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Post-fire fuel succession in a rare California, USA, closed-cone conifer

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Abstract

Background: Increasing frequency and size of wildfires over the past few decades have prompted concerns that populations of obligate seeding species may be vulnerable to repeat, short-interval fires that occur prior to these species reaching maturity. The susceptibility of populations to this risk is partially dependent on the amount and characteristics of fuel loading over time and their influence on fire behavior and effects. This study characterized fuel dynamics and modeled fire behavior across a time-since-fire chronosequence in stands of the rare, serotinous conifer, Baker cypress (*Hesperocyparis bakeri* [Jeps.] Bartel), ranging in age between 3 and 147 years post fire.

Results: Litter and fine woody fuel loading (1- to 100-hour) were highest in the 10-year-old and 147-year-old stands, while coarse fuel loading (1000-hour) peaked in the 10-year-old stand and subsequently decreased with time since fire. Duff loading consistently increased with time since fire. Cone production had not occurred in the first 10 yr of stand development. Foliar moisture content in Baker cypress was inversely correlated with stand age, and older foliage had lower moisture content than younger foliage. Modeled surface fire behavior was highest in the 10-year-old and 107-year-old stands in accordance with higher litter, fine woody fuel, or shrub fuel accumulation. While foliar moisture content was higher in younger stands and influenced the critical fireline intensity, we did not observe changes in fire type.

Conclusions: Fine-fuel loading in Baker cypress stands followed a U-shaped pattern over time (first decreasing, then stable, then increasing), consistent with findings in other forests with stand-replacing fire regimes. Our results indicated that early-successional stages of Baker cypress forests have sufficient fuels to allow for the spread of wildfire and 10-year-old stands could burn with substantive fire behavior prior to cone production. Whenever possible, we recommend suppressing wildfire in stands less than 20 yr old to avoid substantial decreases or local extirpation of these rare Baker cypress populations. Our results highlight the importance of knowing the cone production patterns, fuel dynamics, and corresponding fire behavior over the development of obligate-seeder species to assess the risk of population loss due to short-interval fires.

Keywords: Baker cypress, fuel chronosequence, fuel loading, fuel succession, *Hesperocyparis bakeri*, immaturity risk, senescence risk, serotiny

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Resumen

Antecedentes: El incremento en la frecuencia y tamaño de los incendios en décadas pasadas han causado preocupación sobre las poblaciones de especies que se reproducen estrictamente por semillas y que pueden ser vulnerables a fuegos repetidos a intervalos de tiempo cortos antes de que las mismas lleguen a su madurez. La susceptibilidad de las poblaciones a este riesgo depende parcialmente de la cantidad y características de la carga de combustible en el tiempo, y de su influencia sobre el comportamiento y efectos del fuego. Este estudio caracterizó la dinámica de los combustibles y modeló el comportamiento del fuego a través de una cronosecuencia después de incendios en rodales de una especie de conífera rara y serótina llamada ciprés de panadero (Baker cypress, *Hesperocyparis bakeri* [Jeps.] Bartel), cuyo rango de edades era desde 3 y hasta 147 años después de los incendios.

Resultados: El mantillo y los combustibles leñosos finos (1 a 100 h) fueron los mayores en los rodales de 10 y 147 años, mientras que los combustibles gruesos (1000 h) tuvieron un pico en los rodales de 10 años y decrecieron subsecuentemente con el tiempo en el post-fuego. La carga de hojarasca en descomposición (*i.e.*, duff) se incrementó consistentemente desde el momento del incendio. La producción de conos no ocurrió en los 10 primeros años post-fuego del desarrollo del rodal. El contenido de humedad foliar el ciprés de panadero se correlacionó inversamente con la edad del rodal, y las hojas más viejas tuvieron menor humedad que las nuevas. El comportamiento del fuego modelado en superficie fue mayor en los rodales de 10 y 107 años de acuerdo a la mayor carga de mantillo, material leñoso fino y acumulación de combustible de arbustos. Aunque el contenido de humedad foliar fue más alto en rodales más jóvenes e influenció la intensidad crítica de línea, no observamos cambios en el tipo de fuego.

Conclusiones: La carga del combustible fino en rodales de ciprés de panadero siguió en el tiempo una curva patrón del tipo U (primero decreciendo, luego estable, y posteriormente incrementándose), lo que es consistente con los resultados encontrados para otros bosques con regímenes de fuego que implican el reemplazo total de los rodales. Nuestros resultados indican que en los primeros estadios sucesionales post-fuego los rodales de ciprés de panadero tienen suficiente combustible como para permitir la propagación del fuego, y que rodales de 10 años de edad pueden arder con un comportamiento de mucha intensidad previo a la producción de conos. En lo posible, recomendamos suprimir los incendios en rodales menores a los 20 años de edad para evitar reducciones sustanciales o extinciones locales de estas poblaciones raras de cipreses de panadero. Nuestros resultados subrayan la importancia de conocer los patrones de producción de conos, la dinámica de los combustibles, y el correspondiente comportamiento del fuego de especies que se reproducen estrictamente por semillas, para determinar el riesgo de pérdidas de estas poblaciones debidas a los intervalos de fuego muy cortos.

Introduction

The quantity, quality, and arrangement of live and dead fuels in fire-prone forests are important drivers of fire behavior and effects. In many forest types, these fuel characteristics vary dramatically over time, a process referred to as fuel succession (Fahnestock 1976). Understanding the patterns of fuel succession can aid managers in making wildfire response decisions and developing better fuel management plans to meet resource objectives (Davis et al. 2009), such as managing for the persistence of rare, fire-dependent species. Given ongoing shifts in fire regime characteristics associated with climate change (Westerling 2016; Parks et al. 2017), managers must increasingly rely on fuel succession patterns to make informed decisions.

Fuel succession patterns in fire-prone forests are reflective of fire behavior and effects and the subsequent ability of fuels to accumulate over time. Few studies have examined longer-term fuel succession patterns following fire, but previous research has highlighted substantial variation within and among forest types (Brown and See 1981; Lotan et al. 1985). In forests that experience a high-severity fire, post-fire fuel succession typically has pulses of fine fuel accumulating during the early and late stages of stand development (Fahnestock 1976; Agee and Huff 1987; Kashian et al. 2013). However, other studies conducted in forests characterized by similar fire regimes, but with different climates, have found slower fuel recovery rates. In boreal forests of northern Sweden, fine fuel loading was slow to accumulate in the short term (<30 yr) but progressively increased until reaching a steady state (Schimmel and Granström 1997). In subalpine forests of Yellowstone National Park, USA, fine-fuel loading was persistently low and contributed to limited fire potential over the first 100 yr (Romme 1982). The slower accumulation of fuels over time following a high-severity fire in these ecosystem types is likely due to greater consumption of fine fuels in the fire-killed trees or slower vegetative regrowth that occurs in cooler, higher-latitude climates. By contrast, research examining subalpine forest stands between 22 and 258 yr in Alberta, Canada, found that fine-fuel loading was highly variable over stand age and demonstrated that fire

weather had a greater direct effect on resulting fire behavior than fuel loading or stand age (Bessie and Johnson 1995).

