

INVESTIGATING SEED MATURATION AND MORTALITY: A MECHANISM
FOR POST-FIRE REGENERATION IN NON-SEROTINOUS CONIFERS

By

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A Thesis Presented to

The Faculty of California State Polytechnic University, Humboldt

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Forestry, Watershed, and Wildland Sciences

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May 2022

ABSTRACT

INVESTIGATING SEED MATURATION AND MORTALITY: A MECHANISM FOR POST-FIRE REGENERATION IN NON-SEROTINOUS CONIFERS

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Climate warming and associated dry conditions are contributing to increased fire frequency, severity, and size, for many regions in western North America. These changes in fire activity have prompted concern over the long-term persistence of some conifer species, specifically those not adapted to withstand high-severity fire. However, regeneration of non-serotinous conifer species is possible if the timing of fire occurs following seed maturation, and within a heat range that seeds can withstand, in a regenerative mechanism termed “facultative serotiny.” To address this mechanism, I determined the timing of conifer seed maturation using viability testing for four California conifer species: ponderosa pine (*Pinus ponderosa*), Sierra lodgepole pine (*Pinus contorta* var. *murrayana*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*). The unopened conifer cones were collected for these non-serotinous species throughout three summers near Burney, California. Additionally, I identified the capacity for seed survival relative to heat exposure with seven heat treatments at: no heat (control, ~20°C), 100°C, 150°C, 200°C, 300°C, 400°C, 600°C, followed by viability testing. The accumulated heat sum was significantly associated with seed maturity, indicating over 50% maturity from late July to August (1358°C to

1889°C). Higher heat exposure was negatively associated with seed survival, although seed survival occurred with temperatures as high as 340°C for 150 seconds. My findings identify conditions suitable for the occurrence of facultative serotiny following stand-replacing 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 aid in future non-serotinous conifer forest management in fire-prone ecosystems.

ACKNOWLEDGEMENTS

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 provided by the California Native Plant Society Grant (North Coast chapter), Northwest Scientific Association Grant, and the Dillard-Bailey Graduate Scholarship. I would like to thank my advisor Jeffrey Kane for his support, as well as equal support and guidance from my dedicated committee members David Greene, and Erik Jules. Lastly, I thank my 2018-2019 field crews as well as 2019-2020 volunteer lab assistants Grace Rhoades, Raul Barajas-Ramirez, Katherine Marlin, Jayron Mianji, Abigail Jones, Alex Bairstow, Brittany Long, and Kelsey Fletterick.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	v
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
INTRODUCTION.....	1
MATERIALS AND METHODS.....	8
Site location.....	8
Seed Maturation.....	10
Heat-Induced Seed Mortality.....	12
Data Analysis.....	15
RESULTS.....	18
Seed Maturation.....	18
Heat-Induced Seed Mortality.....	25
Timing of Wildfire.....	29
DISCUSSION.....	32
Seed Maturation.....	32
Seed Survival Relative to Heat Exposure.....	34
Timing of Wildfire.....	36
Implications.....	37
LITERATURE CITED.....	39

LIST OF TABLES

Table 1. The observed maximum absolute viability for the sampled seeds of each species in 2018 and 2019, collected in Shasta County, California. These values were used to calculate relative viability for each collection period for the seed maturation study.	17
Table 2. Accumulated heat sum at 10%, 50%, and 100% relative viability for four non-serotinous conifer species in Shasta County, California, as well as the seasonal timing for 10% relative viability. These values are based on predictions from the top model, which was an additive model including heat sum and species.	22
Table 3. The temperature of heat exposure permitting 10% and 50% relative seed survivorship for the four conifer species studied in Shasta County, California near Burney. These values are based on predictions from the top model, which was an additive model with treatment and species.	28

LIST OF FIGURES

- Figure 1. Locator map of Shasta County, CA, where all the ovulate cones for the four examined species were collected. 9
- Figure 2. The significantly positive relationship based on a generalized linear model, with 95% confidence intervals in gray, between mean heat sum and mean relative viability ($p = 0.0013$, $z = 3.23$). All examined species are pooled together from 2018 and 2019, as the year and species sampled did not significantly impact seed viability as the heat sum increases (year $p = 0.061$; species $p = 0.1749$). The examined species include incense cedar, lodgepole pine, ponderosa pine, and Douglas-fir. All collections were made in Shasta County, California. 19
- Figure 3. The positive relationship between relative seed viability and the accumulating heat sum for each of the studied species in Shasta County of northern California in 2018 and 2019. The examined species include incense cedar, lodgepole pine, ponderosa pine, and Douglas-fir. 21
- Figure 4. The accumulated heat sum by Julian date for the study site near Burney, California, demonstrating the relatively low variability in annual patterns of heat accumulation, from 2000 through 2020 (PRISM, 2021). 24
- Figure 5. Relative seed viability rates, with 95% confidence intervals in gray, for all examined species pooled together, as exposure to heat increases via muffle furnace (used as a proxy for fire). A significant negative relationship is reported for relative seed viability rates with increased heat exposure for all species ($p = 0.0156$, $z = -2.42$). The examined species include incense cedar, lodgepole pine, ponderosa pine, and Douglas-fir, with all cone data collected from Shasta County, California. 26
- Figure 6. Relative seed viability for each examined species, as a function of heat exposure temperature treatments implemented via muffle furnace that was used as a proxy for fire. A consistent negative relationship is shared across each species between increased heat exposure and relative viability rates. The examined species include incense cedar, lodgepole pine, ponderosa pine, and Douglas-fir, with all cone data collected from Shasta County, California. 27
- Figure 7. Fire distribution in the Klamath, Sierra Nevada, and the Cascade ecoregions from 1950 to 2017, delineated by human and natural causes (MTBS, 2018). 30
- Figure 8. Cumulative proportion of annual area burned from 2000 to 2017, based on start dates, in northern California (Klamath, Sierra Nevada, Cascade ecoregions). The yellow represents the temporal window of facultative serotiny (using 10% relative viability as the start and seed abscission as the end), which encompassed 68% (annual range: 39%-

93%) of the burns. The temporal window includes the Julian date of 200 through 265
(mid-July- September). 31

INTRODUCTION

Current climate warming and dry conditions are contributing to an increase in fire frequency, severity, and size, for many regions in western United States (Moritz et al. 2012; Dennison et al. 2014; Westerling, 2016; Parks and Abatzoglou, 2020). Changing fire regimes have prompted concern over the persistence of many woody plant species, specifically those not adapted to withstand high severity fires. An increase in fire frequency can greatly lessen the abundance of non-serotinous species (Enright et al. 2015) and also has the potential to decrease the abundance of serotinous species (Westerling et al. 2011). As a fire interval shortens, the present tree species can face an immaturity risk if individuals are unable to reach reproductive maturity and to contribute progeny to the next generation before the time of fire (Zedler et al. 1983). If the fire interval becomes too short to support the tree species, a stand-type conversion may occur (Keeley and Brennan, 2012; Collins and Roller, 2013).

Serotiny is a fire-adaptive strategy that maintains an abundance of seed within the crown (aerial seed crop) by retaining closed resinous cones for one to 30 years and releasing the crop in the presence of high fire temperatures (Lamont et al. 1991; Johnson and Gutsell, 1993). This convergent trait dates back to the Cretaceous (Keeley, 2012) and has since evolved independently among many southern hemisphere angiosperms (Lamont et al. 1991) but is most prevalent in North America in the two gymnosperm genera, *Pinus* (pine) and *Hesperocyparis* (cypress) (McMaster and Zedler, 1981; Barbour, 2007). Previous work has indicated that the serotinous *Pinus contorta* var. *latifolia* (Rocky

Mountain lodgepole pine) has an aerial seed bank approximately four times the mean annual viable seed production of a non-serotinous species with a similar cone size (Greene and Johnson, 1995; Bates et al. 2002); that is, several decades of serotinous cone production are equivalent to a mast year for these non-masting species.

