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Fire intensity effects on serotinous seed survival

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Abstract

Background In fire-prone environments, some species store their seeds in canopy cones (serotiny), which provides seeds protection from the passage of fire before stimulating seed release. However, the capacity of serotinous cones to protect seeds under high intensity fire is uncertain. Beyond simply "high" versus "low" fire intensity or severity, we must understand the influence of the specific characteristics of fire intensity—heat flux, exposure duration, and their dynamics—on serotinous seed survival. In this study, we tested serotinous seed survival under transient levels of radiant heat to understand the distinct and combined impacts of radiative heat flux and duration of exposure on the survival of seeds from two serotinous obligate seeder species: yellow hakea (*Hakea nodosa* R.Br.) and heath-leaved banksia (*Banksia ericifolia* subsp. *ericifolia*).

Results We found differing impacts of fire intensity treatments on seed survival. Static levels of radiative heat (17 kW/m^2) at long durations (600 s) reduced seed survival by 75.7% for yellow hakea and 1.5% for heath-leaved banksia compared to the control. However, dynamic heat (a short 120-s period of 40 kW/m^2 followed by a slow decline) with an identical total duration (600 s) did not have comparable reductions in seed survival. This is despite both treatments having comparable radiant exposure (10,200 kJ/m^2 for the former and 10,236 kJ/m^2 for the latter). Both species demonstrated remarkable capacity to withstand heat treatments, particularly dynamic fire intensity—both high (40 kW/m^2) and low (19 kW/m^2). While almost all fire exposure treatments reduced survival from the control, most seeds remained viable and germinated upon release.

Conclusions Our study highlights the importance of examining dynamic rather than static fire effects on vegetation, to accurately replicate the conditions of a fire front. Serotinous seeds demonstrate good capacity to tolerate intense fire. Nonetheless, the combined effects of high heat flux at prolonged durations reduces seed survival. We suggest overly prolonged passing fire fronts may cause seed death and are a risk to obligate seeder species that rely solely on seeds for persistence post-fire.

Keywords Seed survival, Serotiny, Obligate seeders, Radiant heat flux, Dynamic heat, Fire intensity, *Banksia ericifolia*, *Hakea nodosa*

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Spanish resumen

Antecedentes: En ambientes propensos al fuego, algunas especies almacenan sus semillas en conos serótinos, proveyéndoles de cierta protección hasta que el pasaje de un fuego estimula la apertura de los conos y libera las semillas. De todas maneras, la capacidad de conos serótinos de proteger las semillas bajo altas intensidades de fuegos, es todavía incierto. Más allá de la simple "alta" o "baja" severidad o intensidad del fuego, debemos entender la influencia de las características específicas de la intensidad del fuego -el nivel de flujo de calor, la duración de exposición al fuego, y su dinámica- en la sobrevivencia de las semillas serótinas. En este estudio, probamos la supervivencia de semillas bajo niveles transitorios de calor radiante para entender los diferentes y combinados impactos del flujo de calor radiante y la duración de la exposición en la sobrevivencia de semillas de dos especies de plantas que se reproducen por semilla y son serótinas obligadas: la hackea nodosa (*Hakea nodosa* R.Br.) y la banksia (*Banksia ericifolia* subsp. *ericifolia*).

Resultados: Encontramos impactos diferentes de los tratamientos de distintas intensidades de fuego sobre la sobrevivencia de semillas. Los niveles estáticos de calor radiante (17 kW/m2) y largos tiempos de exposición (600 segundos) redujeron la supervivencia de semillas comparadas con el control. Sin embargo, el calor dinámico (un tiempo corto de 120 segundos de 40 W/m2 seguido de una leve declinación) con una idéntica duración total de 600 segundos, no tuvo reducciones comparables en la sobrevivencia de las semillas. Esto a pesar de que ambos tratamientos tuvieron una exposición comparable a la radiación recibida (10,200 kJ/m2 para el primer caso y 10,236 kJ/m2 para el segundo). Ambas especies demostraron tener una remarcable capacidad de resistir los tratamientos de calor particularmente el de intensidad de fuego dinámico –ambos tanto a alta (40 kW/m2) como a baja intensidad (19 kW/m2)-. Aunque todos los tratamientos de exposición redujeron su sobrevivencia en relación al control, la mayoría de las semillas permanecieron viables y germinaron luego de su liberación.

Conclusiones: Nuestro estudio subraya la importancia de examinar los efectos dinámicos y no estáticos del fuego sobre la vegetación, para poder replicar exactamente las condiciones de un frente de fuego. Las semillas serótinas demostraron una gran capacidad para tolerar fuegos de alta intensidad. Sin embargo, los efectos combinados de fuegos intensos y prolongados redujeron la supervivencia de las semillas. Sugerimos que frentes de fuegos demasiado prolongados en el tiempo pueden causar la muerte e las semillas y son un riesgo para las plantas que se reproducen estrictamente por semillas y que tienen ese requisito para poder persistir en el post fuego.

Background

Over millennia, fire has evolved the canopy storage of seeds (serotiny) in many plant species (Lamont et al. 2020). Serotinous infructescences (cones) protect internal seeds from the passage of fire, prior to the fire-cued release of seeds (Causley et al. 2016). Serotiny is adapted to historical fire regimes, including high-intensity crown fire in most instances (Pausas 2015). Many serotinous species have demonstrated capacity to tolerate reasonable fire intensity in the context of historical regimes, but very high severity of fire may cause seed death and alter recruitment dynamics (Fernández-García et al. 2019; Gill et al. 2021; Maia et al. 2012; Torres et al. 2006). There is growing evidence that higher-intensity fires are increasing in frequency and will continue to increase as the climate changes (Bowman et al. 2021; Collins et al. 2022). Therefore, a better understanding of the capacity of serotinous cones to preserve seeds under high-intensity fire scenarios is needed (Whelan and Ayre 2022).

