

Seed maturation and mortality patterns support non-serotinous conifer regeneration mechanism following high-severity fire

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Research Article

Keywords: conifer regeneration, Douglas-fir, fire ecology, incense cedar, plant ecology, ponderosa pine, reproductive ecology, seed viability, Sierra lodgepole pine

Posted Date: October 4th, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-4941546/v1>

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Version of Record: A version of this preprint was published at Fire Ecology on March 4th, 2025. See the published version at <https://doi.org/10.1186/s42408-025-00357-4>.

Abstract

Background

Climate warming increases fire activity for many regions around the world, prompting concern over the long-term persistence of conifer species that regenerate poorly from seed after high-severity fire. However, substantive regeneration of non-serotinous conifer species within a large high-severity patch, a process termed facultative serotiny, is possible if the fire occurs in the brief window following seed maturation but before cone opening, the enclosed seeds can withstand the heat range of the fire, and the non-serotinous cone crop is sufficient. To define the temporal window of facultative serotiny, we collected closed cones from June to September over two seasons, examining seed maturation as a function of the heat sum for four non-serotinous California conifer species: ponderosa pine (*Pinus ponderosa*), Sierra lodgepole pine (*Pinus contorta* var. *murryana*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*). Additionally, we examined seed survival based on viability testing in closed cones following heat treatments ranging from ~ 20 to 600°C. Finally, we compared this temporal window of viability to the proportion of area burned during that same interval using recent fire data for northern California to identify the proportion of fires that may be conducive to facultative serotiny.

Results

The accumulated heat sum was positively associated with seed maturity; the proportion of seeds that were viable varied by species but generally ranged from late-July (10%) to mid-September (90%) with heat sums ranging from 1285°C to 2081°C, respectively. Higher heat exposure was negatively associated with seed survival and some withstood temperatures as high as 400°C for 150 seconds. Seeds of the smaller cone species, incense cedar and Douglas-fir, tended to have lower survivability to heat treatments than the larger cone species, lodgepole pine and ponderosa pine. The period of availability of mature seeds overlapped with 60% of the area burned during wildfires for northern California.

Conclusions

We identify conditions suitable for the occurrence of facultative serotiny following high-severity fires for four non-serotinous conifers in northern California. The temporal window that permits facultative serotiny for these species can be incorporated into post-fire regeneration modeling and can aid forest management decision-making in fire-prone ecosystems containing non-serotinous conifers.

Background

Climate warming is contributing to current and projected increases in fire frequency, size, and severity for many regions globally (Moritz et al. 2012; Dennison et al. 2014, Senande-Rivera et al. 2022). Changing fire regimes have prompted concern over the persistence of many non-serotinous and non-resprouting woody plant species, especially for conifer species less capable of adequately regenerating from seed within high severity fire patches. Many recent surveys of post-fire regeneration in areas dominated by non-serotinous conifers have shown that high severity patches have poor regeneration (e.g., Shive et al. 2018, Stevens-Rumann and Morgan, 2019). Continued increases in the size and extent of high severity fire are therefore expected to substantially reduce the abundance of obligate seeder, non-serotinous woody plants over the coming decades (Enright et al. 2015).

Successful regeneration of non-serotinous conifers via seed following high-severity fires typically requires that there are large seed crops available within or near high-severity patches before seedbed quality deteriorates due to forest floor accumulation and competition for light increases due to post-fire vegetation recovery, and that the patch is not too large (Collins and Roller 2013, Hansen et al. 2018). The proximity to living trees has been consistently identified as the most important factor determining the subsequent patch-wide density of recruits of non-serotinous conifers (Agee 1993, Greene and Johnson 1996, Welch et al. 2016, Stevens-Rumann and Morgan 2019). The decline of seed or recruit density with distance from a living forest edge is essentially a negative exponential function over the first 200 m and flattens very strongly at greater distances; the number of seeds at 200 m from the edge will only be about 5–10% of the seed density near the edge (Greene and Johnson 1996).

Serotiny is a fire-adaptive strategy that maintains a large supply of viable seeds within the crown (aerial seedbank) by retaining closed cones for more than 1 year after seed maturation. Following fire, cones are opened and seeds deposit onto mineral soil, an optimal seedbed exposed by litter and duff consumption (Lamont et al. 1991, Johnson and Gutsell 1993, Marlin et al. 2024). Serotinous species can act as a seed source despite fire-caused tree mortality, resulting in high density recruitment even deep within a large high severity patch (Greene and Johnson 1999, de Groot et al. 2004, Turner et al. 2007, Maia et al. 2012, Fernández-García et al. 2019). However, serotiny is known to vary widely within and across species (Lamont 2021), thus, characterizing this trait as a simple dichotomy can be conceptually limiting.

Non-serotinous species are also capable of having viable seeds within closed cones that survive fire, thus, as with serotinous species, relaxing the seed dispersal constraint. A modeling study demonstrated that a sufficient portion of viable non-serotinous seeds should survive a high-severity fire (Michaletz et al. 2013). Protection from fire is largely due to seed depth in the cone, which is known to proportionately increase with ovulate cone size, independent of being serotinous or non-serotinous (Greene et al. 2024). Thus, species that produce larger cones should experience lower rates of seed mortality due to fire. Non-serotinous species may also be exposed to lower temperatures than the average serotinous cone given that new cones tend to reside in the upper, cooler portion of the crown (Greene and Johnson 1994, Michaletz and Johnson 2007). Serotinous cones are often more evenly distributed throughout the crown and thus experience higher average temperatures during the passage of the flaming front. Unlike

serotinous species with their reliable supply of stored seeds, post-fire success of a non-serotinous species would depend greatly on the size of the cone crop that year. Therefore, the density of non-serotinous recruitment from burned trees will depend mainly on the size of the cone crop at the time a fire occurs, with mast years having far greater potential to create high density regeneration following fire.

This alternative post-fire regeneration mechanism, termed facultative serotiny (Greene et al. 2024), is also supported by field observations. As an empirical example of the mechanism, dense regeneration of the non-serotinous Douglas-fir was observed in high-severity burn sites located several hundred meters away from the nearest living conspecific source when a mast crop coincided with fire (Larson and Franklin 2005). Given that non-serotinous species are normally limited to full restocking within approximately 100 m or less of the living seed source at the burn edge (Greene and Johnson 1996), it is improbable that seed dispersal by wind could be responsible for high density recruitment at such great distances away from the burn edges. Additionally, following mast events for the non-serotinous Engelmann spruce (*Picea engelmannii*), abundant regeneration far from living trees was likewise observed at two separate burn sites in the Rocky Mountains (Pounden et al. 2014). Similar findings of high-density post-fire regeneration far from a living edge have also been observed where young serotinous trees have not yet developed persistent closed cones (the first few years after the onset of sexual maturity) or within non-serotinous varieties of *Pinus*. For example, the serotinous lodgepole pine (*Pinus contorta* var. *latifolia*) amply regenerated following fire that burned in a 16-year-old stand of trees with almost entirely non-serotinous cones (Turner et al. 2019). Likewise, abundant regeneration within high severity patches was reported for the non-serotinous Sierra lodgepole pine (*Pinus contorta* var. *murrayana*) following a reburn event (1984 and 2012) in northeastern California (Harris et al. 2020).

