transect length. Litter and duff were calculated (Equation 2.3), given *D* represents depth in meters and BDV is the bulk density value in kilograms per cubic meter. As no BDV for Baker cypress was available in the literature, we used the average values for both duff (173.7) and litter (118.6) from the scale-needled conifers described in a study of Sierra Nevada conifers (van Wagtendonk *et al*. 1998).

Equation 2.1: $$Fine\ Fuel\ Loading\ (Mg/ha) = \frac{\left(1.234*n*d^2*s*a*\left(\sqrt{1+\left(\frac{\%\ slope}{100}\right)^2}\right)\right)}{Nl}$$

Equation 2.2: $$Coarse\ Fuel\ Loading\ (Mg/ha) = \frac{\left(1.234*\sum d^2*s*a*\left(\sqrt{1+\left(\frac{\%\ slope}{100}\right)^2}\right)\right)}{Nl}$$

Equation 2.3: $$Litter\ \&\ Duff\ Loading\ (Mg/ha) = (D * BDV) * 10$$

In 2017, one collection of live foliage was gathered from ten trees at each of the six sites between the 14th and 17th of August, which is within the dry part of the fire season for this region (Knapp *et al*. 2009). From the ground, we also counted the cones on each tree using binoculars when needed. Live foliage samples were collected below 2 m from the south side of each tree to minimize variations associated with crown position (Richardson *et al*. 2000). All sampling was done between 1200 and 1600 hours to limit variation caused by daily moisture fluctuations (Philpot 1963, Gary 1971, Zahn & Henson 2011). New spring foliage was separated from older foliage, meaning two samples were collected for each sample tree in order to account for established differences in FMC amongst foliage ages (van Wagner 1967, Chrosciewicz 1986). Live foliage samples were also collected from 10 specimens of the dominant shrub types at each site in the same manner as the trees (or, from 5 samples of both shrub types per site for codominant shrub understories). Foliage samples were sealed within airtight plastic bags and kept on ice until processing, following the methods of Zahn & Henson (2011). The wet weight of each sample was obtained by subtracting the empty bag weight from the weight of the sealed bag containing foliage (W_l). Subsequently, all samples were dried for 72 h at 60°C and reweighed (W_d). Fuel moistures are expressed as percentages, and calculated using Equation 2.4 (Gary 1971).

Equation 2.4: $$Fuel\ Moisture\ Content\ (\%) = \frac{W_l - W_d}{W_d} * 100$$

Modeling and statistical analyses

Fuel loading patterns across TSF were modeled using local polynomial regression fitting (Loess); a nonparametric predictive modeling method used for characterizing nonlinear patterns. Loess model predictions were made at 1 y increments from 0-150 y TSF for each fuel type including duff, litter, and 1 through 1000 h TL fuels. The models show predicted decreases (presumably decay) in surface fuel loads based on known differences in fuel inputs over time, although actual decay rates of Baker cypress wood are not known.

Values from each site for dead woody fuel loading, live woody and herbaceous fuel loading, and live understory moisture data were used in assigning values to fire behavior models within BehavePlus (Heinsch & Andrews 2010) to compare potential surface fire behavior across stand ages dating from TSF in Baker cypress. For modeling purposes, litter loading was aggregated with 1 h TL fuel loading. Fire behavior models were run with slope values held constant at the average across all sites in all models at 8 percent, and wind speeds at 10 km/h. Dead fuel moistures were assumed to be between “low” and “very low” (Scott & Burgan 2005), at 4.5 percent, 5.5 percent, and 6.5 percent for 1, 10, and 100 h fuels TL, respectively. All other model parameters were initialized from fuel model 184 (Scott & Burgan 2005). To account for possible variation in conditions among the sites, we also tested two alternate scenarios. In one scenario, we adjusted the live woody moisture parameter of the 10 y stand to be the average FMC of the Baker cypress foliage instead of the shrub layer FMC, as Baker cypress regeneration was crowded and may have acted as a shrub fuel in parts of this stand (Figure 2.2). Second, we adjusted wind speed to 5 km/h in the 147 y stand to account for increased drag introduced by the denser canopy (Agee & Huff 1987).