Ovulate cones are primarily distributed in the upper third of the canopy (Greene and Johnson, 1989) and during the time of fire, cones are exposed to prolonged heat from the flaming front. The temperatures associated with the flaming front vary depending on fire type (surface or crown) and intensity, such that field-based studies on crown fires have reported temperatures from 200°C to 1330°C (Hobbs and Gimingham 1984; Habrouk et al. 1999, Butler et al. 2004), with flame temperatures decreasing with height (Michaletz and Johnson, 2007; Splawinski et al. 2019). Serotinous cones have been shown to maintain viable seed crops with temperatures up to 400°C for one minute (Habrouk et al. 1999; Fernandes and Rigolot, 2007). The high temperatures associated with fire promote the weakening of the resinous bond sealing serotinous cone scales shut (Johnson and Gutsell, 1993) which then facilitates the reflex of cone scales and a subsequent release of an abundant seed source. Further, each tree within the burn is able to act as a seed source despite tree mortality, such that the abundant seed source coupled with high quality mineral soil exposure from smoldering combustion, relaxes the dispersal constraint for these serotinous species.

It is possible that non-serotinous species are also capable of relaxing the dispersal constraint following fire, similar to serotinous species. A modeling study from Michaletz et al. (2013) demonstrated that a sufficient portion of non-serotinous seeds should survive

a crown fire if seed maturation precedes the timing of the burn. There is also evidence that suggests non-serotinous ovulate cones retain higher moisture content compared to serotinous species (Greene et al. in prep), giving non-serotinous species an advantage during high severity fires. Non-serotinous species may also be exposed to lower temperatures given that a fresh cone crop placement tends to reside in the upper portion of the crown (Michaletz and Johnson, 2007). Further, cone scales isometrically increase with the size of ovulate cones (Greene et al. in prep), thus species that produce larger cones should experience lower rates of seed necrosis. Therefore, if non-serotinous cone scales are sufficiently protective from the heat of the fire, the density of recruitment is dependent on the size of germinable seed crop, with mast years giving the potential for high-density recruitment.

The driving force that determines population dynamics and regeneration following fire is the availability of viable seeds within or adjacent to the burn site (Habrouk et al. 1999; Hansen et al. 2018). Non-serotinous conifers that reproduce via seed are often reliant on wind and gravity to disperse viable seeds and most studies indicate that post-fire regeneration is primarily based on the proximity to a living forest edge (Agee, 1996; Greene and Johnson, 1996; Welch et al. 2016; Stevens-Rumann and Morgan, 2019). Typical post-fire regeneration patterns have identified the surviving non-serotinous trees within 100 m of adjacent unburned forest to be responsible for the bulk of the non-serotinous regeneration in burn patches (Greene and Johnson, 2000), such that an increase in the size of a severe burn area contributes to lower regeneration rates in the interior of the burned patch, as dispersal distances are exceeded for non-serotinous

species (Greene and Johnson, 1996; Keeley et al. 1999; Hansen et al. 2018; Turner et al. 2016; Stevens-Rumann and Morgan, 2019). Conversely, serotinous species can act as a seed source despite tree mortality, resulting in high density recruitment within the burn area following a severe fire (Lotan, 1967; Greene and Johnson 1999; de Groot et al. 2004; Turner et al. 2007; Maia et al. 2012; Fernandez-Garcia et al. 2019).

Evidence of high-density recruitment in non-serotinous conifers following high severity fires has been reported at great distances from a living seed source. It is possible that non-serotinous tree species have the capacity to disperse viable seeds from trees killed by fire in an alternative mode of regeneration I term facultative serotiny. To exemplify, Douglas-fir, a non-serotinous pine, has demonstrated dense regeneration in high-severity burn sites located several hundred meters away from the nearest living conspecific source (Larson and Franklin, 2005). Given that non-serotinous species are 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 in non-serotinous stages or varieties of *Pinus contorta* far from a living edge have also been observed. For example, Turner et al. (2019) reported well stocked stands of lodgepole pine (*Pinus contorta* var. *latifolia*) following a late season reburn event in Yellowstone National Park (1988 and 2016) when

most of the pines had yet to express serotiny. Furthermore, 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 Lassen Volcanic National Park (Harris et al. 2021).

The abundance of post-fire regeneration via facultative serotiny is dependent on the proportion of seeds that have reached maturity at the time of fire. Previous studies have established that the timing of seed maturation is a function of heat sum $>5^{\circ}\text{C}$ for a specific location, with 5°C allowing for metabolic activity within woody plants (Henttonen et al. 1986; Zasada et al. 1992; Sirois et al. 1999; Fedorkov 2001; Meunier et al. 2007; Michaletz et al. 2013). With the collation of data from studies of maturation on Engelmann spruce and the closely-related white spruce, Michaletz et al. (2013) found that seed viability began with approximately 600°C of accumulated heat in southern Canada, with cone opening varying by location and occurring with a mean accumulation of 1177.29°C . In Sweden, Scots pine (*Pinus sylvestris*) reached 50% maturation at a heat sum of 890°C (Henttonen et al. 1986). Additionally, black spruce follows a similar pattern, with 100% maturation reached by $800\text{-}940^{\circ}\text{C}$ in the northern boreal forest (Sirois et al. 1999). Following seed maturation, the ovulate cone scale tissue expands and begins to reflex the scales in response to decreasing relative humidity (Song et al. 2015). Seeds are primarily disseminated and dispersed in the fall, and far fewer in the winter or spring (Tanaka, 1995; Oliver and Larson, 1996), with the great majority of conifers beginning cone scale flexing and seed abscission in September (Schopmeyer, 1974). If the majority of a population has not had the required time to form a viable aerial seed bank at the time

of fire, contribution to the next generation will be low. Conversely, if a proportion of seeds mature prior to fire, and the cone scales adequately protect the reproductive propagules during a fire such that seed mortality is evaded, then viable seeds should be available to restock the burn patch, without a dispersal constraint, in non-serotinous species. Additionally, the fire regimes of western North America are shifting to become longer with a warming climate and earlier spring snowmelt (Westerling et al. 2016), indicating greater potential for facultative serotiny. That is, as fire occurs later in the season, there are greater proportions of viable seeds available to contribute to future generations.

Understanding post-fire regeneration is essential for predicting future population dynamics of woody plant species. I propose that non-serotinous tree species can regenerate and persist post-fire through contributing abundant, well-protected seed crop to the canopy, in a regenerative mechanism I term facultative serotiny. This research aims to expand the understanding of facultative serotiny by examining seed maturation schedules and the temperature threshold for seed mortality in four common northern California conifers. I investigated and tracked conifer seed development as well as identified the capacity of seeds to survive with increasing levels of heat exposure, for the four non-serotinous California conifers: ponderosa pine (*Pinus ponderosa*), Sierra lodgepole pine (*Pinus contorta* var. *murrayana*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*), throughout multiple growing seasons, in Lassen National Forest. I address the issue of non-serotinous woody plant species persistence and suggest a regenerative mechanism that permits the existence of these species in

landscapes where severe fire dominates. Given that the proportion of available viable seeds is the lead determinant in species composition following fire, it is of utmost importance to understand the mechanism that drives the timing of maturation, and the limitations of heat exposure for seed survival during fire. The characterization of such a mechanism will aid in improving the accuracy for post-fire regeneration modeling and will provide insights for land management techniques (i.e., planting) following a stand-replacing fire.

MATERIALS AND METHODS

Site location

All field collections were made along public roads within the Lassen National Forest near Burney, California (40.8432, -121.7088), at elevations ranging from 980 to 1680 m. This forested region is currently used as a plantation and the trees that supported cone collections were 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 (Figure 1), hosting scattered volcanic soils which give rise to unique plant communities, including a rare Baker cypress (*Hesperocyparis bakeri*) population. Additionally, this region generally is comprised of Holland, Bobbitt, Aquolls, and Skalan soils that support mixed conifer forests, scattered oaks, and Sierra lodgepole pine encroached meadows (Lassen soil survey 1982; NRCS 2020). Multiple conifer species contribute to the composition of Lassen National Forest, however, the selected tree species for study includes those that are common in California and hold commercial value. The species utilized for this research 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, as well as 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 ranged across collection years with 93.2 cm in 2018, 139.5 cm in 2019, and 67.6 cm in 2020.