The abundance of post-fire regeneration via facultative serotiny is partially dependent on the timing of seed maturation and fire. Previous studies have established that the timing of seed maturation is a function of the accumulated heat sum $> 5^{\circ}\text{C}$ (i.e., degree days), such that the greater the heat sum, the increased metabolic activity to permit seed development and maturation (Henttonen et al. 1986, Zasada et al. 1992, Sirois et al. 1999, Fedorkov 2001, Meunier et al. 2007, Michaletz et al. 2013). However, most prior studies have been conducted within higher latitude species, and the relationship between accumulated heat sum and plant phenological development are known to vary with latitude (e.g., Beuker 1994, Gao et al. 2023). Following seed maturation, the ovulate cone scale tissue dries and reflexes until the seeds are abscised (Song et al. 2015). Conifer seeds are primarily dispersed by wind in the fall, with far fewer abscising in the winter or spring (Oliver and Larson 1996, Tanaka et al. 1997). Scale flexing and seed abscission in many North American conifers begins in September (Schopmeyer 1974). Thus, as seed maturation progresses during the growing season, the potential for post-fire regeneration should increase until cone opening or seed release. Therefore, if there is sufficient overlap between the timing of fire and the presence of viable seeds within closed-cones, facultative serotiny should be possible.

The likelihood of successful regeneration via facultative serotiny is not only contingent on viable seed availability (crop size and time of summer) at the time of burning but also on the ability of cones to sufficiently protect mature seeds from the high temperatures of a passing fire. During a fire, closed

ovulate cones within the canopy are exposed to the prolonged heat from the flaming front. The temperatures associated with the flaming front will vary depending on fire type (surface or crown), intensity, and position within the crown. Field-based studies have reported temperatures in the canopy up to 1300 °C during crown fires and up to 750°C during surface fires (Hobbs and Gimingham 1984, Butler et al. 2004). While lab-based studies indicate that serotinous and non-serotinous cones can maintain viable seeds with temperatures up to 500 °C for at least one minute, species vary in their heat exposure tolerance (Habrouk et al. 1999, Reyes and Casal 2002, Milich et al. 2012). The high temperatures associated with fire rapidly dehydrates the cone, thus speeding up the cone opening schedule and promoting seed release (Johnson and Gutsell 1993, Greene et al. 2013). Given the limited empirical research that has examined the relationship between temperature and seed mortality, information on the heat exposure thresholds across a wider range of species, especially non-serotinous cones, is needed.

In this paper, we determine the temporal window for facultative serotiny based on the rate of seed maturation for four common, non-serotinous conifers: ponderosa pine (*Pinus ponderosa*), Sierra lodgepole pine (*Pinus contorta* var. *murrayana*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*) throughout two growing seasons in northeastern California. Specifically, the objectives of this study were to: 1) investigate and track conifer seed maturation to determine the probable temporal window of facultative serotiny, 2) identify the capacity of seeds to survive increasing levels of heat exposure, and 3) estimate the proportion of burned area by wildfire in the region that overlaps the period that cones contain mature seed. This research is the first to examine the conditions necessary to support facultative serotiny across multiple species and should provide information relevant to other fire-prone regions and species.

Methods

Site location

All field collections were made along public roads within or adjacent to the Lassen National Forest near Burney, California (40.8432, -121.7088), at elevations ranging from 980 to 1680 m. Cone collections were made from young mature stands that had been planted for timber, or those that had encroached into adjacent meadows. Burney is located at the base of an inactive volcano in Shasta County, hosting scattered volcanic soils comprised of Holland, Bobbitt, Aquolls, and Skalan soils that support mixed conifer forests, scattered oaks, and Sierra lodgepole pine encroached meadows (NRCS 2020). The selected tree species for the study were limited to common species of commercial value in California and included ponderosa pine, Sierra lodgepole pine, incense cedar, and Douglas-fir. Developing female cones from these four species were collected in 2018 and 2019 for the seed maturation part of the study, and again in 2020 for the heat-induced seed mortality portion of the study. The average temperature during the summer collection months for 2018 (July-September) ranged from 17.5°C to 23.6°C, in 2019 (June-September) it ranged from 15.9°C to 21.1°C, and in 2020 (June-September) it

ranged from 18.1°C to 22.7°C (PRISM 2020). The average annual precipitation across collection years was 93.2 cm in 2018, 139.5 cm in 2019, and 67.6 cm in 2020 (PRISM 2020).

Seed Maturation

The ovulate cone collections for each species were made every other week in June, July, August, and September for both 2018 and 2019, except for Douglas-fir which was only sampled in 2019. Pole pruners were used to collect maturing cones within the crown that had closed cone scales and lacked obvious insect damage. The sampled trees varied in height from 2 to 10 m. The number of sampled cones and trees was dependent on the expected number of seeds per cone for each species. There were four to five trees sampled for Douglas-fir and ponderosa pine, with a minimum of one cone collected per tree during each collection period in both 2018 and 2019. For lodgepole pine, there were ten trees sampled per collection period, and a minimum of one cone collected per tree in both 2018 and 2019. Additionally, five incense cedar were sampled with a minimum of twenty cones collected per tree in both 2018 and 2019. After each collection was made, the cones were transported to the lab and placed in a forced convection oven at 23°C. Once the cone scales reflexed, all seeds were manually extracted from each cone.

Twenty-five seeds from each species and collection date were randomly selected to undergo viability testing. Some of the collections made early in the season had cones with immature seeds that were categorized as undeveloped and nonviable. A 1% tetrazolium solution was prepared using 2,3,5 triphenyl tetrazolium chloride, and the acidic solution was then neutralized to a pH of 7 with potassium chloride (AOSA 2008). The selected seeds for each collection date were scarified by nicking the seed coat with a razor blade, and then submerged in 5 ml of 1% tetrazolium solution in dark conditions, for 72 hours. This process allowed the solution to penetrate the megagametophytic tissue and promoted a hydrogen transfer that stained viable embryos red. After 72 hours, the seeds were rinsed with deionized water, and longitudinally sectioned to excise the embryo. The embryos were then evaluated for stain patterns with a stereoscope and placed into three categories: viable- where the embryos stained an even and vibrant red; probably viable- where most of the embryo displayed a red or pink stain; and nonviable- which included seeds that were hollow and without embryos, or those that did not stain red or pink.