Live FMC patterns across stand and foliage ages in Baker cypress were analyzed using a multiple regression model. Two other regression models were also used to assess the effects of stand age and foliage age on live FMC separately. We compared the models based on change in Akaike Information Criterion (ΔAIC), which is a commonly-used indicator of model quality relative to other models (Burnham & Anderson 2004), and selected the top model based on lowest AIC value. Foliar moisture content data were logarithmically distributed, and therefore log-transformed in order to meet parametric model assumptions. Model predictions of FMC values across stand ages were back-transformed to increase interpretability in visual plots. Statistical analyses were conducted in the R environment (R Core Team 2018).

Results

Fuel succession patterns and fire behavior models

Litter and 1 through 100 h fuel loading peaked in the 10 y and 147 y stand ages (Figure 2.3; Table 2.2), but were lowest initially (in the 3 y stand) and in the 40 y and 107 y stands. Coarse woody fuels were low initially, and peaked in the 10 y stand. After 10 y, coarse woody fuel loading followed a decreasing trend. No duff was observed in the 3 y stand, indicating complete consumption, after which duff loading increased with TSF. Live shrub loading was highest at ages 10 y and 107 y TSF, while herbaceous fuel loading was highest in the 3 y stand age by a wide margin, but low otherwise. Potential ROS and FL in Baker cypress followed similar trajectories as observed for fine fuels, peaking in the 10 y and 147 y ages TSF (Figure 2.4). The parameter adjustment of increased live woody moisture (which assumed the FMC of the small Baker cypress trees instead of the shrub layer) in the 10 y stand modestly decreased expected fire behavior. In this scenario, ROS dropped from 5.4 m/min to 4.4 m/min, and FL decreased from 2.7 m to 2.4 m. When we adjusted wind speed in the 147 y stand, expected ROS decreased from 8.2 m/min to 3.4 m/min, and FL from 2.8 m to 1.9 m. Modeled fire activity was low and nearly identical in the 3 y and 40 y stands. However, ROS and FL more than doubled between the 3 y and 10 y stands, even when site conditions were adjusted.