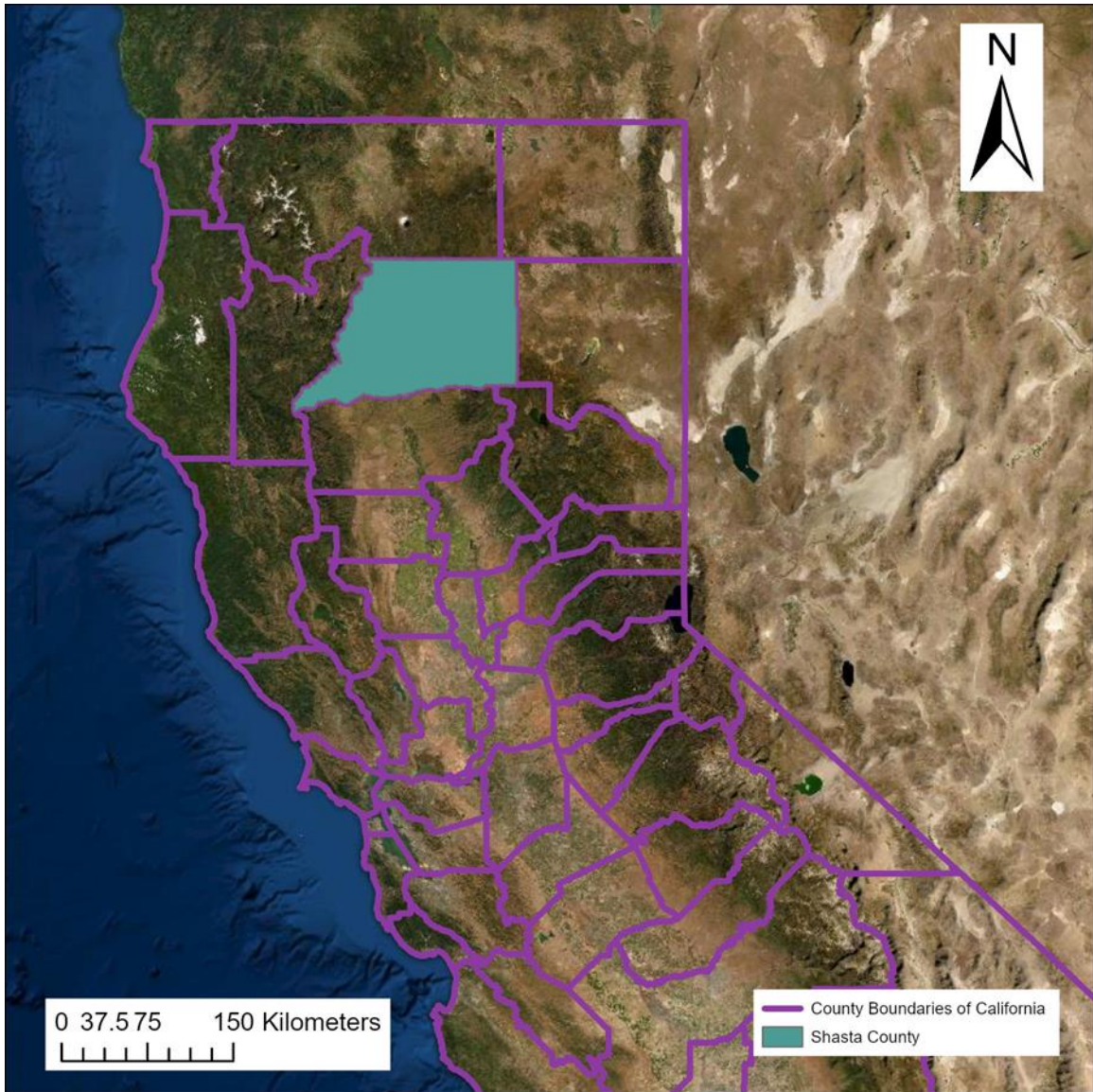


Figure 1. Locator map of Shasta County, CA, where all the ovulate cones for the four examined species were collected.

Seed Maturation

The ovulate cones of each species were collected in their second year of development, except for incense cedar as the cones only take one year to develop. The ovulate cone collections were made every other week in June, July, August, and September for both 2018 and 2019. Pole pruners were used to collect maturing cones within the crown that had closed cone scales, just turned brown, and were absent of obvious insect damage. The sampled trees varied in height, ranging from 2 to 10 m. The number of sampled trees and cones per species were dependent on the cone size and expected amount of seeds per cone. 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 trees were sampled per collection date 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 Cal Poly Humboldt Wildland Fire Lab and immediately placed into a forced convection oven at 23°C. Slowly drying the cones after collection allowed for the cone moisture to evaporate, such that fungal growth was limited and cone opening was enhanced without effect on seed viability. Once the cone scales reflexed, all seeds were manually extracted from each corresponding 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, in which case all 25 seeds 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 edge, 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 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 and site, specifically using localized 2018 and 2019 climate data from a single grid cell (PRISM 2020). Heat sum represented the cumulative thermal sum where the mean daily air temperature exceeded 5°C, thus each day with a mean daily temperature above 5°C was included in the calculation by removing 5°C from $T_{i,mean}$ (Equation 1). Temperatures above 5°C are warm enough to allow for metabolic activity within woody plant species, such that gametophytes and embryos were able to develop (e.g., Meunier et al. 2007). By assigning a heat sum value to each collection date, I was able to understand the heat accumulation pattern across each year and apply it to future seasons in spite of variable and shifting

annual temperatures. The annual heat sum was also calculated for this region spanning from 2000 to 2021, to identify the typical pattern of accumulation and associated variation of timing between years. The equation used to calculate heat sum (HS) was:

$$HS = \sum_{i=1}^n [(T_{i,mean}) - 5] \quad \text{Equation 1}$$

Such that $T_{i,mean}$ represents the daily average temperature (°C).

With the identification of the timing of fires in these ecoregions, and the timing of seed maturation, I was able to estimate the temporal period that permits regeneration via facultative serotiny. I obtained the 2000-2017 fire perimeter data of all wildfires in northern California from the Monitoring Trends in Burn Severity (MTBS 2020) program. The annual cumulative proportion of area burned (ha) was assigned to the Julian start date, assuming a steady state of fire growth from the start date for fires that spanned more than one month. I then overlaid the temporal window of seed maturation to identify the proportion of area burned that may be conducive to facultative serotiny. This window was defined as the onset of seed maturation (10% viability) to the typical time for seed abscission for these conifers (September; Schopmeyer, 1974).

Heat-Induced Seed Mortality

To examine heat-induced seed mortality thresholds among cones of the four species examined, I used a muffle furnace to generate heat as a proxy for fire temperatures. Cones for this part of the study were collected in 2020 based on accumulated heat sum and seed maturation data from 2018-2019. I determined the

optimal cone collection date (period of maximum viability prior to seed abscission) using tracked heat sum data based on 2020 PRISM temperature data and calculated using Equation 1. The seed maturation study from 2018 and 2019 indicated that an accumulated heat sum of approximately 2200°C would correspond with maximum seed viability for all four species. Therefore, the 2020 cone collections were made on September 5th when 2146.2°C had accumulated. The developed ovulate cones were then collected with pole pruners from the canopy, following the same methods as seed maturation. I sampled a minimum of 50 cones from 2 to 13 trees for each species, which ranged from 3 to 10 m in height. The cones were kept cool until testing could be conducted to maintain cone closure and the state of seed maturity.