Previous studies have focused primarily on surface and crown fuel loading changes with time since fire, while far less attention has been given to factors that may influence the moisture content of live fuels (Jolly and Johnson 2018). Changes in the live-fuel moisture content of shrubs and trees at different stand development stages may influence potential fire behavior. In fact, some young or recently burned stands experience a period of limited fire spread, presumably due to insufficient fuel (Romme 1982; Parks et al. 2015) or high live-fuel moisture (Catchpole and Catchpole 1991; Davies et al. 2009). Conversely, some ecosystems lack a strong fuel-age limitation in the recurrence of fire (Keeley et al. 1999a; Moritz et al. 2005). For instance, fire hazard in young chaparral stands (≤20 yr) was ~2.4% while fire hazard in 60-year-old stands only increased to ~4.9%, indicating that fire-weather conditions (*e.g.,* Santa Ana winds) or sufficient vegetation regrowth (*e.g.,* resprouting or fire-obligate shrubs) were more influential in promoting fire spread (Moritz et al. 2005). While it is widely known that new foliage has higher moisture content than older foliage (Agee et al. 2002; Keyes 2006), we are unaware of studies that have examined patterns of foliar moisture content with time since fire (*i.e.,* stand age).

Given the recent shifts in many western US fire regimes toward more frequent and larger, high-severity fires (Miller et al. 2009; Westerling 2016; Parks et al. 2017), the persistence of certain species has become a point of concern (Turner 2010; Buma et al. 2013), especially for obligate-seeding species that take a long time to reach sexual maturity. While the prolonged absence of fire in obligate seeders can allow overstory transition to more shade-tolerant species (*i.e.,* senescence risk), obligate seeders could also burn prior to the onset of seed production, eliminating the stand (*i.e.,* immaturity risk; Keeley et al. 1999b). Previous studies have documented immaturity risk in many obligate seeders for which short-interval (<40 yr) fires caused substantial decreases in populations (Zedler 1977; Zedler et al. 1983; Keeley et al. 1999b; de Gouvenain and Ansary 2006; Bowman et al. 2014; Fairman et al. 2017). The potential for immaturity risk to occur is partially dependent on how rapidly plants reach reproductive maturity (*e.g.,* Enright et al. 1996). While some species produce reproductive structures quickly, many tree species can take a decade or more to do so. Information that characterizes the time to maturity in most species is largely lacking but is essential to determine the potential for immaturity risk under changing fire conditions. Along with increases in fire frequency, increased temperatures associated with climate change may result in extending the time to maturity (*i.e.,* the time it takes an individual to produce viable seeds) due to reduced water availability, slowing

growth, and thus potentially extending the duration of immaturity risk (Buma et al. 2013; Enright et al. 2015). However, the frequency with which these events might occur is unknown for most areas and previous observations of immaturity risk may simply represent accounts of low-probability events. Thus, understanding fuel and fire behavior changes can provide further insight into the potential impacts following a short-interval fire.

Baker cypress (*Hesperocyparis bakeri* [Jeps.] Bartel) 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 and disjunct populations, with the oldest stand approximately 156 years old at the time of this study (Merriam and Rentz 2010; Bower and Hipkins 2017). Given their serotinous character, retention of lower branches, relatively even-aged structure, and other characteristics, Baker cypress forests are typically classified as having a low-frequency, high-severity fire regime (Skinner and Taylor 2018), although fire history studies quantifying the fire regime characteristics for this species have not been conducted. Following fire, mature Baker cypress will typically die because the heat is sufficient to kill the cambium beneath their thin bark. The heat of the fire also serves to release seeds from the serotinous cones that disperse onto fire-exposed mineral soil and facilitate the establishment of the next cohort. Forest types adjacent to Baker cypress are quite varied, with some having more frequent, low- to mixed-severity fire regimes, such as mixed-conifer, ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), and red fir (*Abies magnifica* A. Murray bis) forests, and others having less frequent, mixed- to high-severity fire regimes, such as lodgepole pine (*Pinus contorta* ssp. *murrayana* [Grev. & Balf.] Critchf.) forests.

In the prolonged absence of fire, these forests are prone to senescence risk because shade-tolerant competitors can overtop and kill mature Baker cypress (Merriam and Rentz 2010), but the extent of this occurrence is not well characterized. However, many sites contain low-productivity soils (serpentine, volcanic lava flows) that inhibit substantial recruitment of competing conifers and likely act as refugia from the influence of fire exclusion. Seeds can release upon tree death, but the presence of a dense litter and duff layer often inhibits seed germination and survival. While some Baker cypress populations have experienced a prolonged period of fire exclusion that has caused senescence (Merriam and Rentz 2010), six of the nine California, USA, populations have burned in large wildfires since 2006 (J.M. Kane, Humboldt State University, Arcata, California, USA, unpublished data), prompting concern about the potential for short-interval fires that may facilitate population reduction or loss.

McNamara *et al. Fire Ecology*   (2019) 15:39

Page 4 of 14

This study examined post-fire fuel succession patterns in the rare, serotinous Baker cypress of northern California, across a time-since-fire chronosequence ranging from 3 to 147 years. The specific objectives of this study were to (1) characterize surface fuel loading by category (*e.g.,* litter, duff, woody fuels, etc.) across the chronosequence; (2) examine changes in foliar moisture content of shrubs and trees across the chronosequence;(3) determine the amount of cone production across the chronosequence; and (4) model changes in predicted fire behavior across the chronosequence. While our research focused on the rare, serotinous Baker cypress, results from this study may have implications for the many other obligate-seeder species in fire-prone ecosystems.