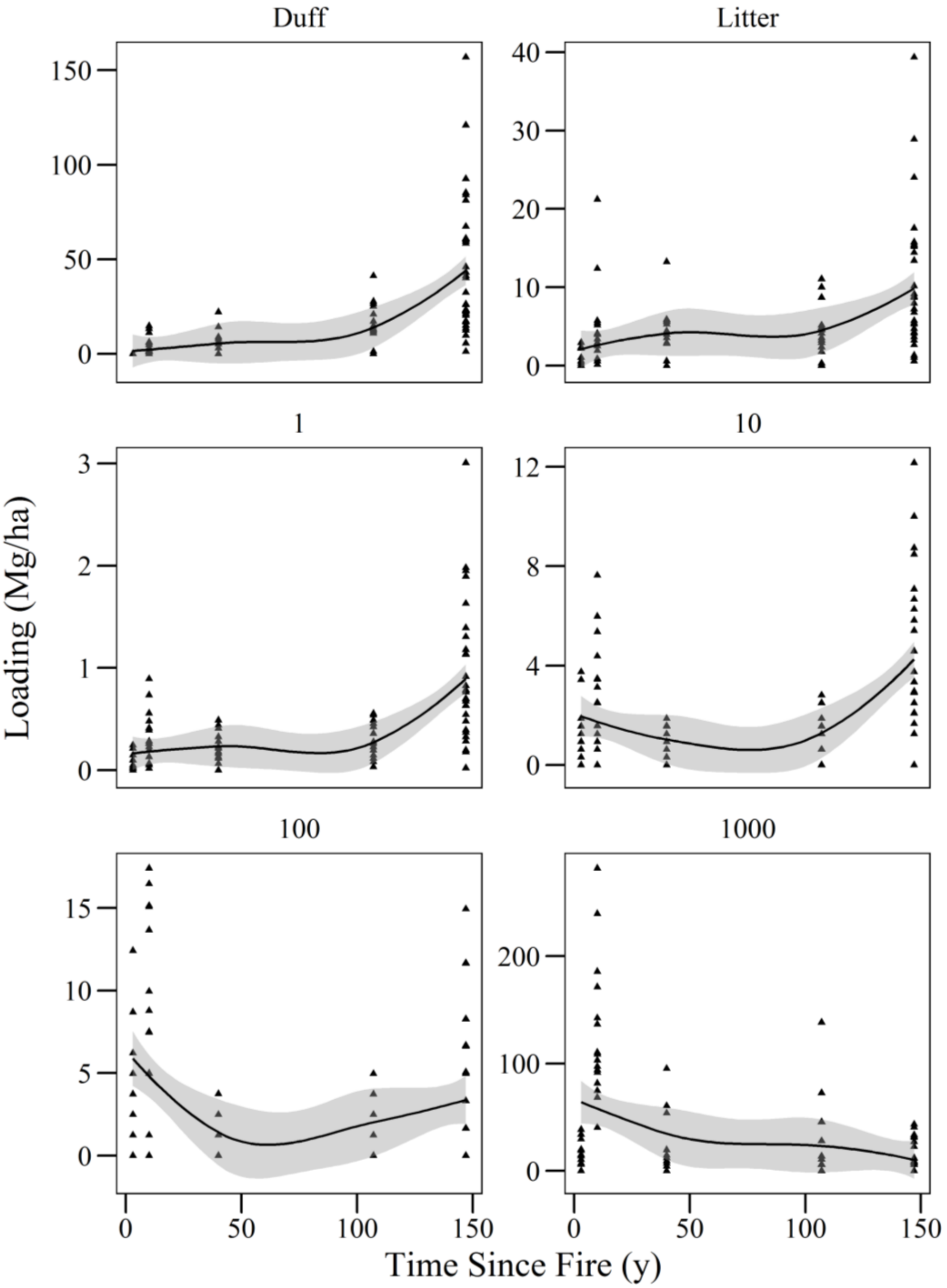

Figure 2.3. Fuel loading changes by fuel type with time since fire for Baker cypress stands in northern California. Solid lines represent local polynomial regression fitting (Loess) models: shaded areas represent 95 percent confidence intervals.

Table 2.2. Fuel profiles observed by stand age in the time since fire (TSF) chronosequence of Baker cypress forests. Values were used to parameterize fire behavior models. Values in parentheses are standard error.

TSF (y)	**3**	**10**	**40**	**107**	**147**
Dominant shrub genus	*Arctostaphylos / Ceanothus*	*Ceanothus*	*Arctostaphylos*	*Arctostaphylos / Purshia*	*Arctostaphylos*
Shrub FMC (%)	101.81 (2.84)	104.27 (2.36)	84.98 (3.77)	73.82 (1.44)	107.16 (2.82)
Fuelbed Height (cm)	20.3	31.2	6.6	6.6	19.5
Live Herb Mg/ha	0.5791 (0.25)	0.0042 (<0.01)	0.0162 (0.01)	0.1741 (0.07)	0.0146 (<0.01)
Live Shrub Mg/ha	2.62 (0.80)	9.74 (2.97)	2.76 (2.06)	8.85 (5.14)	0.86 (0.31)
Duff Mg/ha	0.00 (0.00)	8.21 (2.40)	9.77 (3.06)	27.39 (5.99)	86.35 (12.41)
Litter Mg/ha	1.63 (0.67)	12.45 (3.56)	9.66 (2.25)	12.08 (2.10)	26.51 (4.07)
1's Mg/ha	0.07 (0.02)	0.31 (0.06)	0.2 (0.04)	0.27 (0.04)	0.90 (0.11)
10's Mg/ha	1.11 (0.30)	2.87 (0.53)	0.74 (0.16)	1.29 (0.26)	4.25 (0.48)
100's Mg/ha	3.26 (0.88)	8.29 (1.45)	0.55 (0.28)	2.02 (0.44)	3.37 (0.63)
1000's Sound Mg/ha	12.03 (3.25)	118.07 (12.75)	10.01 (4.10)	14.37 (5.34)	9.49 (2.35)
1000's Rotten Mg/ha	0.00 (0.00)	8.65 (4.25)	7.27 (2.90)	8.84 (4.07)	0.82 (0.39)