To define the threshold of heat that permits mortality for each species, heat exposure treatments were used as a proxy for fire temperatures. The use of all four species allowed for a thorough investigation across a range of cone sizes, with incense cedar being the smallest and ponderosa pine being the largest. The heat exposure tests were performed in a muffle furnace using a total of seven heat treatments at: no heat (control, ~20°C), 100°C, 150°C, 200°C, 300°C, 400°C, 600°C. These temperatures were selected to represent air temperatures typically experienced at the height of cones based on observed and modeled wildfires (Butler et al. 2004; Michaletz et al. 2013). I used Omega type K thermocouples, with a testable temperature range that spanned from 200°C to 1250°C, connected to a Campbell Scientific CR1000 data logger, to record the maximum temperature ($\pm 10^\circ\text{C}$) within the muffle furnace. For each heat treatment, five cones were randomly selected from each species, with the exception of 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 divot of the metal pan, which was then placed into the muffle furnace. Once the proper temperature was reached, the selected cones were exposed to 150 seconds of the treatment temperature, this exposure time was chosen as it is representative of the duration of a flaming front in simulated (Michaletz et al. 2013) and observed crown fires (Butler et al. 2004). Following exposure, the cones were removed promptly from the muffle furnace. If any cone ignited upon exposure to oxygen, it was then smothered in sand to extinguish the flames. Increasing heat treatments were implemented for all species until complete seed death was observed, such that none of the seeds sampled were found to be viable. Upon removal from the furnace, all seeds from each cone were quickly extracted and five seeds per cone were subjected to viability testing. 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 cones per heat treatment and species were examined for viability. Robust seeds that appeared to have an abundance of megagametophytic tissue, indicating high potential for a viable embryo, and those that were free of insect damage, were biasedly 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 carefully and categorized by viability. This data was obtained for all of the 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. The mean percentage of viable seeds were then relativized to calculate the survival rates among treatments.

Data Analysis

Data from the seed maturation and heat-induced mortality studies for all four species were gathered and separately analyzed in R (R Core Team, 2022). Both the seed maturation data from 2018 and 2019, as well as the 2020 seed mortality data, were analyzed using a generalized linear model assuming a binomial distribution. The main effects for both projects were then analyzed with ANOVA in the *car* package (Fox and Weisberg, 2019), which provided the significance level for the species and year term. To identify seed maturation timing, the accumulated heat sum was used to explain the relativized proportion of viable seeds. 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 fair comparisons among the examined species variability. To identify the threshold of heat for seed mortality, heat treatments among species were used to explain relative seed viability. 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, I

considered the parameters of species and treatment and again selected the most parsimonious generalized linear model using the lowest AIC values.

Table 1. The observed maximum absolute viability for the sampled seeds of each species in 2018 and 2019, collected in Shasta County, 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 a cumulative increase in air temperature over the growing season (Figure 2). As the total cumulative heat sum increased, a positive relationship with seed maturation was observed for 2018 and 2019 ($p = 0.0013$, $z = 3.23$, $df = 42$). The top model selected for seed maturation included an additive generalized linear model with heat sum and species. The collection year was not included as it did not have a significant effect ($p = 0.061$, $z = -1.87$, $df = 42$), such that the increase in viability was consistent between years.

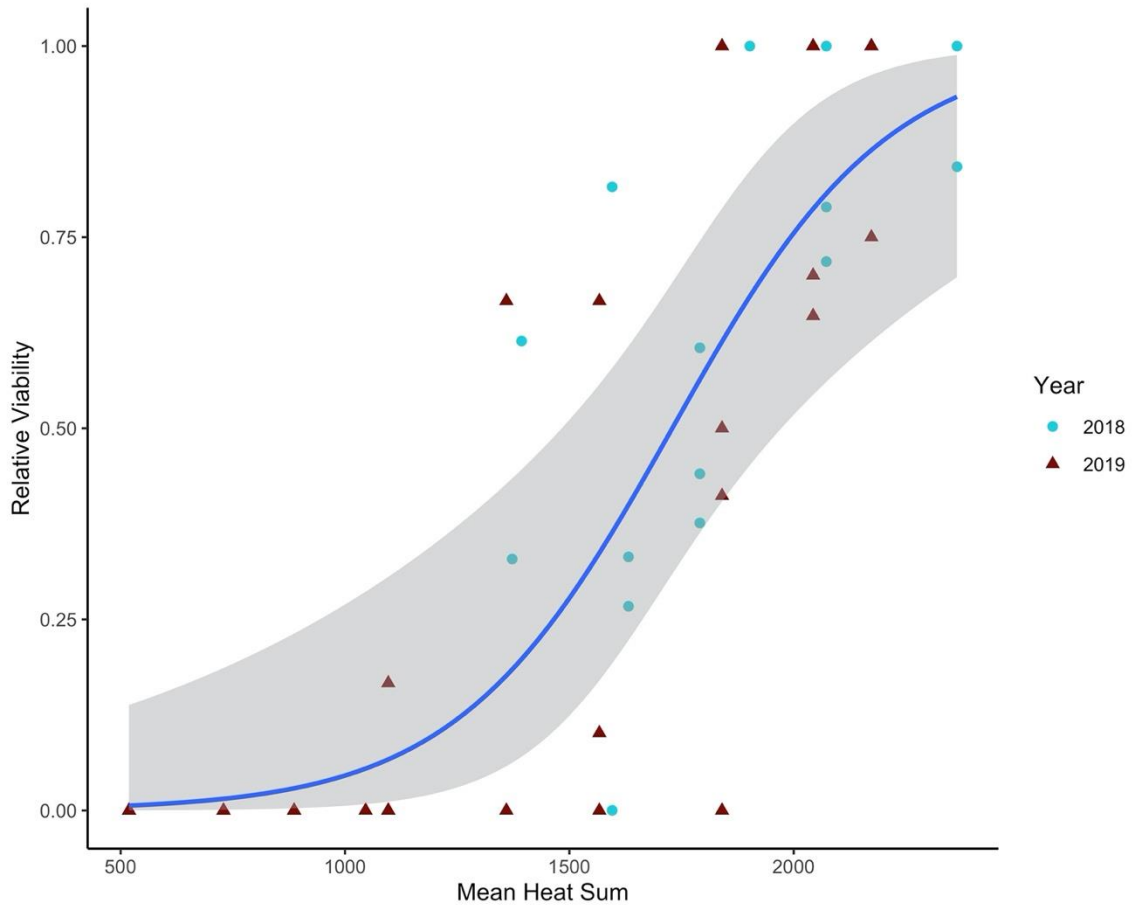


Figure 2. The significantly positive relationship based on a generalized linear model, with 95% confidence intervals in gray, between mean heat sum and mean relative viability ($p = 0.0013$, $z = 3.23$). All examined species are pooled together from 2018 and 2019, as the year and species sampled did not significantly impact seed viability as the heat sum increases (year $p = 0.061$; species $p = 0.1749$). The examined species include incense cedar, lodgepole pine, ponderosa pine, and Douglas-fir. All collections were made in Shasta County, California.

The onset and rate of seed maturation varied among species (Figure 3; Table 2). Species were included and informative in the top model, although I did not detect differences in relative seed viability among species ($p = 0.1749$, $\chi^2 = 4.96$ $df = 3$). Across all four species examined, 50% relative seed viability was reached with a cumulative heat sum between 1358°C (Douglas-fir) and 1889°C (incense cedar), which is typically early-August to mid-September. The onset of seed maturation (10% relative viability) came the earliest for Douglas-fir (959°C heat sum) and lodgepole pine (1205°C heat sum) in early-July, and latest for incense cedar in mid-August (1491°C heat sum), with ponderosa pine following closely behind (1484°C heat sum).