The heat sum was calculated for each cone collection date, specifically using localized 2018 and 2019 interpolated climate data for the grid cell that included the collection site (PRISM 2020). The heat sum is simply the cumulative sum of the mean daily air temperature ($Ti, mean$) that exceeded 5°C (Eq. 1).

$$\text{Heat Sum} = \sum_{i=1}^n [(Ti, mean) - 5] \text{ Eq. 1}$$

Temperatures above 5°C are warm enough to allow for metabolic activity within woody plant species, such that gametophytes and embryos are able to develop (e.g., Meunier et al. 2007). By assigning a heat sum value to each collection date, we were able to examine the heat accumulation pattern across each year, so that it could be applied to future seasons despite variable annual temperatures. The annual heat

sum was also calculated for this region spanning from 2000 to 2020, to identify the patterns of accumulation and associated variation of timing among years.

Heat-Induced Seed Mortality

Additional cones were collected in 2020 to examine heat-induced seed mortality thresholds of the same four species. We determined the optimal cone collection date (period of maximum viability prior to seed abscission) based on results of accumulated heat sum and seed maturation relationships from 2018 and 2019 and then tracked the daily heat sum for 2020 calculated using Eq. 1 using PRISM temperature data for the site. As such, the 2020 cone collections were made on September 5th when 2146°C had accumulated. The developed ovulate cones were then collected with pole pruners from the canopy, following the same methods as the seed maturation portion of the study described earlier. We sampled a minimum of 50 cones from 2 to 13 trees for each species. The cones were kept cool until testing could be conducted to maintain cone closure and the state of seed maturity.

The heat exposure tests were performed in a muffle furnace using a total of seven heat treatments: no heat (control, ~ 20 °C), 100 °C, 150 °C, 200 °C, 300 °C, 400 °C, 600 °C. These temperatures were selected to represent a wide range of temperatures that would occur during wildfires (Butler et al. 2004, Michaletz et al. 2013). We used Omega type K thermocouples (Omega Engineering, Norwalk, CT, USA), with a testable temperature range that spanned from 200 °C to 1250 °C, connected to a Campbell Scientific CR1000 data logger (Campbell Scientific Inc., Logan, UT, USA), to record the maximum temperature (± 10 °C) within the muffle furnace. For each heat treatment, five cones were randomly selected from each species, except incense cedar, which had fifteen cones selected per treatment due to a maximum of four seeds produced per cone. Each cone was placed individually in a metal pan and placed into the muffle furnace at the desired temperature for 150 seconds. This exposure time was chosen as it was representative of the duration of simulated fire (Michaletz et al. 2013) and observed data in an experimental crown fire (Butler et al. 2004). Following exposure, the cones were removed promptly from the muffle furnace. Increasing heat treatments were implemented for all species until complete seed death was observed. Upon removal from the furnace, all seeds from the cone were extracted and five seeds per cone were tested for viability. If the cone scales failed to reflex during the heat treatment (commonly found at low heat treatment levels), the cones were placed in a drying oven at 23°C until the cone scales reflexed enough to free the seeds. In total, 25 randomly selected seeds across five or 15 (incense cedar) cones per heat treatment and species were examined for viability. Only seeds that were free of insect damage and appeared to have abundant megagametophytic tissue, indicating a high potential for a viable embryo, were selected to undergo viability testing. Using the same viability test methods as the seed maturation portion of the study, the seed embryos from the mortality experiment were examined and categorized by viability. This data was obtained for all seeds in each treatment, the number of viable and probably viable seeds were combined to find the proportion of viable seeds per treatment and species.

Timing of Fire

To estimate the temporal window that may permit post-fire regeneration via facultative serotiny, we first obtained the 2000–2017 fire perimeter data of all wildfires greater than 200 ha for the Klamath Mountains, northern Sierra Nevada, and southern Cascade ecoregions in northern California from the CalFire FRAP fire perimeter database (<https://www.fire.ca.gov/>). Each fire included a total area burned as well as the start and end date. From this data, we calculated the daily cumulative proportion of area burned for each year assuming a constant rate of fire growth based on fire size and duration. For example, if a fire began on July 20 and was declared as ended on July 27 then 1/7th of the area burned was assigned to the cumulative total for each of those days. However, it is important to note that this approach will tend to bias our cumulative area burned estimates towards later dates as the “mop-up” phase of a wildfire is often protracted despite little additional area burned. We then overlaid the temporal window of seed maturation with the window of fire activity to identify the proportion of area burned that could permit facultative serotiny. We defined the window of facultative serotiny as the period between the onset of seed maturation (10% viability) and 90% seed maturation based on our two study years. We expect that the ending period of this window should correspond to the typical time for cone opening and the onset seed abscission for these conifers which appears to be around early September (Schopmeyer 1974).

Data Analysis

Data from the seed maturation and heat-induced mortality studies for all four species were analyzed in R (R Core Team 2022). Seed maturation data from 2018 and 2019, seed mortality data from 2020, and cumulative area burned data from 2000–2017 were all analyzed using a generalized linear model assuming a binomial distribution. The significance level ($\alpha = 0.05$) of the main effects of each analysis were examined with the Anova function in the *car* package (Fox and Weisberg, 2019). Both seed maturation and heat treatment analysis included relative seed viability as the response variable. Relative viability was calculated as the proportion of observed viability for each collection period divided by the maximum observed viability for each species, with values ranging from 0 to 1 (Pereira 2020). With the wide variation in maximum absolute seed viability observed (Table 1), relativized proportions of viability were calculated to allow for comparisons among the examined species. The most parsimonious generalized linear model for the seed maturation study was selected based on the lowest Akaike information criterion (AIC) value (Burnham and Anderson 2004), with consideration for the parameters of heat sum, species, and year. For the heat induced seed mortality study, we considered the parameters of species and treatment and again selected the most parsimonious generalized linear model using the lowest AIC values. The same approach was used to examine the relationship of Julian date and year with cumulative area burned.

Table 1

The observed maximum absolute viability for the sampled seeds of each species in 2018 and 2019, collected in northeastern California. These values were used to calculate relative viability for each collection period for the seed maturation study.

Species	Maximum viability (%)
incense cedar	68
Douglas-fir	24
lodgepole pine	76
ponderosa pine	52

Results

Seed Maturation

Seed viability across all four species increased over time in association with the increase in heat sum over the growing season (Fig. 1) for both 2018 and 2019 ($p = 0.0013$, $z = 3.23$, $df = 42$). The best generalized linear model of seed maturation included an additive model with heat sum and species. The collection year was not included in the top model and did not quite have a significant effect ($p = 0.061$, $z = -1.87$, $df = 42$).