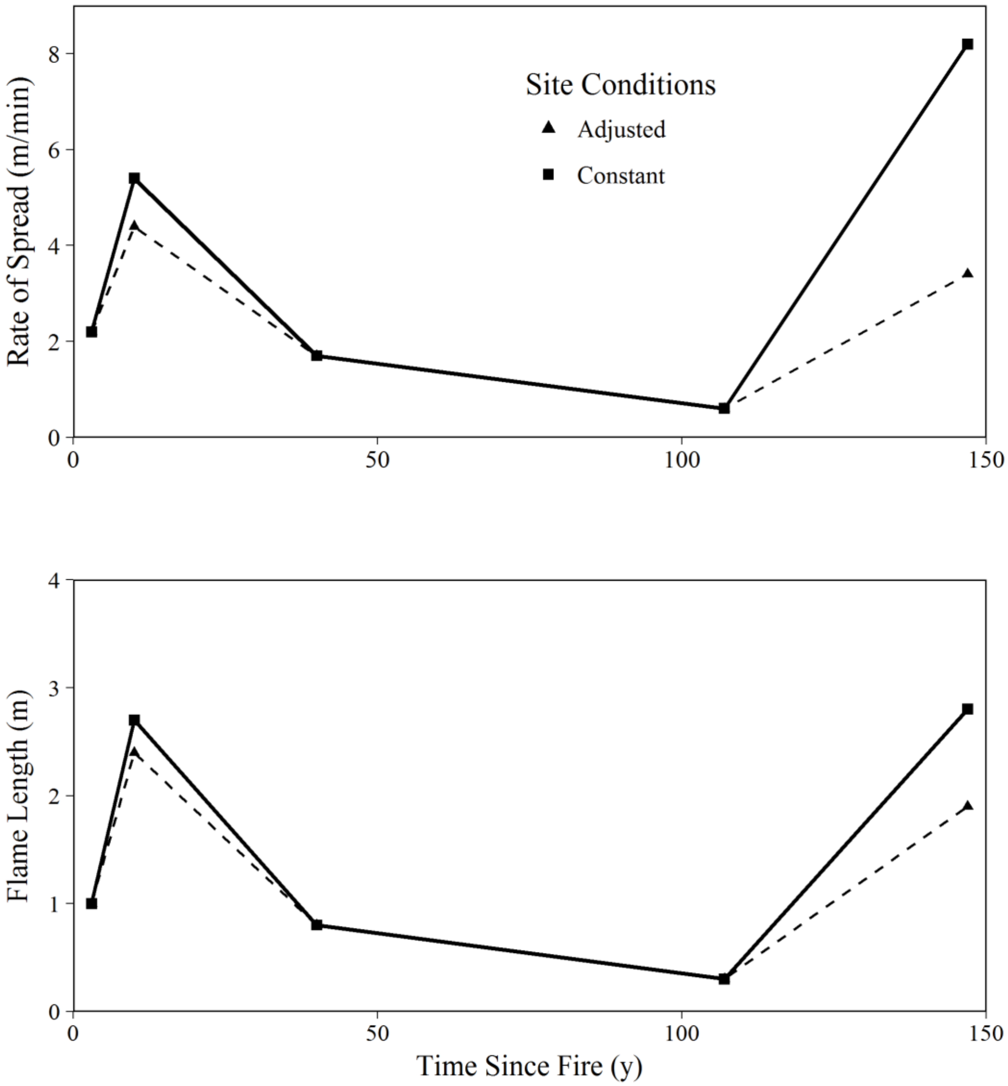

Figure 2.4. Modeled surface fire behavior in Baker cypress stands at various post-fire stand ages (y) in terms of rate of spread (m/min) and flame length (m) based on predictions from BehavePlus. Parameter adjustments to account for possible variations in among-site conditions are shown (dashed line and triangle) in the 10 y and 147 y stands. The adjustment in the 10 y stand substituted the FMC of the Baker cypress trees for the FMC of the shrubs in the live woody moisture parameter. The adjustment in the 147 y stand decreased the wind speed parameter from 10 km/h to 5 km/h.

Models of live fuel moisture across stand ages

In 2017, we sampled live foliage of Baker cypress in six stand ages and analyzed trends in live FMC using a multiple regression model which accounted for changes in stand age and foliage age (AIC = -23.17; Table 2.3). The multiple regression model indicated the relationship between live FMC and stand age was significant ($R^2 = 0.42$, $p < 0.0001$; Table 2.4). The model also indicated live Baker cypress FMC exhibited significant differences between foliage <1 y old and >1 y old ($p < 0.0001$; Figure 2.5). When the effects of stand age and foliage age on live FMC were separately tested, they were also significant ($p < 0.0001$), though the top model (with the lowest AIC) accounted for both independent variables (Table 2.3). Among all stand ages in 2017, the highest FMC values were observed in the 3 y seedlings, averaging 150.0 percent (±7.00 SE). In the 148 y stand, live FMC values averaged 102.5 percent (±5.11 SE). Live FMC values were noticeably lowest in the 40 y stand, averaging 80.5 percent (±3.29 SE). Live FMC values from the dominant shrub type at each site indicated that shrub FMC was highest at the 147 y stand and lowest in the 107 y stand (Table 2.2).