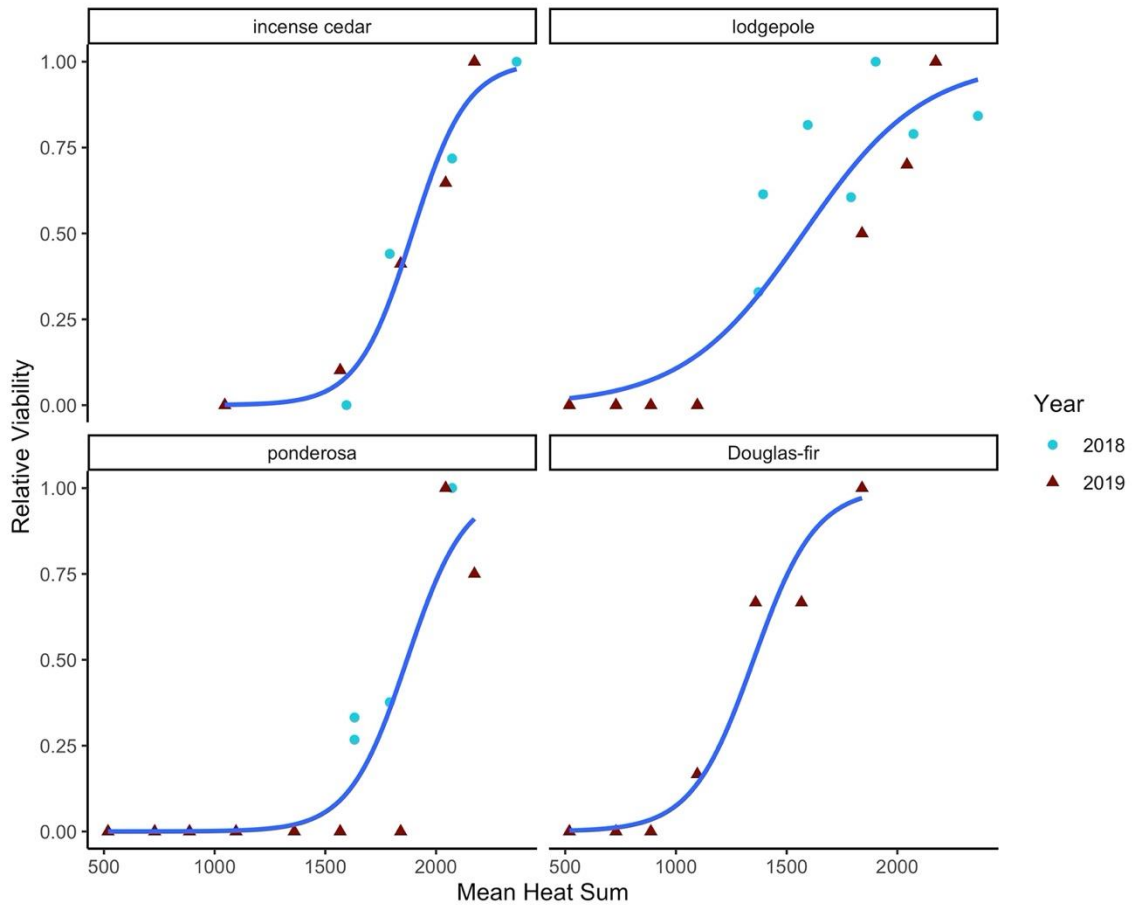


Figure 3. The positive relationship between relative seed viability and the accumulating heat sum for each of the studied species in Shasta County of northern California in 2018 and 2019. The examined species include incense cedar, lodgepole pine, ponderosa pine, and Douglas-fir.

Table 2. Accumulated heat sum at 10%, 50%, and 100% relative viability for four non-serotinous conifer species in Shasta County, California, as well as the seasonal timing for 10% relative viability. These values are based on predictions from the top model, which was an additive model including heat sum and species.

Species	Heat Sum at 10% Viability (°C)	Heat Sum at 50% Viability (°C)	Heat Sum at 100% Viability (°C)	Timing at 10% relative viability
incense cedar	1491	1889	2173	Mid-August
Douglas-fir	959	1358	1840	Late July
lodgepole pine	1205	1603	1902	Late July
ponderosa pine	1484	1883	2072	Mid-July

Annual variation in the heat sum accumulation from 2000 through 2020 at the study site in northeastern California followed a similar accumulation pattern each year (Figure 4). Despite year-specific variation in heat accumulation patterns, around 190 to 220 Julian dates (early-July to early-August) there is typically an accumulated heat sum of 959°C to 1491°C. A heat accumulation of 1358°C to 1889°C is typically reached with 220 to 245 Julian dates (early-August to early-September).

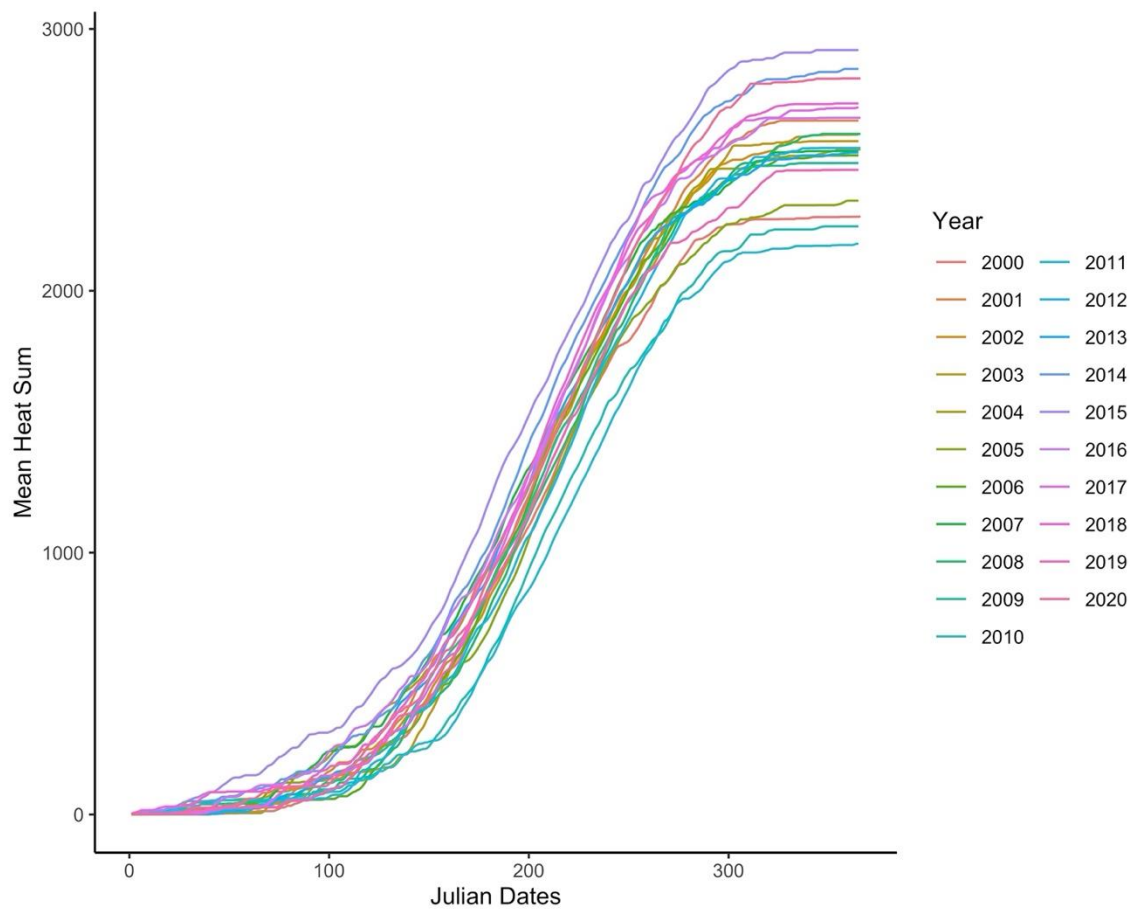


Figure 4. The accumulated heat sum by Julian date for the study site near Burney, California, demonstrating the relatively low variability in annual patterns of heat accumulation, from 2000 through 2020 (PRISM, 2021).