The onset and rate of seed maturation varied among species (Table 2). Species were informative in the best model, although we did not detect significant differences in relative seed viability with heat sum among species ($p = 0.1749$, $\chi^2 = 4.96$, $df = 3$). The onset of seed maturation (10% relative viability) was earliest for Douglas-fir (959°C heat sum, early-July) and lodgepole pine (1205°C heat sum, mid-July), and latest for ponderosa pine (1484 °C heat sum) and incense cedar (1491°C heat sum) in early August. For the four species examined, 90% relative seed viability was reached with a cumulative heat sum between 1756 °C (Douglas-fir) and 2287 °C (incense cedar), which is typically mid-August to mid-September. Based on these findings, the temporal window for facultative serotiny (10–90% relative viability) with cumulative heat sum values ranging from 1285°C and 2100°C typically occurred between the Julian dates of 200 and 260 or generally mid-July to mid-September.

Table 2

Accumulated heat sum at 10%, 50%, and 90% relative viability for four non-serotinous conifer species in Shasta County, California, as well as the seasonal timing for 10% and 90% relative viability. Heat sum values are based on predictions from the top selected model that included heat sum and species. Timing estimates for each species and viability category represent the average Julian dates associated with accumulated heat sums generated from modeled temperature data from 2000–2020 for the study site in northeastern California.

Species	10% Viability (°C)	50% Viability (°C)	90% Viability (°C)	Timing at 10%	Timing at 90%
incense cedar	1491	1889	2287	Early-August	Late-September
Douglas-fir	959	1358	1756	Early-July	Mid-August
lodgepole pine	1205	1603	2002	Mid-July	Early-September
ponderosa pine	1484	1883	2281	Early-August	Late-September

Annual variation in the heat sum accumulation from 2000 through 2020 at the study site in northeastern California varied strongly among years (Fig. 2). For instance, the heat sum for the average onset of viability (10%; 1285°C) across all species had an average Julian date of 206 (± 4.0 days 95% CI), or late July. An accumulated heat sum of 1683 °C represented the average 50% viability across all species and occurred on the Julian date of 230 (± 4.3 days 95% CI), or mid-August. Our estimate of the closing period of facultative serotiny (90% relative viability) occurred around an accumulated heat sum of 2100°C, or the Julian date of 259 (± 6.4 days 95% CI), or mid-September.

Heat-Induced Seed Mortality

Seed survival was negatively associated with increasing convective heat (Fig. 3). As the heat treatment temperature increased, relative seed viability significantly decreased across all species ($p = 0.0156$, $z = -2.42$, $df = 27$). The most informative seed mortality model included heat treatment and species. While species was informative in the most parsimonious model, it was not statistically significant ($p = 0.1895$, $\chi^2 = 4.77$, $df = 3$). Seeds of the smaller cone species, incense cedar and Douglas-fir, tended to have lower survivability to heat treatments than the larger cone species, lodgepole pine and ponderosa pine (Table 3). Douglas-fir and incense cedar were only able to maintain 50% relative seed viability up to 60°C and 105°C, respectively. Ponderosa pine and lodgepole pine maintained 50% relative viability at temperatures of 215°C and 240°C, respectively. And ponderosa pine, our largest cone, had some seeds that could survive as much as 400°C.

Table 3

The temperature of heat exposure permitting 10%, 50%, and 90% relative seed survivorship for the four conifer species studied in northeastern California. These values are based on predictions from the top generalized linear model, containing heat treatment and species.

Species	10% Survival (°C)	50% Survival (°C)	90% Survival (°C)
incense cedar	230	105	20
Douglas-fir	185	60	20
lodgepole pine	360	240	120
ponderosa pine	340	215	90

Timing of Wildfire

Recent fires in the Klamath Mountains, northern Sierra Nevada, and southern Cascade ecoregions of northern California from 2000 to 2017 mostly burned between June and September, with both lightning and human-caused fires having their highest area burned in August. However, a secondary peak was observed in June for lightning fires. During this same time and geographic area, the cumulative proportion of burned area varied significantly among years ($p < 0.0001$, $z = -5.4$), with the cumulative area burned in more recent years occurring slightly later than in earlier years. Almost all the area burned (> 99%) across the years examined occurred between 125 and 350 Julian days (Fig. 4). A total of 60% ($\pm 7.6\%$ 95% CI), of the cumulative area burned was within our estimated window of facultative serotiny (200 and 260 Julian date); that is, more than half the area burned had the capacity for in-situ regeneration by non-serotinous conifers following high severity fire.

Discussion

Here we provide support for the possibility of facultative serotiny in northeastern California across the four conifer species examined. Within this region, we demonstrated the timing of seed maturation (approximately mid-July to mid-September) coincided with the time when most fire occur (60% by area) and that seeds within cones can be protective of the heat experienced during wildfires. In combination, these results are aligned with our expectations that non-serotinous conifer species can colonize the interior portions of high severity burn patches from seed that survives in the canopy. Yet, the temporal and geographic extent of facultative serotiny remains uncertain as its occurrence will depend on several factors including the probability of a fire occurring when closed cones contain viable seed, the number of cones and viable seeds available, cone characteristics of the species (e.g., size and placement), and the intensity of the fire.

Seed Maturation

We provide the first known study to examine the relationship between heat sum and seed maturation in lower latitude temperate forests across multiple conifer species. While our findings align with previous

research that seed viability increases with accumulated heat sum (Henttonen et al. 1986, Zasada et al. 1992, Sirois et al. 1999, Fedorkov 2001, Meunier et al. 2007, Michaletz et al. 2013), there were marked differences in the timing and duration of seed maturation from other studies. The onset of seed maturation in our study began in late July with heat sums ranging between 959 °C to 1491 °C and closed around mid-September with heat sums ranging between 1756 °C to 2287 °C. However, other studies have demonstrated a more abbreviated schedule where seed maturation began with heat sums around 600°C and closed around 1100°C (e.g., Henttonen et al. 1986, Michaletz et al. 2013). A tendency for the required heat sum for a phenophase to decrease with latitude has been reported elsewhere for phases such as budburst or leaf fall (e.g., Beuker 1994, Gao et al. 2023), and it is likely that these observed differences are attributable to latitudinal variation across reported study sites. These differences highlight the importance of considering the local climate (i.e., temperature) and topography (i.e., elevation and latitude) context when examining seed maturation schedules and the potential for facultative serotiny.