Methods
Experimental design
The study took place in Baker cypress populations occurring in Shasta, Siskiyou, and Plumas counties of northeastern California, USA. Stand selection for this study was based on a current map of Baker cypress populations (K. Merriam, USDA Forest Service, Quincy, California, USA, unpublished data) overlaid with fire perimeter data (CalFire 2018) so that we could survey a wide range of time since fire and stand development stages in Baker cypress ecosystems (Fig. 1). Since the 147-year-old stand preceded fire records, we approximated time since fire based on a tree-ring count of the oldest tree cored at the site during a stand inventory that we conducted in 2016. Attempts to
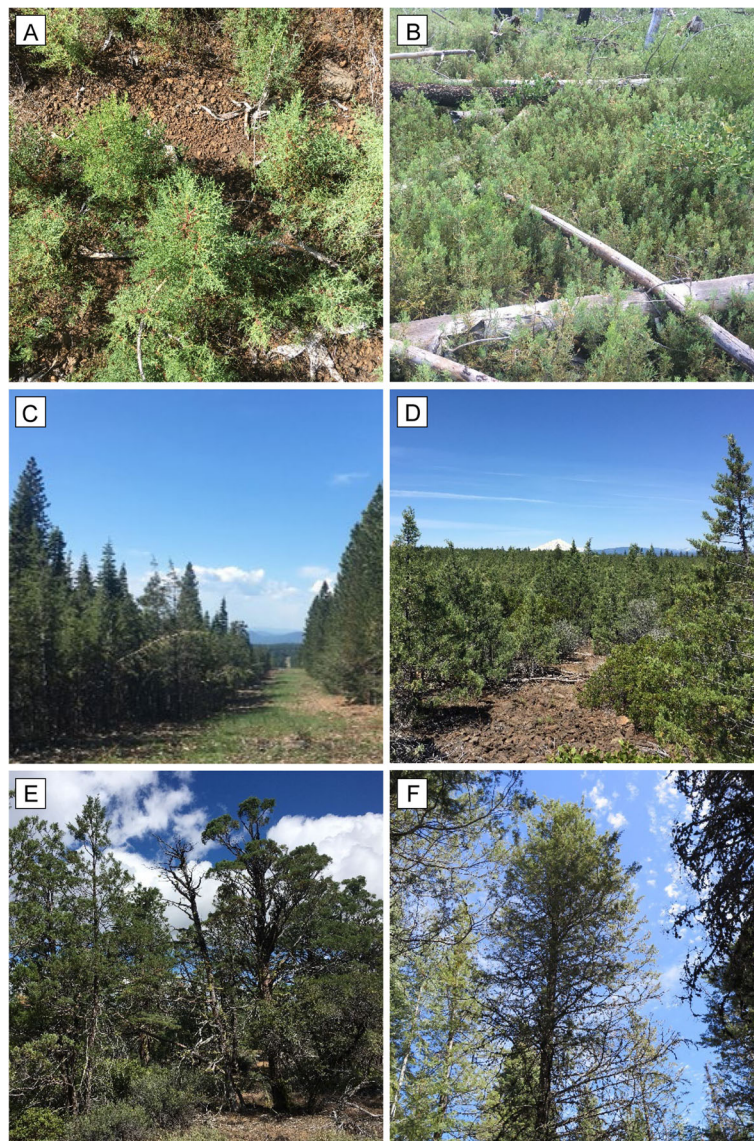
Fig. 1 Representative Baker cypress stand conditions for our study sites along the time-since-fire chronosequence in northern California, USA, that were sampled in 2015 or 2016. Stand ages include (**A**) 3 yr, (**B**) 10 yr, (**C**) 26 yr, (**D**) 40 yr, (**E**) 107 yr, and (**F**) 147 yr. Photographer credits: (**A** through **E**) B. McNamara; (**F**) J. Kane

cross-date tree rings at this site were unsuccessful, thus our age estimate for this site may be conservative. An additional 26-year-old planted stand adjacent to the 147-year-old stand was included for some measurements (*e.g.,* foliar moisture content, cone production) as it offered us the opportunity to add an important stand age that was otherwise not available.

Similar to many previous studies on fuel succession, we employed a chronosequence approach that substitutes time for space to examine potential changes in fuel characteristics and cone production. While we recognized the limitations of the chronosequence approach (Walker et al. 2010), we minimized these impacts by selecting stands that had similar site characteristics. Slope and aspect for each site were derived using raster data from a 10 m resolution digital elevation model within a geographic information system. We used this information to select study sites that had minimal variation in among-site topographical characteristics, resulting in all study sites having gentle to moderate slopes and generally north-facing aspects (Table 1). All soil types were volcanic in origin; however, the 40 and 107-year-old sites at Timbered Crater Wilderness Study Area in northeastern California, USA, contain lava flows with younger and presumably lower-productivity soils than the other sites. Greenleaf manzanita (*Arctostaphylos patula* Greene) was the dominant or codominant shrub species at most sites, with the exception of the 10-year-old stand where tobacco brush (*Ceanothus velutinous* Douglas) was the most common shrub. Stand density index was calculated based on Reineke (1933), and values increased with time since fire (Table 1). At the oldest study site, which had substantial Baker cypress mortality among the canopy trees due to overtopping by other species, the stand density index was 492. This value is consistent with heavy competition-induced mortality in other shade-intolerant species (Woodall et al. 2005).

Data collection and calculations

We first conducted a stand inventory within a 12 ha area at the 147-year-old site in 2016 using a systematic grid design containing sixteen 0.025 ha, fixed-area circular plots (radius = 8.92 m) that were spaced 40 m apart. Plot locations for the remaining sites surveyed in 2017 were generated from 25 random points in ArcMap 10.2 (ESRI, Redlands, California, USA) within a 12- to 15-hectare area. Of the original 25 selected points, we established twelve 0.025 ha fixed-area circular plots (radius = 8.92 m) that contained live or dead Baker cypress and had an average minimum distance of 59 m (range 5.8 to 195.9 m) from another plot. Within each plot, we recorded species, status (live or dead), height, and crown base height for all trees >3 cm diameter at breast height (DBH), while smaller trees (<3 cm DBH) were simply tallied.

Surface fuel loading data at all sites were collected using the planar intercept method (Brown 1974). At the 3-, 10-, 40-, and 107-year-old sites, 16 m planar intercept transects were established along random azimuths originating at the center of each tree plot. In every third tree plot, we established a second planar intercept transect that was 90° from the first transect, for a total of 16 transects per stand age. At the 147-year-old site, data was collected the previous year with slightly different methods: we used two 12 m transects originating at the center of each tree plot (32 total), with the first planar intercept being a randomly selected azimuth from plot center and the second being established 120° from the first. Coarse woody fuels (1000-hour, >7.62 cm) were recorded along the full transect length, 100-hour fuels (2.54 to 7.62 cm) were counted along the first half of the transect, and 1-hour (<0.63 cm) and 10-hour (0.63 to 2.54 cm) fuels were counted along the first quarter of the transect in all stands. Litter and duff depths were measured at the quarter, half, and full mark length of each transect. The highest fuelbed depth (to a maximum of 2 m height) was also measured three times per transect along 1 m planes preceding the quarter, half, and full transect length marks. For all 1000-hour fuel particles, we measured the diameter where the particle intersected the transect, categorized each as rotten or sound, and identified each to species. Live surface fuels, including shrubs and herbaceous plants, were collected in a 1 m^2 circular plot at the end of all 32 transects for the 147-year-old site, and at the end of nine systematically selected transects for the remaining sites. Live surface fuels collected for each plot were separated into woody shrub or

Table 1 Site attributes at each Baker cypress stand measured along a chronosequence in northern California, USA, surveyed in 2015 or 2016 Note that the Pipeline site was planted and excluded from fuel loading and stand density measurements. SDI = stand density index, n/a = not available

Fire or site name	Latitude, longitude (°)	Age (yr)	Aspect (°)	Slope (%)	Elevation (m)	Metric SDI	Cones per tree (*n*)
Eiler	40.76, −121.6	3	27	8	1560	0	0
Moonlight	40.18, −120.7	10	5	23	2034	22	0
Pipeline	40.78, −121.7	26	336	8	1344	n/a	120
Horrs Corner	41.18, −121.5	40	13	7	1130	94	210
Glass Mountain	41.19, −121.8	107	333	1	1098	210	240
Burney	40.78, −121.7	147	336	8	1344	492	1290

herbaceous categories and all samples were dried for at least 72 hr at 60 °C, weighed, and values were converted to megagrams per hectare (Mg ha^{-1}).