Table 2.3. Covariate combinations of the regression models which test the effects of stand age and foliage age on live foliar moisture content in Baker cypress. The lowest Akaike's Information Criterion (**Δ**AIC) value was used for selecting the most appropriate (top) model.

Model	**AIC**	**ΔAIC**	R^2	p
Stand Age + Foliage Age	-23.17	0	0.42	<0.001
Stand Age	9.98	33.15	0.22	<0.001
Foliage Age	13.7	36.87	0.2	<0.001

Table 2.4. The summary table of the top model used to assess the effects of foliage age and stand age on live foliar moisture content in Baker cypress. *F*-statistic = 42.44 on 2 and 117 degrees of freedom, ($R^2 = 0.42$, $p < 0.0001$).

Coefficients	**Estimate**	**SE**	***t*-statistic**	***p***
Intercept	4.9592	0.0345	143.7	<0.001
Stand Age	-0.0025	0.0004	-6.7	<0.001
Foliage Age >1 year	-0.2489	0.0393	-6.3	<0.001

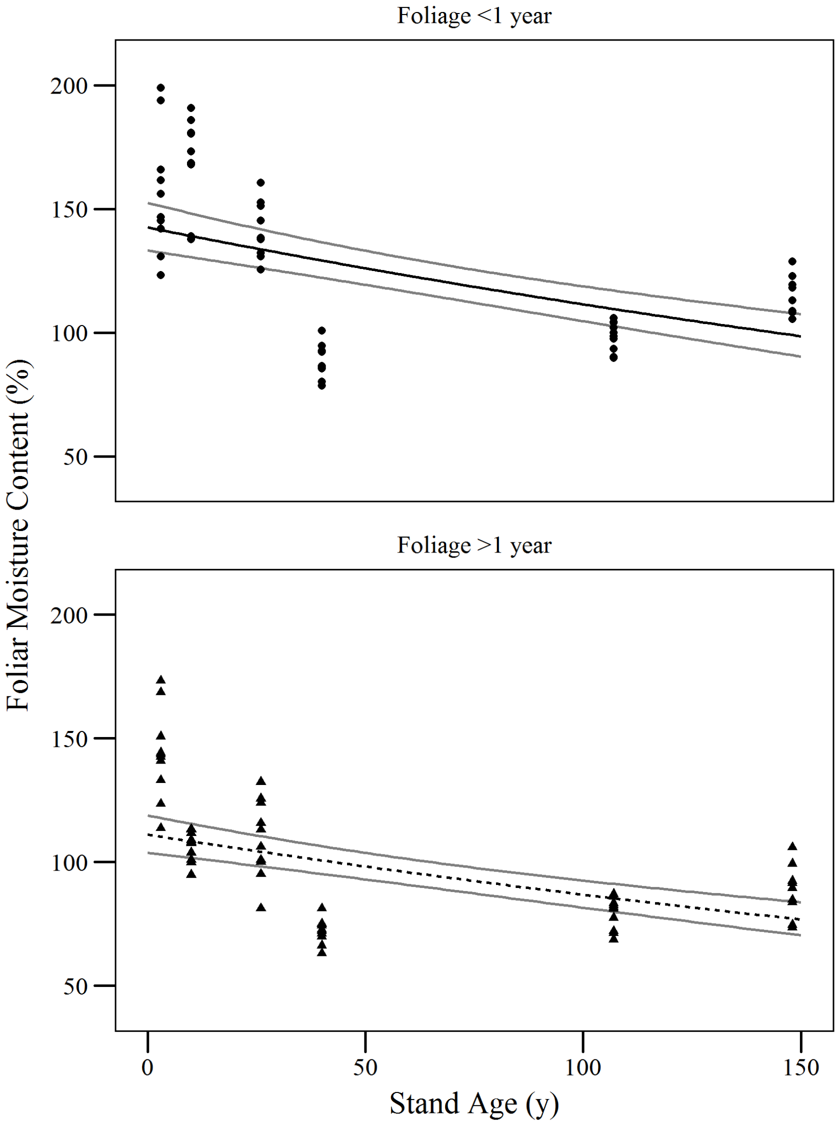

Figure 2.5. The prediction made by the top model of younger (<1 y) and older (>1 y) live foliar moisture content (percent) per year across the stand age chronosequence in Baker cypress. Semi-transparent lines denote 95 percent confidence intervals.