Our estimated temporal window for facultative serotiny (late-July to early-September) will vary annually. Based on examination of 20 years of recent temperature data at our site, the window of facultative serotiny can vary by 4 to 7 days. We also note that the closing period of our estimate is based on the timing of 90% seed viability and that this may be a conservative estimate considering that cones may not open and release seeds until later. While reports indicate that seed abscission commonly begins in early-September for many species (Schopmeyer 1974), direct examination of cone opening and seed release schedules would provide better estimates and is an area of future research we are pursuing.

The lack of a substantial influence of species on the relationship between cumulative heat sum and seed maturation in our study suggests that the timing of seed maturation, and thus the propensity for facultative serotiny, may be relatively consistent across conifer species in northeastern California. While we were unable to detect a strong influence of species, it was informative in our best model of relative seed viability, suggesting that species may differ in their maturation schedules. Future studies that consider larger sample sizes may increase the power to detect differences among species.

Seed Survival Relative to Heat Exposure

The observed decline in seed survival with increasing temperature corroborates previous studies across a wide range of species (e.g., Zasada et al. 1979, Johnstone et al. 2009, Milich et al. 2012, Michaletz et al. 2013). While differences in seed survival among species were subtle in our study, we observed that species with smaller cones tended to have lower heat tolerances than species with larger cones. These observations confirm recent results from a fire simulation study that found smaller cones with less protected seeds (i.e., shallower seed depth) experienced higher potential seed mortality rates (Greene et al. 2024). However, our findings are somewhat limited due to relatively small sample sizes in only four species. Future studies might consider examining more species across a wider range of cone sizes with larger sample sizes to better examine the potential relationships between cone traits and seed mortality due to heat exposure.

We note that our heating treatments do not fully reflect the heat flux cones typically experience during high severity crown fire conditions. Maximum temperatures associated with high intensity fires within the mid- to upper canopy can be over 1000°C (Butler et al. 2004). Based on our study, this implies that most seeds would not survive these upper temperatures. However, these temperatures rarely last more than 10 to 20 seconds. Cones in high severity wildfires likely experience a wider range of temperatures and durations that could permit seed survival, especially if heat pulses are shorter than the 150 seconds we selected. Additionally, the heat pulses from wildfire are difficult to reproduce in a lab setting and the static temperatures of a muffle furnace are unlikely to replicate the dynamic heat fluxes experienced during a wildfire. However, our study included a high of 600 °C for 150 seconds to reflect the potential upper bounds of heat exposure during high intensity fire, which is higher than the rapid heat flashes over 1000°C experienced for 10 to 20 seconds (Butler et al. 2004). That is, survival may be more likely in the rapidly varying temperature regime of a flaming front than in the uniform environment of a muffle furnace. Furthermore, most ovulate cones are in the upper portion of the crown, which can result in lower heat-induced seed mortality due to exposure to lower plume temperatures and durations when compared to cones in the lower and middle crown positions (Splawinski et al. 2019).

Our finding that viable seeds should be able to survive fire within cones must be tempered by the fact that seed survival will be highly dependent on fire intensity. One study in black spruce estimated 86% seed survival following fire (Zasada et al. 1979). In another study seed viability in black spruce following fire similarly ranged between 61% and 81% based on crown position, such that the side of the crown with more intense charring had greater seed mortality (Splawinski et al. 2019). Although a separate study with black spruce indicated much lower seed viability (< 10%) following the highest severity fires examined (Johnstone et al. 2009). Similarly, a computational study for white spruce cones estimated that only 12% of the seeds should survive representative crown temperatures during fire (Michaletz et al. 2013). Given this wide range of empirical outcomes, it is likely that post-fire seed survival will depend on the intensity of fire. Additional research is needed to determine the thresholds and circumstances that contribute to this variation.

Timing of Wildfire

Sixty percent of the area burned in northern California forests from 2000 to 2017 occurred from late-July to early-September (our estimated window for facultative serotiny) with lightning fires contributing to a higher proportion of this total area than human ignitions. Our findings are similar to the estimated 50% of the area burned in lightning fires that overlapped seed maturation in white spruce in Canada (Michaletz et al. 2013). Given that lightning-ignited fires tend to result in lower intensities than human ignitions (Hantson et al. 2022), it is plausible that facultative serotiny may be more common following high severity lightning-ignited fires that occur during this time.

The occurrence of facultative serotiny will also be influenced by changing climatic conditions given the likelihood of continued warming and further seasonal shifts in fire activity, but the direction and magnitude of this change remains uncertain. Increased warming will likely result in earlier seed maturation and abscission, shifting the window of facultative serotiny to earlier in the year. Conversely, it

is presumed, based on previously described shifts in fire activity, that fires will increasingly burn more frequently later in the season (Westerling 2016), potentially resulting in proportionately less burned area overlapping with the window of facultative serotiny. This observation is consistent with our results that show cumulative area burned for northern California between 2000 and 2017 has shifted to slightly later in the year. If both trends hold true, we expect that the incidence of facultative serotiny would decline under future climate and fire conditions.

Many regions in western North America have experienced increases in fire frequency and severity (Westerling 2016, Parks and Abatzaglou 2020), resulting in a greater need to consider reforestation (North et al. 2019). However, given the limited availability and increasing demands on nursery stock (Fargione et al. 2021), improved post-fire regeneration modeling that considers facultative serotiny may better inform replanting efforts. For instance, areas resulting in regeneration from facultative serotiny could represent a lower priority for reforestation.

Areas for future inquiry

While we have demonstrated that facultative serotiny is mechanistically supported across multiple conifer species, it is uncertain how frequently this process occurs. We can expect that the incidence of facultative serotiny is much less than the 60% of fires that would permit its occurrence or else it would have been more commonly documented in previous studies. The incidence of this regeneration mechanism is likely lower due to variation in cone production and fire intensity. Cone production in most non-serotinous conifers is highly right-skewed, with most years having lower levels of cone production with less frequent mast years (Greene and Johnson 2004). Thus, the more frequent occurrence of low cone producing years would expectedly result in low post-fire regeneration density that would be indistinguishable from long-distance dispersal. It is also likely that the intensity of fire often exceeds the ability of cones to protect seeds, and so we would also expect lower incidence and detectability of facultative serotiny, especially in species with very small cones such as *Tsuga* or *Larix* (Greene et al. 2024). Future research that examines the role of cone production and fire intensity are necessary to advance our understanding of the frequency with which this mechanism occurs.