We calculated fuel loading (Mg ha^{-1}) for 1- to 100-hour fuels (Eq. 1) and 1000-hour fuels (Eq. 2) using values for particle diameter, particle angle, and specific gravity of conifers provided by Brown (1974):

$$Fine\ Fuel\ Loading = \frac{\left(1.234 \times n \times d^2 \times s \times a\left(\sqrt{1 + \left(\frac{\%slope}{100}\right)^2}\right)\right)}{Nl} \quad (1)$$

$$Coarse\ Fuel\ Loading = \frac{\left(1.234 \times \sum d^2 \times s \times a\left(\sqrt{1 + \left(\frac{\%slope}{100}\right)^2}\right)\right)}{Nl}, \quad (2)$$

where 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 loading (Mg ha^{-1}) were calculated following Eq. 3:

$$Litter\ and\ Duff\ Loading = (D \times BDV) \times 10, \quad (3)$$

where D represents depth in meters (m) and BDV is the bulk density value in kilograms per cubic meter (kg m^{-3}). Since bulk density values for Baker cypress were not available in the literature, we used the average values of scale-needled conifers from the Sierra Nevada, California, USA (van Wagtendonk et al. 1998), for both duff (173.7 kg m^{-3}) and litter (118.6 kg m^{-3}) loading estimates.

Crown fuel characteristics were determined based on field observations and model estimates for each plot across all sites. We measured tree height and crown base height in the field and calculated the average crown base height across all plots for each site. Average crown bulk density was determined using Fuels Management Analyst Plus (FMA+; Carlton 2005), based on species and the diameter distribution across all plots for each site. Since crown mass equations were not available for Baker cypress, we used western juniper (*Juniperus occidentalis* Hook.) values as a proxy since it was the species with the most similar crown characteristics available.

In 2017, live foliage was collected from 10 trees and shrubs at each of the six sites between 14 and 17 August, which is in the driest time of the wildfire season for this region. For each site, tree and shrub collections occurred within approximately 1- to 2-hectare area of the broader fuel sampling areas mentioned above. We chose a smaller

area for live fuel sampling because we wanted to limit potential differences in climate conditions over time across sites. Live foliage samples were collected within 2 m from the ground on the south side of each tree to minimize variation associated with crown position (Richardson et al. 2000). All sampling occurred between 1200 and 1600 hours to limit variation caused by daily moisture fluctuations (Zahn and Henson 2011). New (<1 yr) and old (>1 yr) foliage were separately collected to account for established differences in foliar moisture content amongst foliage ages (Van Wagner 1967; Chrosciewicz 1986). For each of the 10 trees that were sampled for fuel moisture, we also counted all cones on each tree, using binoculars when needed, to approximate average cone production per tree for each site. We also collected live foliage samples from 10 specimens of the dominant shrub species at each site or from five samples of the codominant shrub species per site. Foliage samples were contained within airtight plastic bags and kept on ice until weighed (Zahn and 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 hr at 60 °C and reweighed (W_d). Fuel moisture, expressed as a percentage, was calculated using Eq. 4 (Gary 1971).

$$Fuel\ Moisture\ Content = \frac{W_l - W_d}{W_d} \times 100. \quad (4)$$

Modeling and statistical analyses

We used a locally estimated scatterplot smoothing (Loess) function to visualize the non-linear patterns of fuel loading across the time-since-fire chronosequence. Loess fits were made at 1 yr increments from 0 to 150 yr since fire for each fuel type including duff, litter, shrubs, and 1- through 1000-hour woody fuels. The resultant patterns represented estimated surface fuel loads based on the collective change of fuel inputs and outputs over time.

Live foliar moisture content patterns for shrubs and Baker cypress foliage were analyzed using simple linear and multiple regression. Each individual sampled tree or shrub was considered an independent replicate to account for variation in live foliar moisture content associated with differences among trees within a site (*e.g.*, physiological, competitive environment). We examined the influence of time since fire for shrub foliar moisture content and the influence of time since fire and foliage age, including an interaction term, for Baker cypress foliar moisture content. Model selection for Baker cypress foliage was determined using the change in Akaike Information Criterion (ΔAIC; Burnham and Anderson 1998), a common indicator of model quality relative to

other models. The top regression model was selected based on the lowest AIC value and we report the resultant *F*- and *t*-statistics. Foliar moisture content data were log-transformed in order to meet parametric model assumptions. Model predictions of foliar moisture content across the chronosequence were back-transformed in visual plots for interpretability. All statistical analyses were conducted in the R environment (R Development Core Team 2018).

We used BehavePlus version 6 (Andrews 2014) to assess potential surface and crown fire behavior in Baker cypress stands. We reported surface fire rate of spread and flame length based on the Rothermel (1972) fire spread equations. This model assumes that fuels are evenly distributed throughout a stand and that fire behavior is temporally static (*i.e.,* consistent over time). Potential fire behavior was modeled across the time-since-fire chronosequence of Baker cypress stands using field and model-based observations of slope, fuel characteristics, fuel moisture, and wind speed. Slope at our study sites ranged from 1 to 23%; we used a value of 8%, the average slope across all sites, for all model runs. For the 107-year-old stand, we used a fuelbed depth of 0.3 m because of the prevalence of a shrub fuel layer. We used both custom fuel models generated from observed fuel characteristics at each site and representative fire behavior fuel models from a subset of Scott and Burgan (2005). Fire behavior fuel models were selected by a combination of observed fuel characteristics (primarily fuelbed depth and fine woody fuel loading) and our expectations of how fire might carry through the respective stands under the modeled fire-weather conditions. As a result, we used low-load shrub models, SH1 and SH2, to characterize the two youngest stands, 3- and 10-year-old stands, respectively. The 40-year-old stand was modeled using TU1, while the 107-year-old stand was modeled with TU5. The oldest stand (147 yr) was characterized by relatively high fuel loads and fuelbed depth due to substantial Baker cypress mortality and was modeled using a slash-blowdown model, SB3. The custom fuel models used for each site were initialized from the selected Scott and Burgan (2005) fire behavior fuel models, including surface area-to-volume ratios (1-hour, herbaceous, and shrub fuels), heat content, and moisture of extinction. The main difference was that we modified these models to include field-based observations of fuel loading by type and fuelbed depth.