Heat-Induced Seed Mortality

Seed survival was significantly impacted by increasing convective heat (Figure 5). As the temperature increased, relative seed viability significantly decreased across all species ($p = 0.0156$, $z = -2.42$, $df = 27$). The most informative model selected for seed mortality utilized an additive generalized linear model with the treatment and species. While species was again informative in the most parsimonious model, it was not statistically significant ($p = 0.1895$, $\chi^2 = 4.77$, $df = 3$). The threshold of seed survival for each of the four California conifers studied was dependent on the temperature of heat exposed to the surface of the ovulate cones (Figure 6). With minor differences in seed survival among species, it is observed that relative seed survival ranged widely by species at 10 and 50% survival (Table 3). It was observed that lodgepole pine can withstand the greatest amount of heat prior to mortality (235°C to 342°C), while Douglas-fir experienced mortality at a lower threshold of heat (64°C to 171°C; Table 3). With a maximum heat exposure of 342°C, 10% survivorship was recorded for lodgepole pine.

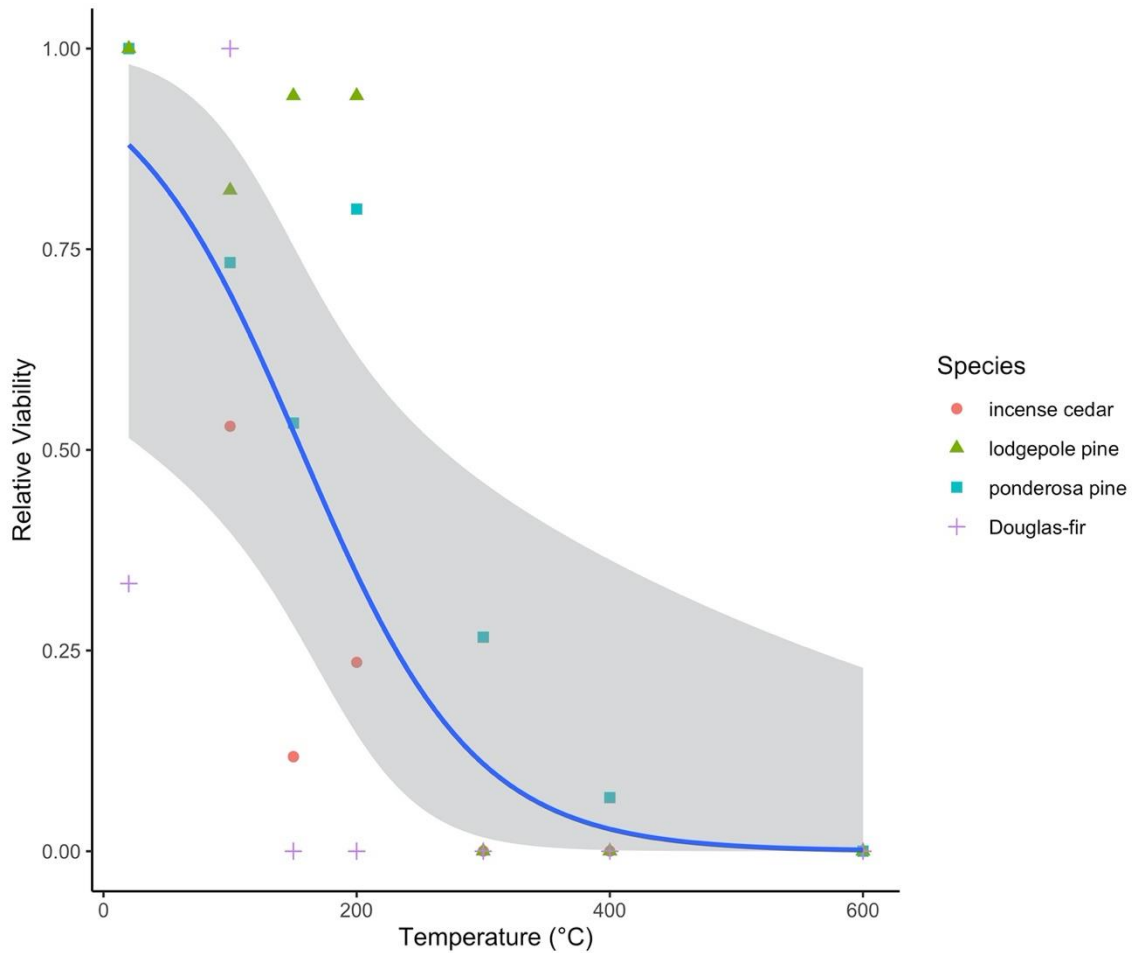


Figure 5. Relative seed viability rates, with 95% confidence intervals in gray, for all examined species pooled together, as exposure to heat increases via muffle furnace (used as a proxy for fire). A significant negative relationship is reported for relative seed viability rates with increased heat exposure for all species ($p = 0.0156$, $z = -2.42$). The examined species include incense cedar, lodgepole pine, ponderosa pine, and Douglas-fir, with all cone data collected from Shasta County, California.

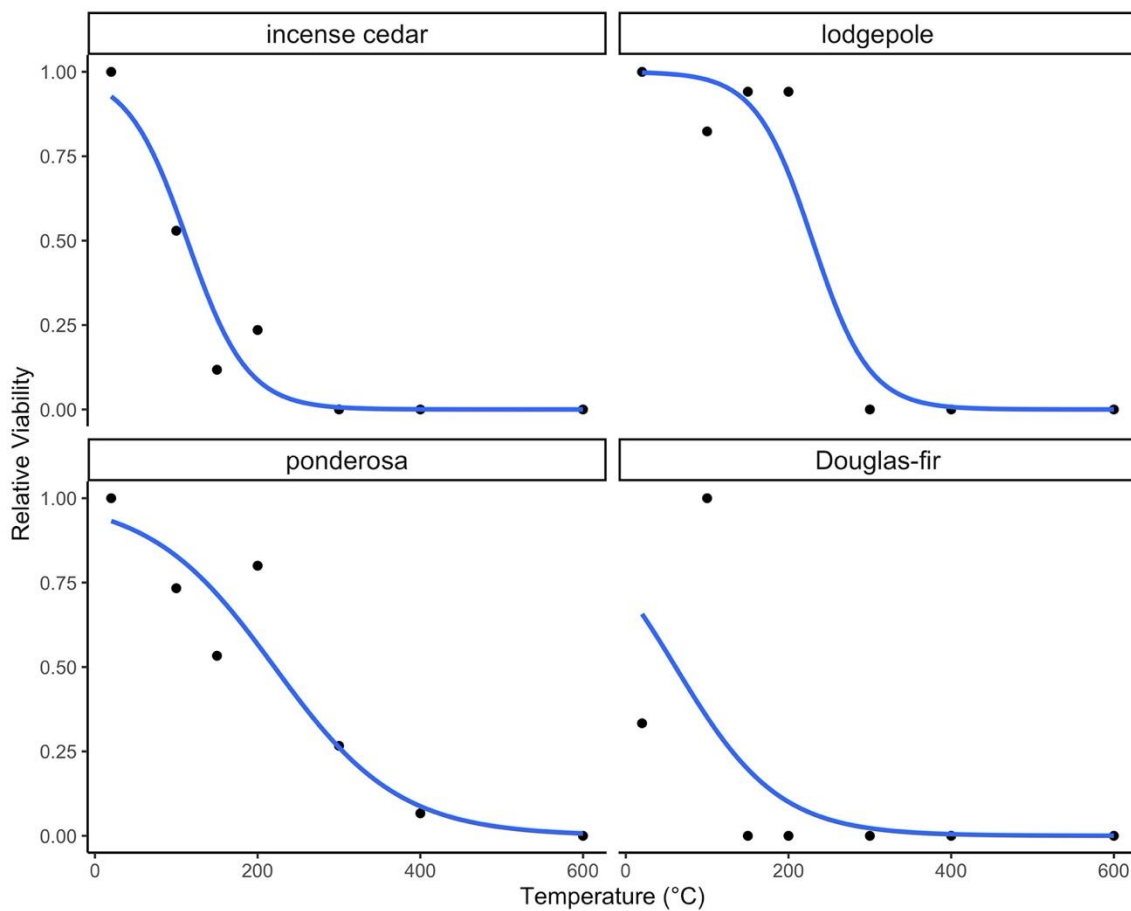


Figure 6. Relative seed viability for each examined species, as a function of heat exposure temperature treatments implemented via muffle furnace that was used as a proxy for fire. A consistent negative relationship is shared across each species between increased heat exposure and relative viability rates. The examined species include incense cedar, lodgepole pine, ponderosa pine, and Douglas-fir, with all cone data collected from Shasta County, California.