Still, we think that facultative serotiny is not entirely rare either. It is likely that facultative serotiny has been underrepresented in the literature due to the limited number of deliberate studies intended to examine it. Here we suggest several methods for detecting this regeneration mechanism in locations where the timing of fire and seed maturation are conducive. The first method would be to monitor seedling regeneration in non-serotinous species along transects perpendicular to the living forest edge and extending deep (> 300 m) into a large high severity patch (e.g., Pouden et al. 2014). Facultative serotiny will be evident where seedling densities do not steeply decline with distance from the living edge. A second method would be to examine regeneration around stands of isolated conspecifics in a matrix of other species within a high severity patch. One could extend transects from the center of each stand outward, counting recruits as well as recently fallen and still-appended cones. If facultative serotiny is apparent, then there will be a positive relationship between recruit density and cone density throughout the high severity patch. Third, one could promptly (before seed abscission) visit a recently

burned site and cut burned trees down, collect the cones, and test the seeds for germinability (e.g., Splawinski et al. 2019). This approach must be done very soon after the burn because the heat from fire greatly accelerates the drying of the scales and thus the rate at which they open; for serotinous pines, Marlin et al. (2024) and Greene et al. (2013) reported that most of the seeds were on the ground within two months. Summarizing, we feel that if researchers started employing these methods or others, the number of reported examples of facultative serotiny would increase.

Conclusions

Our research provides support for the potential of facultative serotiny to contribute to substantive post-fire regeneration following high severity fire across four non-serotinous species in northeastern California, with the potential to more broadly apply to other fire-prone regions globally. While more research is needed to determine the extent and magnitude of facultative serotiny, the development of future post-fire conifer regeneration models would likely benefit from considering factors such as cone and seed production, timing of wildfire, and fire intensity. Inclusion of these factors could explain observed incidences of high-density post-fire regeneration far from the living forest edge (e.g., Larson and Franklin 2005, Pouden et al. 2014) that are not captured by current post-fire regeneration models (e.g., Shive et al. 2018, Stevens-Rumann and Morgan, 2019).

Throughout this paper, we have emphasized the central role of timing in determining the density of post-fire recruits. Particularly, the timing of fire and seed maturation are key. We conclude that the mechanism should be uncommon but not rare. We normally think of the fire-prone, conifer-dominated landscape as one where the serotinous species are found at high density in the younger stands while the non-serotinous species are mainly in the older patches or the edges of more recent fires (due to limited dispersal). But facultative serotiny allows a non-serotinous species to occasionally develop high recruit densities across a high severity patch if (as with serotinous species) it was major component of the site before fire. The emphasis on timing also underscores that the subsequent composition of the canopy stratum decades later is contingent on the weather-driven dynamics of cone production and fire. Early arrival of regeneration after fire confers an advantage in the subsequent competition for light and the probability of becoming a canopy tree. The size of the crop and fire activity are differentially weather-dependent, with fire patterns influenced by weather of the current summer (Williams and Abatzaglou 2016) and cone production influenced by weather in the preceding two growing seasons (LaMontagne et al. 2020).

Declarations

Ethics approval and consent to participate

not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Funding

This work was supported by the USDA National Institute of Food and Agriculture, McIntire-Stennis Cooperative Forestry Research Program, Project #CALZ-170. Additional funding was awarded to M. Lopez by the California Native Plant Society Grant (North Coast chapter), Northwest Scientific Association Grant, and the Dillard-Bailey Graduate Scholarship.

Authors' contributions

MAL: investigation, supervision, formal analysis, writing- original draft, writing-review and editing; JMK: conceptualization, funding acquisition, supervision, formal analysis, writing-review and editing; DFG: conceptualization, funding acquisition, supervision, writing-review and editing.

Acknowledgements

Erik Jules provided helpful comments on an earlier draft of the manuscript. Field and lab work was provided by G. Rhoades, R. Barajas-Ramirez, K. Marlin, J. Mianji, A. Jones, A. Bairstow, B. Long, and K. Fletterick.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Figures

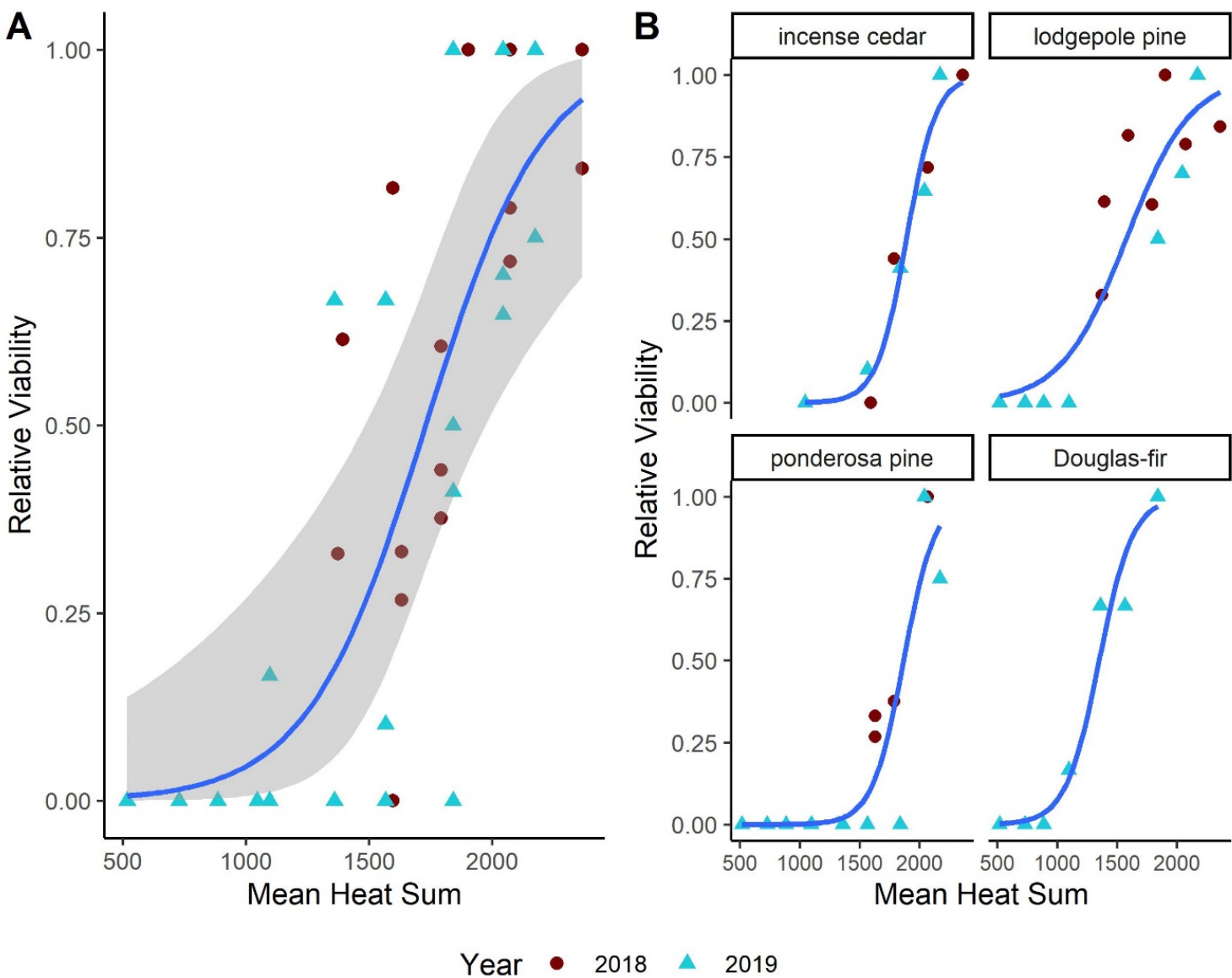


Figure 1

The positive relationship between mean heat sum and mean relative viability ($p = 0.0013$, $z = 3.23$) in 2018 and 2019, based on a generalized linear model, with 95% confidence intervals in gray for A) all

species combined and B) each individual species. All cone collections were from northeastern California.