To model fire behavior, we extracted fire-weather data for each Baker cypress field site from gridMET, a 4 km surface meteorological dataset available on a daily time scale from 1979 to the present for the contiguous US (climatologylab.org; Abatzoglou and Brown 2012; Abatzoglou 2013) and accessed through Google Earth Engine (earthengine.google.com/datasets). From this data, we calculated the 97th percentile 10 m wind speed, maximum temperature, minimum relative humidity, and 100-hour fuel moisture for the

wildfire season (June through September) between 2000 and 2017. The 10 m wind speeds were then adjusted to estimate mid-flame wind speeds following the equation provided by Andrews (2012) to account for differences in stand and fuelbed characteristics among sites. Wind adjustment factor (*WAF*) accounts for fuelbed depth (*H*), canopy closure (*CC*) and crown ratio (*CR*), depending on whether sites were unsheltered (WAF_u; Eq. 5) or sheltered (WAF_s; Eq. 6):

$$WAF_u = \frac{1.83}{\ln\left(\frac{20 + 0.36H}{0.13H}\right)}. \tag{5}$$

$$WAF_s = \frac{1.83}{\sqrt{\frac{CC}{3} \times CR \times H} \ \ln\left(\frac{20 + 0.36H}{0.13H}\right)}. \tag{6}$$

Using minimum relative humidity (*RH*) and maximum temperature (*TEMP*), we calculated the equilibrium moisture content (*EMC*) based off the equation provided by Cohen and Deeming (1985) that is used as part of the National Fire Danger Ratings System (Eq. 7) as well as FireFamilyPlus (Bradshaw and McCormick 2000):

$$EMC = [0.03229 + (0.281073 \times RH)] - (0.000578 \times TEMP \times RH) \tag{7}$$

After calculating *EMC*, we multiplied *EMC* by either 1.03 or 1.28 to estimate 1- and 10-hour fuel moisture, respectively. The 97th percentile fine woody fuel moisture content was 2.2%, 2.7%, and 5.1% for 1-, 10-, and 100-hour fuels, respectively. Shrub fuel moisture inputs were based on fuel moisture samples collected from each site and herbaceous fuel moisture content was set at 30%. The 97th percentile wind adjusted speeds used for fire behavior modeling were 6.2, 6.7, 6.7, 7.8, and 3.7 km hr^{-1}, for each stand in order of increasing stand age.

Representation of crown fire behavior was estimated based on calculations of critical fireline intensity following Van Wagner (1977). This measure represents the fire intensity necessary for transition from surface fire to crown fire. Determination of the fire type (surface, passive crown, conditional crown, and active crown fire) was based on the equation of Scott and Reinhardt (2001), which was selected due to its ability to better estimate the incidence of active crown fires (Scott 2006). We also provided predicted crown fire flame length and rate of spread. Additionally, we modeled potential post-fire tree mortality based on the average stand characteristics for each site with the First Order Fire Effects Model version 6.5 (Lutes 2019),

which predicts mortality based on bark thickness estimates specific to tree species by DBH and percent crown volume scorched. Since bark thickness estimates are not available for Baker cypress, we used western juniper as a proxy based on its similar bark thickness characteristics. Crown volume scorched was based on scorch height, tree height, and crown ratio.

Results

Fuel loading patterns

Litter and fine woody fuel (1- to 100-hour) loading was highest in the 10- and 147-year-old stands (Table 2, Fig. 2), but were lowest in the 3-year-old stand. Fine-fuel loading was lower in the 40- and 107-year-old stands compared to the 10- or 147-year-old stands. Coarse woody fuel loading was low initially, and peaked in the 10-year-old stand. After 10 yr, coarse woody fuel loading followed a decreasing trend. We did not observe any duff in the 3-year-old stand, after which duff loading increased with time since fire. Live shrub fuel loading was more variable over time (Table 2), with the highest values recorded at the 10- and 107-year-old stands. Herbaceous fuel loading was persistently low across all stands, but 333% higher in the 3-year-old stand compared to the 10-year-old stand, which had the lowest herbaceous fuel loading.

Crown fuels were not present in the 3- and 10-year-old stands because of the low stature of the existing seedlings and saplings and we did not encounter any trees that survived the preceding wildfire within our study sites. Crown base height was 1 m in the 40-year-old stand, increasing to 3 to 4 m in the older stands. Estimates of crown bulk density ranged from 0.43 to 0.88 kg m^{-2}, with the oldest stand having the highest value.

Live fuel moisture patterns

Live fuel moisture patterns varied along the time-since-fire chronosequence. Average observed shrub foliar moisture content ranged from 74 to107% across sites and was highest at the 147- and 3-year-old stands and lowest in the 40- and 107-year-old stands (Table 2), but differences were not linearly related to time since fire ($P = 0.74$). Average live foliar moisture content for Baker cypress ranged from 72 to 143% in old foliage and from 89 to 169% in new foliage, across all sites. The 40-year-old stand had the lowest observed foliar moisture values and the two youngest stands (3- and 10-year-old) had the highest foliar moisture content (Fig. 3). Foliar moisture content in new foliage (<1 yr) was 9 to 59% higher than older foliage (>1 yr) across the chronosequence (Fig. 3). An additive model that included stand age and foliage age better predicted Baker cypress live foliar moisture content than models of either variable alone or with an interaction between stand and foliage age. Time since fire had a strong and negative relationship with live foliar moisture content ($R^2 = 0.42$, $P < 0.0001$; Table 3).

Cone production

Cone production in Baker cypress increased with time since fire across all stands (Table 1). However, we did not observe cone production in either of the two youngest stands (3- and 10-year-old). The 26-year-old stand, by contrast, had an average of 120 cones per tree. The two intermediate-aged stands, 40- and 107-year-old, had 210 and 240 cones per tree, respectively. The oldest stand had substantially more cone production, with an average of 1290 cones per tree.

Table 2 Fuel characteristics along a time-since-fire chronosequence of Baker cypress stands in northern California, USA, surveyed in 2015 or 2016. Values were used to parameterize fire behavior models. Values in parentheses are standard error. FMC = foliar moisture content