Table 3. The temperature of heat exposure permitting 10% and 50% relative seed survivorship for the four conifer species studied in Shasta County, California near Burney. These values are based on predictions from the top model, which was an additive model with treatment and species.

Species	10% Survival (°C)	50% Survival (°C)
incense cedar	214	107
Douglas-fir	171	64
lodgepole pine	342	235
ponderosa pine	318	211

Timing of Wildfire

Given the distribution of fire in the Klamath, Sierra Nevada, and Cascade ecoregions from 1950 to 2017, the peak timing of fire occurred from late-July to mid-September (Figure 7). The fire distribution indicates that lightning acts as a prominent ignition source as early as May and spanning into August. Fires caused by humans span the entire year, and peaks from July to September. Cumulative proportion of area burned between 2000 and 2017 for the same geographic area, annually occurred between 125-350 Julian days (Figure 8). A total of 68% of the cumulative area burned fell within the estimation of the seed maturation window, such that more than half the area burned had the capacity for regeneration via facultative serotiny.

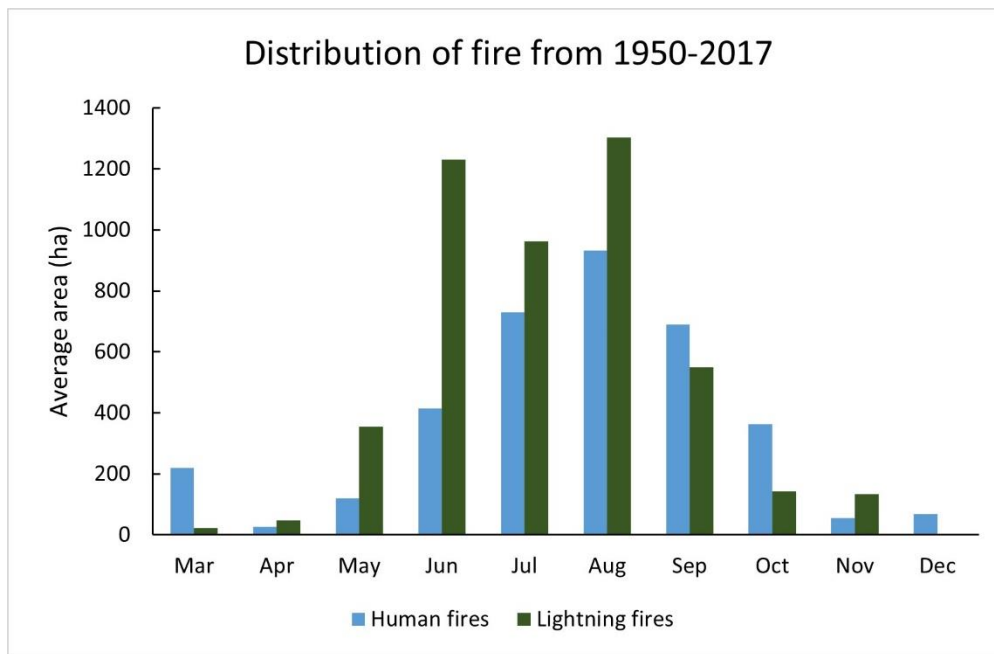


Figure 7. Fire distribution in the Klamath, Sierra Nevada, and the Cascade ecoregions from 1950 to 2017, delineated by human and natural causes (MTBS, 2018).

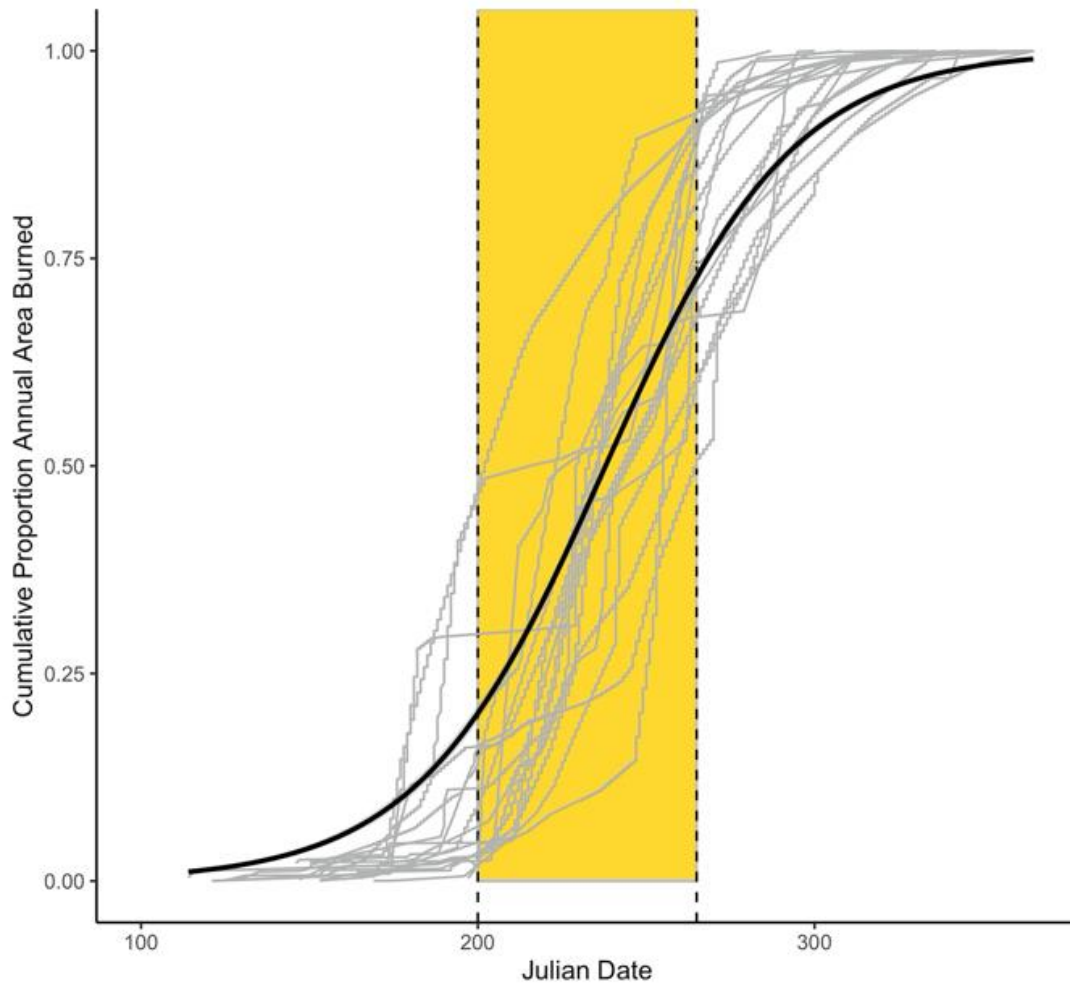


Figure 8. Cumulative proportion of annual area burned from 2000 to 2017, based on start dates, in northern California (Klamath, Sierra Nevada, Cascade ecoregions). The yellow represents the temporal window of facultative serotiny (using 10% relative viability as the start and seed abscission as the end), which encompassed 68% (annual range: 39%-93%) of the burns. The temporal window includes the Julian date of 200 through 265 (mid-July- September).