Discussion

Surface fuel loading and fire behavior patterns

There is a noticeable dearth of available information regarding fuel succession trends in rare serotinous forest types. Given that the natural regeneration of these forests is fire-dependent and fire behavior predictions are heavily influenced by fuel loading, this knowledge informs conservation management actions. In this study, the first major surface fuel contributions resulted from the natural falling of fire-killed snags, as observed during the substantial pulse of 1 through 1000 h TL fuels in the 10 y stand. Duff increased with TSF, while litter inputs behaved more similarly to the fine fuels with TSF. Decay rates for Baker cypress are not known, though decreased fuel loads in the 40 y through 107 y stands likely reflect the rate of dead woody fuel decay outpacing inputs from other sources. The second major contribution to dead woody surface fuel loading was likely the result of competition-induced mortality, as seen in the form of increasing fuel loads in the 147 y stand. The SDI was highest in the 147 y stand, at 491.9, which is consistent SDI maximums of other shade-intolerant species (Woodall *et al*. 2005), and may be approximately the SDI maximum for Baker cypress.

The increase of fine fuel inputs observed in the 10 y stand corresponded predictably with increased fire behavior. Both ROS and FL were predicted to be highest in the 10 y and 147 y stands. Interestingly, a similar study of fuel succession in western hemlock (*Tsuga heterophylla*) / Douglas-fir (*Pseudotsuga menziesii*) forests predicted an increase in potential surface fire behavior between 1 and 3 y TSF (Agee & Huff 1987). A subsequent reduction in fire behavior was predicted until 110 y TSF in the western hemlock / Douglas-fir forest, followed by a gradual increase to the end of a 515 y post-fire chronosequence (Agee & Huff 1987). Our models also predicted this steep increase in potential surface fire behavior during the first post-fire decade, followed by a reduction in fire behavior until 107 y post-fire in the Baker cypress forest type. At 147 y post-fire, fire behavior had increased again, probably resulting from maximum density and a stem-exclusion phase being reached. Notably, both Baker cypress and western hemlock / Douglas-fir forests exhibit high severity (>75 percent mortality) historical fire regimes (Hann & Bunnell 2001, Sugihara *et al*. 2006, Merriam & Rentz 2010). Though, with the maximum age of existing Baker cypress being approximately 156 y, the natural span of Baker cypress seral stages is likely shorter than the larger, longer-lived species such as western hemlock and Douglas-fir.

The task of managing fire-prone forests has become complicated by the onset of rapid climate change (Stephens *et al*. 2013) and changing fire regimes (Westerling *et al*. 2006, Westerling 2016). Time to stand maturity is also expected to increase as a result of intensified droughts in these forests (Enright *et al*. 2015). However, detrimental impacts can be minimized provided there is enough information to enact informed strategies (Noss *et al*. 2006, Flannigan *et al*. 2009). Rare species are of particular concern. In the case of Baker cypress, reburn of stands within the temporal window before cones are produced would likely eliminate the stand. Our results suggest this scenario is possible in this forest type. The probability of reburn before stand maturity is reached could be relatively low, but could increase in the future due to climate change (Enright *et al*.

2015). When we adjusted the fire behavior model to test for the effects of higher live FMC in the 10 y stand, (which was crowded with small trees approximately the same size as shrubs), fire behavior was only modestly reduced.