Fuel characteristic	Time since fire (yr)				
	3	10	40	107	147
1-hour (Mg ha^{-1})	0.07 (0.02)	0.31 (0.06)	0.2 (0.04)	0.27 (0.04)	0.90 (0.11)
10-hour (Mg ha^{-1})	1.11 (0.30)	2.87 (0.53)	0.74 (0.16)	1.29 (0.26)	4.25 (0.48)
100-hour (Mg ha^{-1})	3.26 (0.88)	8.29 (1.45)	0.55 (0.28)	2.02 (0.44)	3.37 (0.63)
1000-hour, sound (Mg ha^{-1})	12.03 (3.25)	118.07 (12.75)	10.01 (4.10)	14.37 (5.34)	9.49 (2.35)
1000-hour, rotten (Mg ha^{-1})	0.00 (0.00)	8.65 (4.25)	7.27 (2.90)	8.84 (4.07)	0.82 (0.39)
Litter (Mg ha^{-1})	1.63 (0.67)	12.45 (3.56)	9.66 (2.25)	12.08 (2.10)	26.51 (4.07)
Duff (Mg ha^{-1})	0.00 (0.00)	8.21 (2.40)	9.77 (3.06)	27.39 (5.99)	86.35 (12.41)
Live herbaceous (Mg ha^{-1})	0.5791 (0.25)	0.0042 (<0.01)	0.0162 (0.01)	0.1741 (0.07)	0.0146 (<0.01)
Live shrub (Mg ha^{-1})	2.62 (0.80)	9.74 (2.97)	2.76 (2.06)	8.85 (5.14)	0.86 (0.31)
Shrub FMC (%)	101.81 (2.84)	104.27 (2.36)	84.98 (3.77)	73.82 (1.44)	107.16 (2.82)
Fuelbed depth (cm)	20.34 (4.40)	31.22 (4.35)	6.64 (1.77)	6.64 (1.20)	37.28 (5.87)
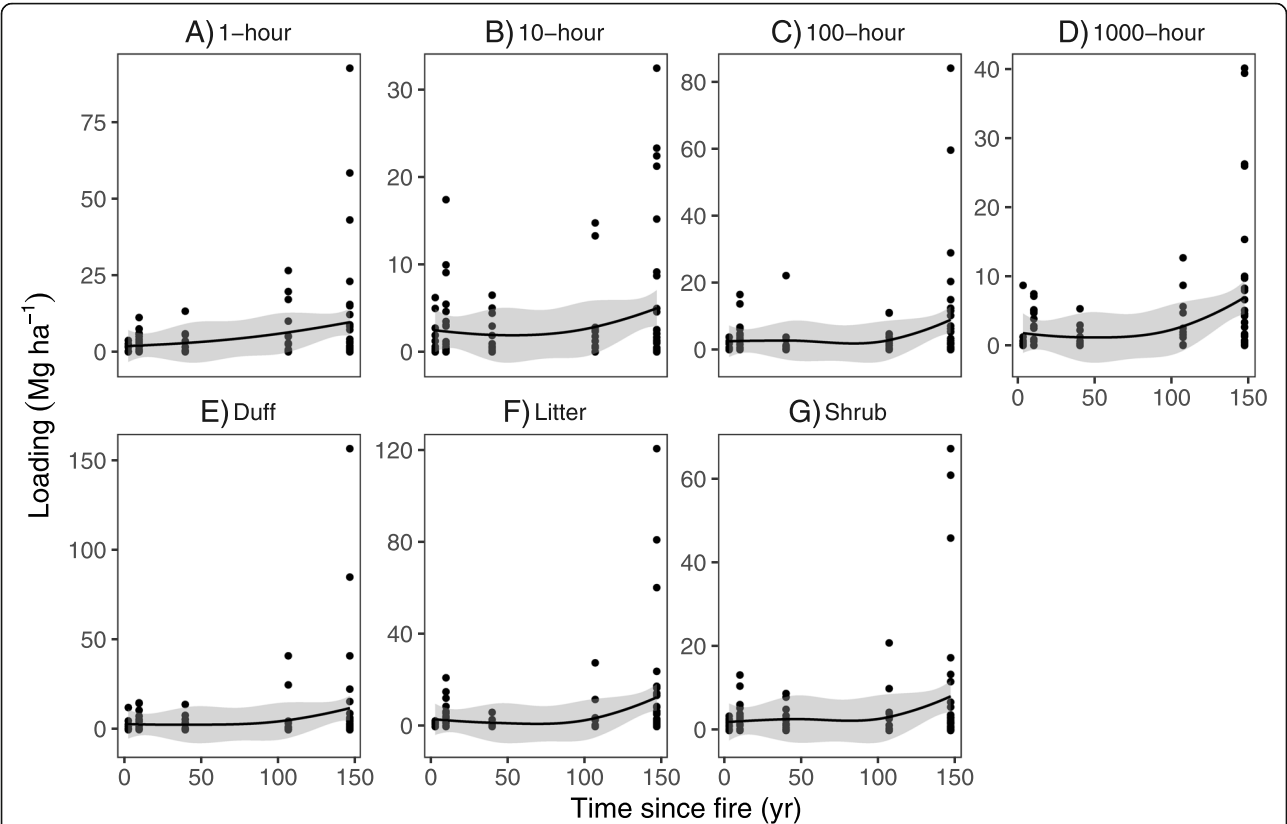
Fig. 2 Change in (**A**) 1-hour, (**B**) 10-hour, (**C**) 100-hour, (**D**) 1000-hour, (**E**) duff, (**F**) litter, and (**G**) shrub fuel loading sampled in 2015 or 2016 along a Baker cypress time-since-fire chronosequence in northern California, USA. Solid lines represent locally estimated scatterplot smoothing (Loess) functions and shaded areas represent 95% confidence intervals. Dots represent fuel loading samples within each site
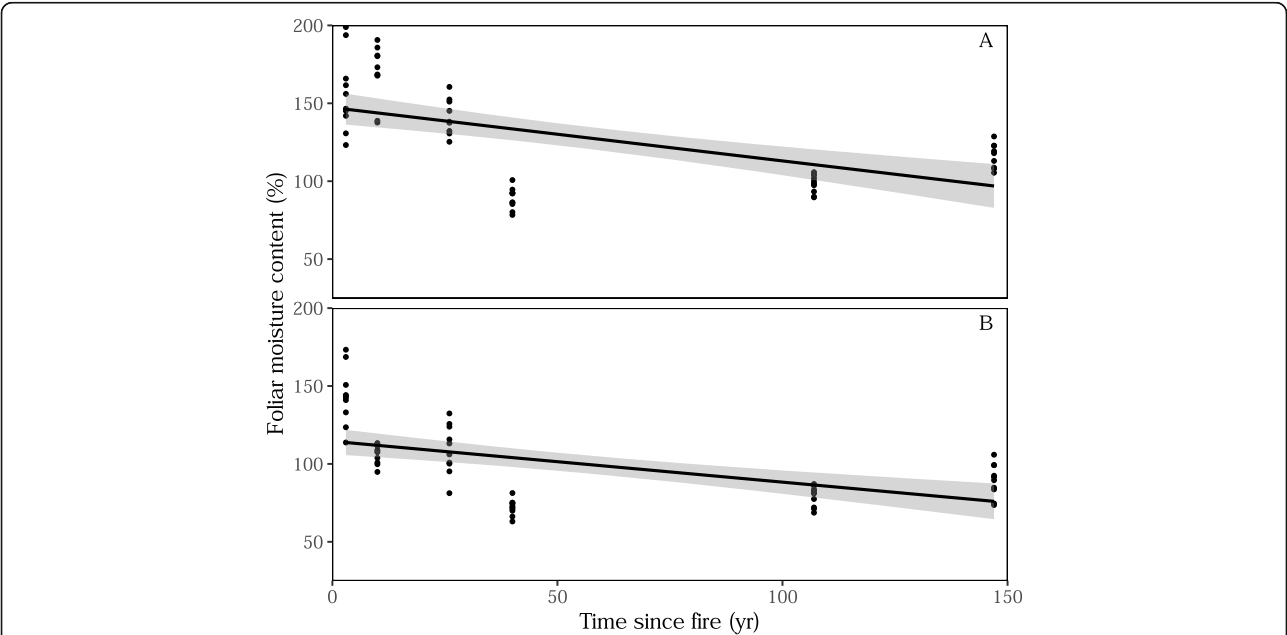
Fig. 3 Top model predictions of (**A**) new foliage (<1 yr), and (**B**) old foliage (>1 yr) live foliar moisture content (%) collected in August 2016 across the Baker cypress time-since-fire chronosequences of northern California, USA. Dots represent observed foliar moisture content values of individual tree samples within each site

Table 3 Summary of the top multiple regression model for Baker cypress live foliar moisture content that included foliage age and stand age. Sites were sampled in August 2016 and located in northern California, USA. Old = foliage >1 yr, F-statistic = 42.44 on 2 and 117 degrees of freedom, (R^2 = 0.42, P < 0.0001). SE represents standard error

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-Old	−0.2489	0.0393	−6.3	<0.001