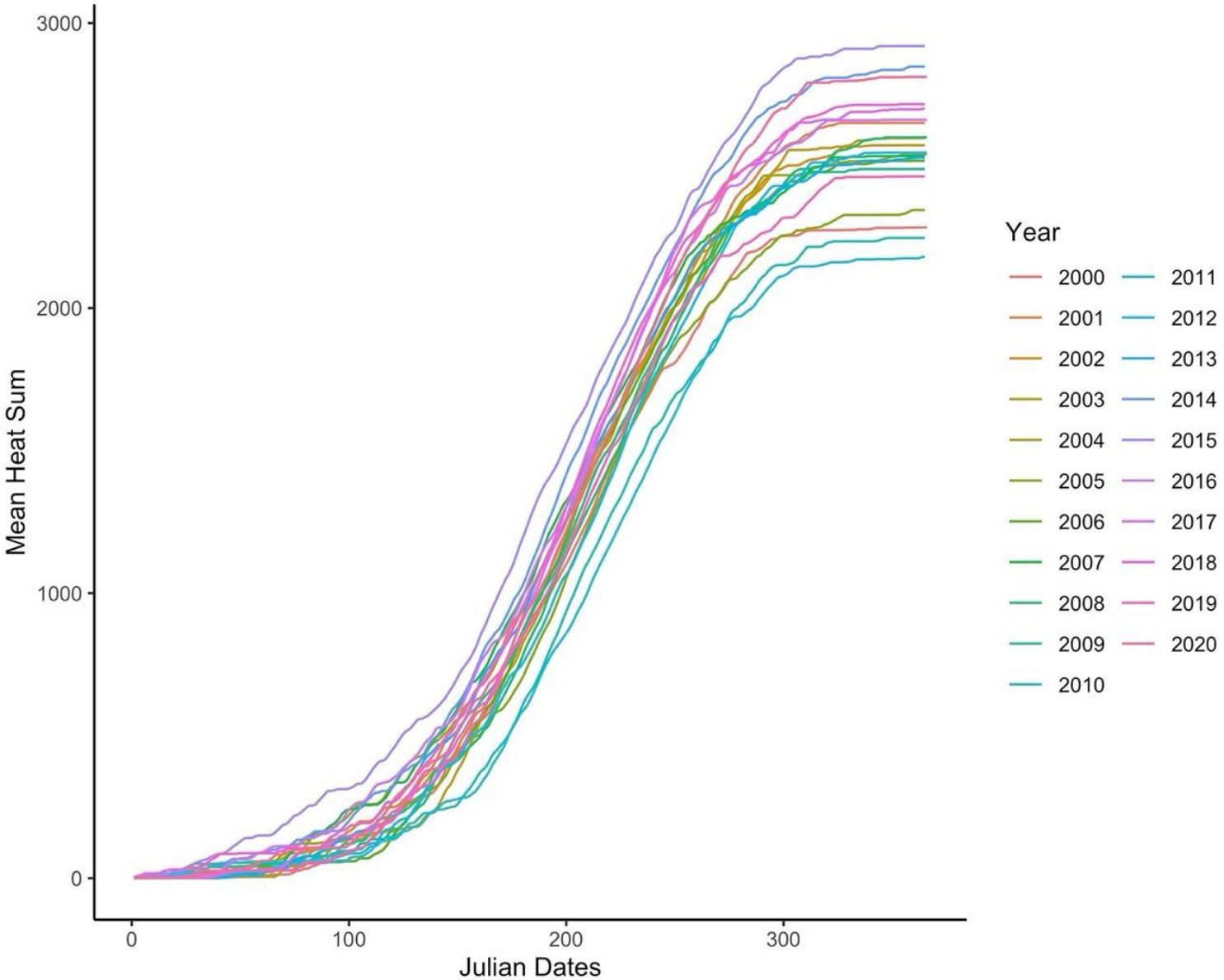


Figure 2

The accumulated heat sum by Julian date for the study site in northeastern California demonstrating the variability in annual patterns of heat accumulation from 2000 through 2020 (PRISM, 2020).