At what age Baker cypress begins consistent cone production is not well documented, though this information could refine the interpretation of this study. Anecdotally, we witnessed a couple of 10 y old Baker cypress with a seed cone (among thousands observed in a non-systematic manner while traversing the site) at the Mud Lake population. However, none of the trees in our sample were cone bearing until 26 y, at which point the average amount of cones per tree was approximately 120. Merriam & Rentz (2010) observed trees 16 years old that did not yet bear cones, so consistent cone production in Baker cypress probably does not occur for roughly two decades. As demonstrated by our study, fuel profiles in these forests within this temporal window could carry fire. Regions where Baker cypress exist are currently undergoing an increasing trend of area burned per year (Westerling *et al*. 2006, Dennison *et al*. 2014) with most ignitions caused by humans and lightning (Komarek 1968, Stephens 2005, Westerling 2016). Future studies of fuel succession in closed-cone forests coupled with detailed information about the ages at which cones are produced would greatly increase our understanding of immaturity risk in rare serotinous conifers, and help inform interventions that could prevent population losses.

Live foliar moisture patterns

Trends in FMC observed in our study agreed with the anticipated difference between younger and older foliage on a tree (van Wagner 1967, Chrosciewicz 1986), in that FMC was lower in older foliage than younger foliage. However, a unique trend was observed, in that live FMC in Baker cypress generally decreased with stand age. We have not attempted to determine mechanisms driving this relationship, but possible mechanisms could be increased competition for water (we observed only increases in SDI as stands aged), changes in foliar morphology with tree age (Apple *et al*. 2002), or both. If the trend of decreasing FMC with stand age is true in other fire-prone forest types, it could have implications for predicting crown-fire ignition in those forests, and model accuracy may be increased by accounting for stand age.

While the higher FMC in younger Baker cypress trees may modestly reduce fire behavior, we would still expect their mortality in the case of a fire, because modeled FL was taller than any living Baker cypress at that site. Live FMC below 100 percent is associated with higher likelihood of crown fire behavior (Woodward et al. 1983, Agee 1993), and we observed live FMC values for Baker cypress ranging between 63.1 percent and 198.9 percent in this experiment. Our samples recorded average FMC levels lower than 100 percent for all foliage greater than 1 year old in stand ages 40 and older, suggesting higher ignitability in the older trees. Crown fire in mature Baker cypress forests may have been a natural part of the fire regime pre-exclusion, and high-severity crown fire has been associated with dense regeneration in the species (Merriam & Rentz 2010).

References

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SUMMARY

Chapter 1 demonstrated the spatial limitations to Baker cypress dispersal. The seedling shadow we observed following the Eiler fire was in general agreement with the seed dispersal curve predicted by the mechanistic model of anemochory. This suggests that secondary dispersal of the Baker cypress seeds, which would increase dispersal distances, was probably minimal at the site. Overall, this dispersal constraint in Baker cypress is an attribute that is probably shared by the other endemic serotinous cypress species that exist as scarce metapopulations and exhibit wingless or marginally winged seeds. Short seed dispersal modeled in the species will spatially impede its ability to occupy new spaces or track shifts in suitable habitat as the climate changes. While competitive in fire-prone environments, the range expansion event we observed in this species was restricted mainly to 2 years following the wildfire. Compared to species that can establish a new cohort (and therefore expand their range) each year, heavily fire-dependent conifers may be not be able to pace spatial shifts in their suitable habitat as easily, since they depend on wildfire events and a subsequent period of growth and cone development which takes roughly a quarter-century.

Chapter 2 found a combination of elevated surface fire potential and inadequate (or absent) cone crops in early-seral Baker cypress stands, meaning they could risk burning prior to reaching reproductive age. The remaining populations of Baker cypress are widely spaced, and all are small enough to completely burn in a single wildfire (as the

Seiad population did in 2017, and the Mud Lake population did in 2007). Since complete reburn during early seral-stages is possible, whole populations could be lost in a single event. This refinement in understanding of the fuel succession patterns and life history processes in Baker cypress forests can inform management decisions regarding their conservation, such as timing of fuel treatments. Fuel loading and fire behavior potential are expected to decrease for a period of time following the initial fuel loading input from fire-killed trees seen in the 10 y stand. In the oldest stand we observed, at approximately 147 years TSF, potential surface fire behavior had once again increased, probably resulting from competition-induced mortality (from high SDI) and increased aboveground biomass. Silvicultural removal of interspecific competition in Baker cypress forests would likely improve their health extend their lifespan. Further, managed wildfires in stands older than 40 y TSF could be allowed, as the cone crops in these stands had matured. Future work could include a detailed record of *Hesperocyparis* stand ages and the average number of cones observed on a sample of trees in each. Coupled with further studies of fuel succession, this information could clarify courses of action for conservation management of rare serotinous conifers.