Fire behavior and mortality patterns

Potential fire behavior varied with time since fire across all stands. Potential surface fire behavior in Baker cypress followed a trajectory similar to that of the changes observed in fine fuels, with higher flame lengths and faster rates of spread occurring in the 10- and 147-year-old stands (Fig. 4). Surface flame length and rate of spread increased from 0.9 m and 1.6 m s^{-1}, respectively, in the 3-year-old stand to 2.3 m and 3.5 m s^{-1}, respectively, in the 10-year-old stand, based on custom model results. We would assume that this fire behavior would result in substantial mortality of Baker cypress in these young stands; however, modeled mortality estimates were not available for the small trees (<1.37 m in height) at these two sites. Potential flame lengths based on custom models decreased from 3.5 m in the 10-year-old stand to 0.03 m in the 40-year-old stand, although a conditional crown fire was predicted for the latter stand. The 107-year-old stand was predicted to sustain an active crown fire with a substantial increase in surface flame length and rate of spread compared to the 40-year-old stand. The oldest stand (147 yr) also was predicted to sustain an active crown fire. Crown fire rate of spread was predicted to be 11.9 m s^{-1} for the three oldest stands, and predicted crown fire flame length increased from 10.6 m in the 40-year-old stand to 22.8 m in the 147-year-old stand. Surface and crown fire behavior between custom models and fire behavior fuel models was largely in agreement, but custom models predicted slightly greater rates of spread and flame lengths at most sites (Fig. 4). Post-fire mortality was estimated to be 100% for all stands 40 yr or older based on custom fuel model inputs and modeled fire behavior. Modeling fire behavior using observed live Baker cypress foliar moisture content for woody fuels did not substantially change predictions of fire type (surface or crown fire). However, the critical fireline intensity values based on observed foliar moisture content were 14 and 23% lower for the 40- and 107-year-old stands, respectively, than estimates based on the standard use of 100% foliar moisture content.

Discussion
Fuel loading patterns

The patterns of fuel succession in Baker cypress were consistent with previous findings from other empirical studies following stand-replacing fire, providing further evidence that time since fire or stand age can be a useful predictor of fuel patterns over time (Fahnestock 1976; Brown and See 1981; Agee and Huff 1987). Fine-fuel loading across the 147-year chronosequence in our study indicated a U-shaped pattern. The first major surface fuel contributions likely resulted from the decaying of fire-killed snags, as observed through the substantial pulse of fine and coarse woody fuels in the 10-year-old stand. Other studies corroborate this initial pulse in the first post-fire decade (Agee and Huff 1987; Kashian et al. 2013; Dunn and Bailey 2015). The second major contribution to dead woody surface fuel loading was likely the result of competition-induced mortality that developed from the post-fire cohort of this very shade-intolerant species. Interspecific competition from more shade-tolerant species may accelerate the fuel accumulation process in Baker cypress stands of sufficiently advanced age and declining health (*i.e.,* senescence risk), an on-going conversion observed in some of the older Baker cypress populations (Merriam and Rentz 2010). The lower fine woody fuel loads observed within the 40- and 107-year-old stands likely reflects decomposition of dead woody fuels without substantive inputs from the new stand. However, these two stands possibly differed in their productivity compared to the others, due to the younger, less productive volcanic substrate (*i.e.,* lava flows) that was present at these two sites, which may have partially contributed to the lower fuel loads at these intermittent stand ages. While the 107-year-old stand lacked substantial fine woody surface fuels, an increase in shrub fuel loading was observed at this site.

Live fuel moisture patterns

Live foliar moisture content at the stand scale in Baker cypress generally decreased with stand age independent of foliage age—a finding, to our knowledge, that has not been previous reported. We speculate that increased competition for water in a moisture-limited ecosystem may be one possible mechanism for this trend. In our study, we observed increases in stand density index, and thus live tree biomass, with time since fire, suggesting increased competition for soil moisture and other nutrients during the dry northeastern California summer. Changes in foliar anatomy and physiology with tree age may have also contributed to these observed patterns. For instance, the amount of non-photosynthetic cell area within a needle decreased with tree age in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco; Apple et al. 2002), and thus needles in younger trees may require more water storage (*i.e.,* higher foliar moisture content) to maintain what is presumably a higher rate of photosynthetic activity. There is greater recognition that physiological changes, possibly in association with tree age, can strongly influence patterns of foliar moisture content (Jolly and Johnson 2018), but this topic requires further investigation.
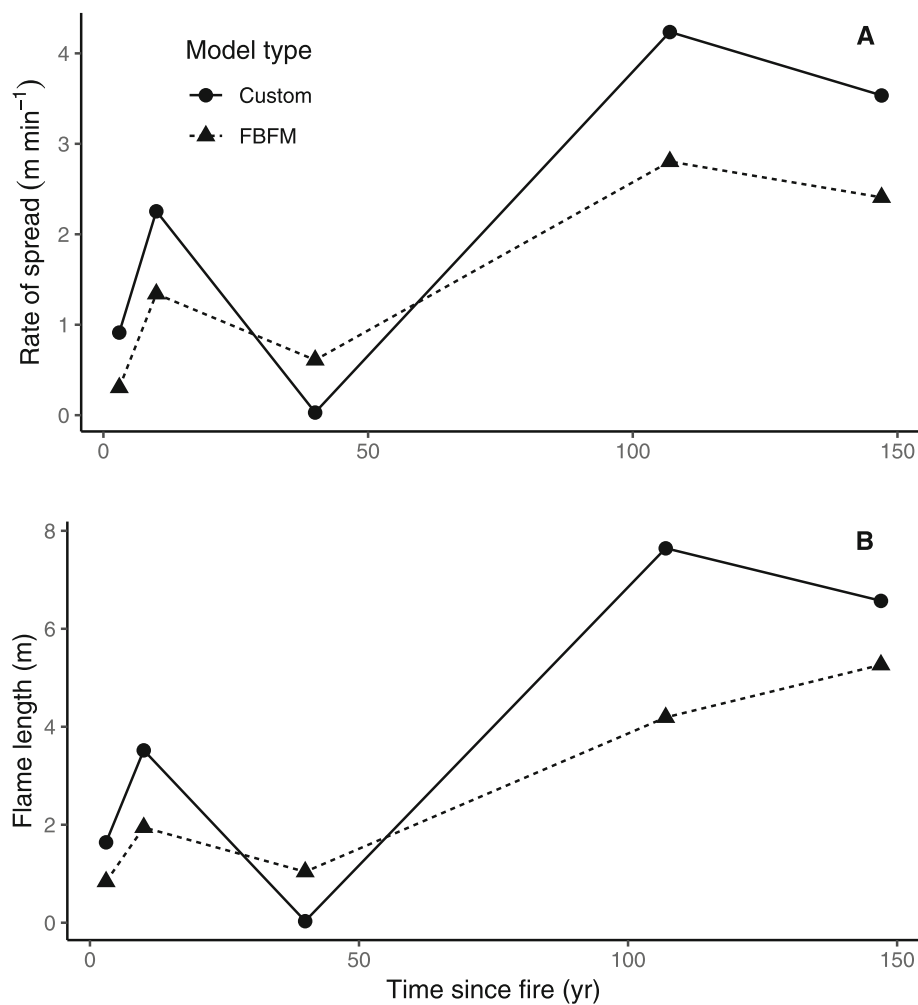
Fig. 4 Modeled surface fire behavior, (**A**) rate of spread and (**B**) flame length, across a time-since-fire chronosequence of Baker cypress stands in northern California, USA. Predictions are based on predictions from custom fuel models (solid line and dots) generated from field-based observations made in 2015 or 2016 and the best matched fire behavior fuel model (FBFM; dashed line and triangles) from Scott and Burgan (2005)