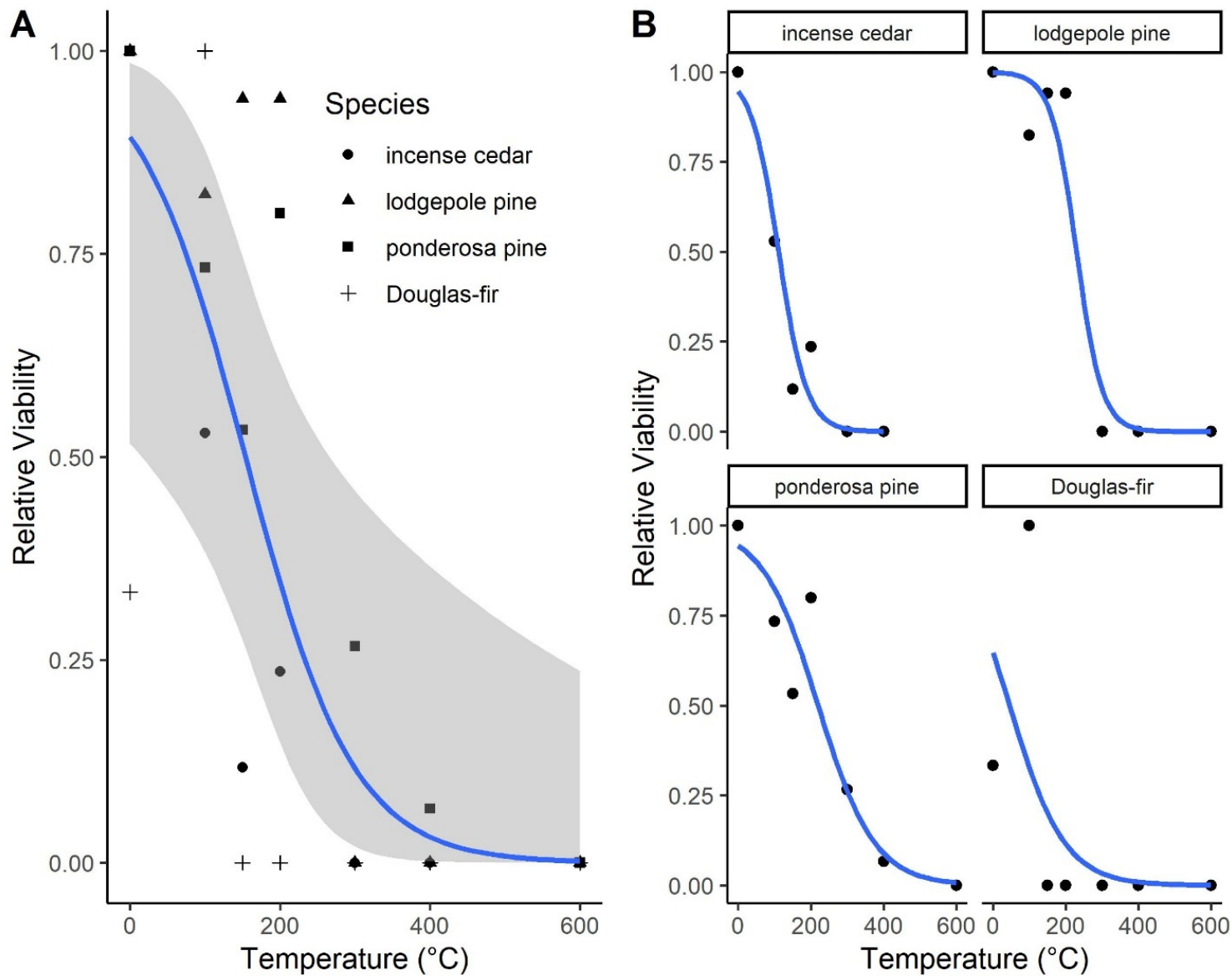


Figure 3

A negative relationship between relative seed viability and heat exposure temperature ($p = 0.0156$, $z = -2.42$), based on a generalized linear model, with 95% confidence intervals in gray for A) all species combined and B) each individual species. Cones were collected in 2020 from northeastern California.

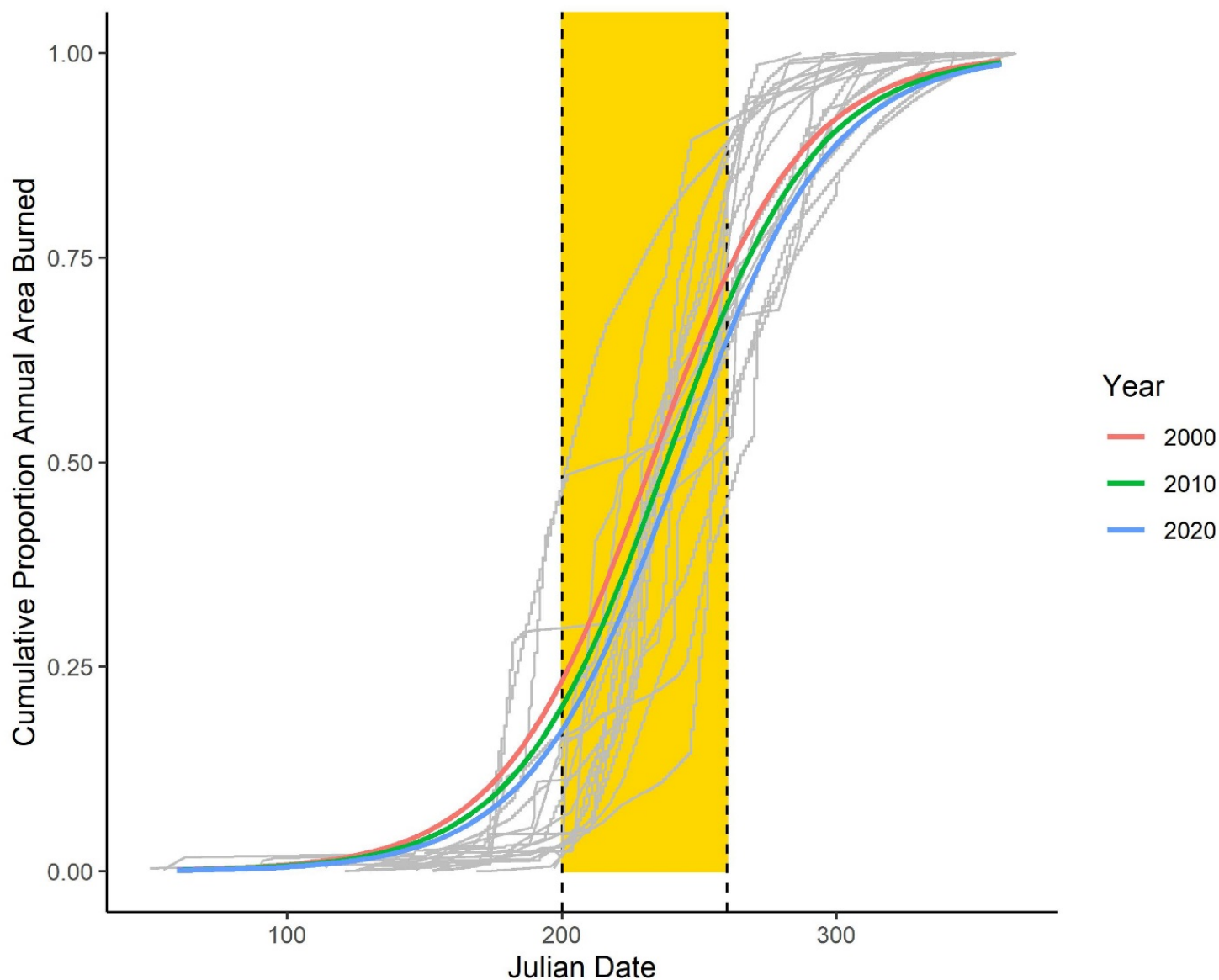


Figure 4

Cumulative proportion of annual area burned from 2000 to 2017, based on start dates, in northern California (Klamath, northern Sierra Nevada, southern Cascade ecoregions). The yellow area represents the temporal window of facultative serotiny (using 10% relative viability as the start and 90% viability as the end), which encompassed 60% (annual range: 33% to 86%) of the burns. The temporal window for facultative serotiny includes the Julian date of 200 through 260 (late-July to mid-September). Gray lines represent cumulative area burned by year and colored lines represent the generalized linear model results of the year effect.