DISCUSSION

I provide mechanistic support for the possibility of facultative serotiny, an alternative post-fire mode of regeneration in non-serotinous conifers, in northeastern California. Facultative serotiny is defined as the capacity of a non-serotinous species to disperse viable seeds from trees killed by fire. The mechanism is made possible when seed maturation precedes the timing of fire, and when ovulate cone scales adequately protect the viable crop. The onset of seed viability for the studied species occurred around mid-July to mid-August (Table 2), and the timing of the reported fires occurred from late-June to mid-September (Figure 7). As such, I identify the window for this regenerative mechanism to occur with the onset of seed viability starting in mid-July and spanning to September with respect to the timing of seed abscission (Figure 8).

Seed Maturation

Given the positive relationship between seed viability and accumulating heat sum of the four studied conifer species, it is evident that larger quantities of viable seed become available later in the summer, as heat accumulates. This relationship has likewise been demonstrated in other species such as Engelmann spruce (*Picea engelmannii*) in Canada (Pounden et al. 2014) and in the Rocky Mountains (Buechling et al. 2016), Scots pine (*Pinus sylvestris*) in Finland (Henttonen et al. 1986), as well as multiple northern boreal tree species including black spruce (*Picea mariana*; Sirios 2000; Meunier et al. 2007), white spruce (*Picea glauca*; Michaletz et al. 2013), and Norway spruce (*Picea*

abies; Selas et al. 2002). Additionally, warmer temperatures during the period of reproductive bud initiation have been documented to increase seed production (Selas et al. 2002; Buechling et al. 2016; Ibáñez et al. 2017), indicating that climatic warming may increase seed availability. When a fire occurs later in the season, greater opportunity is made available for conifers to produce seed that can then contribute to future generations following a fire. This window of opportunity, termed facultative serotiny, is marked by the onset of viability (10% relative viability) and ends with the reflex of cone scales and the abscission of seeds.

The positive trends among species and cumulative heat sum indicate subtle differences among species (Table 1) as the effect of species was informative in the best model. Albeit there is potential for stochastic variability in the timing of ovulate cone fertilization which could have limited the ability to detect a species effect, meaning that certain cones within the collection may have had better access to pollen clouds and were fertilized earlier in the season (Niklas, 1985), and therefore developed earlier in the final growing season. Conversely, the onset of viability in the species examined was reached by late July (959°C to 1491°C) and maximum viability occurred by late August (1840°C to 2173°C; Meunier et al., 2007; Michaletz et al. 2013). Likewise, the compendium of Schoepfer (1974) shows that, while the reports are anecdotal, most North American tree species (with the exception of spring seed dispersers, such as *Populus*) begin abscising seeds in September. Thus, if onset and ending dates are similar, then the sigmoidal curves depicting seed maturation should be similar. Given that the small sample size decreased the power to detect statistical differences, future studies should also include larger sample

sizes to account for species-specific variability in seed maturation while also considering a sampling design where collections are made from the same trees over time to account for intra-specific variability.

Seed Survival Relative to Heat Exposure

Seed survival rates expectedly decreased with higher exposure to heat for the studied non-serotinous species. This inverse relationship has been documented previously with black spruce (Zasada et al. 1979; Johnstone et al. 2009), multiple cypress species (Milich et al. 2012), as well as the Engelmann spruce in a modeling study (Michaletz et al. 2013). There are few studies that have been completed to obtain temperature data associated with high severity crown fires. The reported temperatures associated with low to moderate severity fires range from 200°C to 1000°C (Butler et al. 2004; Hobbs and Gimingham, 1984; Habrouk et al. 1999). Conversely, high intensity fires within the crown shift temperatures to 600°C to 1300°C (Butler et al. 2004), implying that no seeds should survive for these species based on my study's findings (Figure 6). However, these temperatures were experienced in rapid flashes, spanning only 20 to 100 seconds. Rapid heat fluxes experienced during wildfires are difficult to replicate in lab settings, given that high temperatures produced in a muffle furnace remain insulated in the oven and cannot be released to the surrounding environment quickly. However, the study included a high of 600°C for 150 seconds to reflect the upper bounds of heat exposure, which is comparable to the rapid heat flashes over 1000°C experienced for 20 to 100 seconds in 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 an oven. Furthermore, most ovulate cones are located in the upper portion of the crown, which can result in exposure to lower fire temperatures when compared to cones in the lower and middle crown positions (Butler et al. 2004). Field-based studies provide evidence of viable seeds in burned cones following fire, this has been completed twice for the serotinous black spruce (e.g., Zasada et al. 1979; Johnstone et al. 2009), from which Zasada et al. (1979) determined 86% seed survival following fire. A computational study by Michaletz et al. (2013) conversely found 12% of cones with viable seeds following a crown fire, however this difference can likely be attributed to the lack of consideration for cone characteristics (e.g., cone size, moisture content) in their simulations. A beneficial next step would be a study based on the widespread collection of cones following fire from a large number of non-serotinous species varying in cone size. This would permit the ability to ascertain whether seeds can survive inside closed cones, as well as test the hypothesis that the proportion of seeds surviving varies with cone size.

Evidence indicates higher moisture content in the fresh annual non-serotinous cones (Greene et al. in prep). That is, greater energetic input is required for cone combustion to occur, even when faced with high temperatures. The moisture acts as an additional protective force for the reproductive propagules (Splawinski et al. 2019), allowing greater potential for seed survival at the time of fire. Further, cone scales isometrically increase with the size of ovulate cones (Greene et al. in prep) which offer greater protection for seeds. Thus, non-serotinous species with larger cones should tend towards higher seed survival rates. Additionally, given that cone size and moisture

content play an important role in protecting seeds (de Groot et al. 2004; Splawinski et al. 2019), the larger cones of ponderosa and lodgepole pine should have the greatest seed survival rates following heat exposure. With that said, species was informative to my top model but did not have a statistically significant effect on seed survival, which is attributed to the small sample size. If these seeds have matured at the time of fire and remain protected by the moisture content and cone scales following the time of fire, facultative serotiny can ensue.

Timing of Wildfire

The bulk of the area burned in the reported ecoregions from 1950 to 2017 occurred from late July to early September in California. As climate warms, this may change with more area burning earlier in the season. Thus, surviving non-serotinous seeds will be available in increasing numbers until late August, and maintained for a few weeks until seed abscission begins. It should be noted that a late August fire in a poor crop year would lead to minimal recruitment, such that regeneration would be indistinguishable from long-distance dispersal. Likewise, an early August (too few viable seeds) or late Autumn (too few seeds remaining) fire during a very large seed crop may also yield little recruitment.

Almost 70% of the area burned from 2000 to 2017 for the examined ecoregions occurred during the window for facultative serotiny, although detectable recruitment from this mechanism will occur much less than 70% of the time. To estimate the occurrence of this mechanism within forest population dynamics would require an

approximation of the probability of a fire burning coinciding with the production of an abundant seed crop and identification of seed abscission at the population level in Autumn.

The occurrence of facultative serotiny will also be influenced by changing climatic conditions given the continued warming, lengthening of fire seasons, and earlier occurrences of fire in the season (Westerling, 2016). The reported timing of lightning ignitions is conducive to facultative serotiny, as these fires occur later in the season. Conversely, as fires occur earlier, facultative serotiny may become more likely if the phenology of seed maturation shifts to earlier in the season. Thus, the expansion of seed maturation studies with more species is crucial for defining the rate of change in phenology of seed maturation as climatic conditions shift over time. As the conditions change, the prevalence of this mechanism will be influenced by the temporal distribution and intensity of fires, the timing of seed maturation phenology, and the rates of cone production.

Implications

As fire regimes continue to shift given climatic warming, and concern of local extirpation in species lacking fire adaptations increases, I offer a regenerative mechanism that allows for non-serotinous conifer persistence in landscapes prone to high-severity fire. My research indicates that the mechanism may operate commonly in the western half of this continent. My characterization of this mechanism will not only aid in improving the accuracy of post-fire regeneration modeling but also offers new research

on the timing of seed maturation for four non-serotinous conifer species, in addition to providing insights for land management techniques following a stand-replacing fire.

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