Assuming that decreases in foliar moisture content with time since fire also apply to other forest types that experience stand-replacing fires, values adjusted for stand age may more accurately predict transition of a surface fire to a crown fire. In addition, use of 100% for foliar moisture values, as recommended when other information is not available (*e.g.,* Finney 1998), may lead to overestimations in critical fireline intensity for stand ages that contain values lower than 100%, such as we observed in the 40- and 107-year-old stands. A somewhat surprising result of our study was that shrub foliar moisture content did not follow a similar pattern to tree foliar moisture across sites. The reason for the absence of a time-since-fire pattern in shrub foliar moisture content is unknown but may reflect differences in the species present across sites, different physiological processes among tree and shrub species, or access to different water sources in the soil horizon.

In accordance with previous findings, foliar moisture content was lower in old foliage than in new foliage (Van Wagner 1967; Gary 1971; Chrosciewicz 1986; Agee et al. 2002; Jolly et al. 2014). Young foliage typically contains higher moisture content due to lower non-structural carbohydrates and crude fats compared to older foliage (Gary 1971; Jolly et al. 2014). However, it is important to note that younger stands have a higher proportion of younger foliage than older stands and, thus, would have higher foliar moisture content at the whole-tree scale, a distinction that is not typically accounted for when modeling fire behavior, as has been noted by others (Agee et al. 2002; Jolly et al. 2014).

Fire behavior and mortality patterns
Fire behavior modeling for the stands observed along the Baker cypress time-since-fire chronosequence indicated that these conditions could sustain combustion that is sufficient to kill Baker cypress and that these stands do not

appear to be fuel or moisture limited. In other words, there was sufficient fuel to carry fire and the elevated foliar moisture content of Baker cypress on younger sites did not affect potential fire spread. It is important to point out that our results are strictly based on modeled fire behavior, which can be quite sensitive to the fuel models selected to represent fuel conditions across the chronosequence. Our results indicated that fire behavior would take a U-shaped distribution as stand age increased, which is consistent with the observed fine woody loading and fuelbed depth patterns. However, there is a possibility that the density of the young cypress trees in the 40-year-old stand may be better represented as a shrub fuel model due to their short stature. We opted to characterize this stand as a TU1 fuel model because of the large distances between trees (Fig. 1d). Additionally, the surface fire behavior model employed assumed a uniform distribution of fuels (Rothermel 1972) and did not account for the observed patchiness of fuels in some stands. For instance, in the 3-year-old stand, we did not observe litter loading on 62.5% of the transects, suggesting that, if burning is sustained, it may be quite patchy, possibly allowing some Baker cypress to survive. Based on our modeled fire behavior and stand information, post-fire mortality in Baker cypress was 100% for the three oldest sites and would likely extend to younger sites if modeling was possible for these size classes. The persistently thin bark of Baker cypress is unlikely to provide sufficient protection from even modest fire behavior.

Time since fire had a strong influence on modeled surface fire behavior in Baker cypress forests. These results were consistent with another study of fuel succession following stand-replacing fire in western hemlock (*Tsuga heterophylla* [Raf.] Sarg.)–Douglas-fir forests: Agee and Huff (1987) found increased surface fire behavior in young stands, a subsequent reduction in fire behavior in intermediate-aged stands, and a gradual increase in the oldest stands of the post-fire chronosequence. While the specific timing of fine fuel and surface fire increases differed compared to our study, both forest types followed a more or less U-shaped distribution in fine woody fuels, and fire behavior that spanned the range of stand developmental stages.

Conclusions

The onset of rapid climate change, changing fire regimes (Westerling 2016; Parks et al. 2017), and intensified droughts (Enright et al. 2015) have prompted concerns for the persistence of obligate-seeding species (Turner 2010; Buma et al. 2013). In the case of Baker cypress, populations that experience a short-interval fire before a sufficient production of cones would be substantially reduced or eliminated. While our modeling indicates that fuel conditions are suitable for these types of events to occur, it does not indicate the likelihood of fire occurring (*i.e.,* ignition). Recent projections of annual fire probability for 2026

to 2050, based on a model of fire occurrence developed for California (Mann et al. 2016), suggest that the probability of fire occurring for most of the Baker cypress range is < 1% per year (CalFire 2019). Thus, the probability of a fire burning a second time before the stand reaches maturity is likely extremely low, and we are unaware of any population that has experienced such a short-interval fire in Baker cypress; however, recurrent fire within seven years that resulted in no regeneration was recently observed for Tecate cypress (*Hesperocyparis forbesii* [Jeps.] Bartel) in southern California (Brennan and Keeley 2019).

The possibility of immaturity risk occurring in Baker cypress is also dependent on the time at which a sufficient number of cones are produced to replace the stand. We did not observe cone production within stands in our study sites younger than the 26-year-old stand, which had an average of 120 cones per tree (Table 1). However, it is important to note that trees at this site were planted and likely represent a higher level of cone production than would occur in most post-fire regenerated stands at this stand age. There were no cones on the sampled trees at the 10-year-old site, but we did observe that some (very few) individual trees bore a single cone at this age. Assuming that there are only about four viable seeds per cone (McNamara 2018) and an expected seedling survival rate of about 10% (Greene and Johnson 1998), young stands like this that have few individuals bearing cones may be incapable of replacing the population after fire. Likewise, Merriam and Rentz (2010) observed a 16-year-old stand that did not yet bear cones. Consistent cone production in Baker cypress probably does not occur for at least two decades and possibly longer for less productive sites. Estimates for a related species, the Tecate cypress of southern California, indicated that a fire return interval shorter than 40 yr would result in a substantial population reduction (Rodríguez-Buriticá and Suding 2013).

Our study demonstrates that fuel conditions in young Baker cypress stands are conducive to burning and can result in substantial fire behavior and post-fire mortality, but likely represent relatively low probability events. Still, given that Baker cypress is quite rare, the loss of any population is problematic. As such, we recommend the exclusion of fire in stands younger than 20 yr to prevent the potential loss of a population due to immaturity risk. Treating adjacent areas around Baker cypress populations may also help facilitate the ability to suppress fire in younger stands. In stands older than 20 yr, fuel conditions and sufficient cone production would promote stand replacement following fire and eliminate the competitors that would eventually overtop Baker cypress.

Authors' contributions
JK and DG conceived of the project idea and procured funding to support the work. BM and JK analyzed the data, interpreted the findings, and wrote the major portions of the manuscript. All authors read and reviewed earlier drafts of the manuscript and approved the final version.

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