An important part of understanding the effects of fire intensity is moving beyond "high" versus "low" intensity, to the specific patterns of fire intensity such as heat flux, duration, and their dynamics. This allows investigation of the mechanisms through which fire intensity influences biota. Fire intensity refers to the rate of energy released during combustion, measured in kilowatt per square meter (kW/m^2; Rossi et al. 2018). The total energy flux—or total heat exposure—can be made up of different combinations of heat flux and durations, forming different exposure profiles that equal the same total heat exposure (Rossi et al. 2018). Even if equal to the same total heat exposure, different fire intensity dynamics may have incomparable effects on serotinous cones. For example, a short duration of high levels of radiative heat, or "heat shock," may promote seed release and germination, or kill seeds if exceeding the threshold of heat tolerance (Ayan et al. 2020; Bell and Williams 1998; Hanley and Lamont 2000), as is the case for soil-stored seeds (Ooi et al. 2014). A long duration of a high level of radiative heat may kill seeds (Habrouk et al. 1999), but a similar duration of low or medium levels of radiative heat might not. The influence and relative importance of these different fire intensity components—duration, maximum heat flux, and the total heat flux—are not clear. Typically, static heat is used to study the effects of fire intensity on seeds in the laboratory (Cochrane 2017; Emery et al. 2011), which is different from the dynamic heat of wildland fire. Thus, it is essential to understand how fire behavior characteristics impact seed survival during the "approaching," "passing," and "leaving" stages of a fire front.

Serotinous obligate seeders do not resprout post fire, and therefore are considered particularly at risk to fire regime change, due to their sole reliance on seeds for persistence post-fire (Bowman et al. 2014; McColl-Gausden et al. 2022). Recent work has demonstrated the vulnerability of serotinous obligate seeders under increased fire frequency (Agne et al. 2022; Turner et al. 2019). However, fewer studies have investigated the influence of fire intensity on their sole persistence trait—survival of seeds retained in serotinous cones (Bradstock et al. 1994; Habrouk et al. 1999; Huss et al. 2019; Milich et al. 2012). Vulnerability to fire is often tested on isolated seeds, which does not account for the fire-protection awarded within the complex serotinous fruit structures.

In this study, we investigate how fire intensity influences seed survival within serotinous cones. We used a novel variable heat flux apparatus (VHFlux; Miller et al. 2022) to test serotinous seed survival under transient levels of radiant heat exposure in laboratory conditions. We test our hypotheses for two serotinous obligate seeders: heath-leaved banksia (*Banksia ericifolia* subsp. *ericifolia*) and yellow hakea (*Hakea nodosa* R.Br.). We formulated the following research questions: How do various characteristics of fire intensity, including heat flux, duration, and their dynamics, affect seed survival? and Does the effect vary depending on the species? To address these questions, we developed four competing hypotheses:

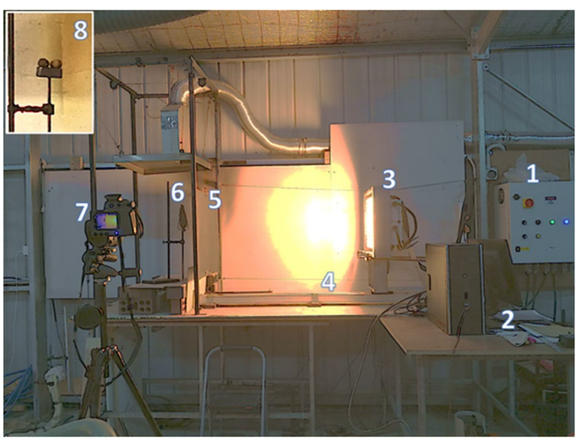

Fig. 1 Configuration of VHFlux apparatus. (1) Switchboard, (2) PC control system, (3) radiative panel, (4) linear stage, (5) shutter, (6) rotisserie to hold Banksia cones, (7) thermal imaging camera for observation purposes, and (8) stage to hold Hakea cones

A) *High level of radiative heat causes seed death, irrespective of "short" or "long" duration and "dynamic" or "static" exposure.* Previous studies have demonstrated seed death when exposed to high temperatures for a short duration (Bell and Williams 1998)
B) *Static exposure cause seed death at long exposure duration only.* Contrary to evidence supporting hypothesis A, other studies have demonstrated the capacity for seeds to survive short periods of time at relatively high static temperatures, analogous to heat shock (Huss et al. 2019; Tangney et al. 2020)
C) *Long exposure duration causes seed death, irrespective of "static" or "dynamic" exposure, or "low" or "high" heat level.* Once heat opens protective cones, it could damage seed tissue at long durations, regardless of the level and type of heat exposure, across "passing" or protracted "leaving" stages (Milich et al. 2012)
D) *High total radiant exposure (calculated from exposure duration and heat level) causes seed death.* This hypothesis suggests that exposure duration and heat flux are just components that equate to total radiant exposure or total intensity. High total radiant exposure—regardless of duration and heat level alone but combined—could form a threshold at which higher values cause seed death

Methods

Study design and sampling procedures

We focused on two fire-killed species that are thus most vulnerable to fire: heath-leaved banksia and yellow hakea. We selected these species as they grow in the same

Table 1 Different heat treatments and their total duration of exposure (seconds), total radiant exposure (kJ/m^2), maximum heat flux (kW/m^2), and duration of maximum heat flux (seconds)

Treatment	Total duration of exposure (seconds)	Total radiant exposure (kJ/m^2)	Maximum heat flux (kW/m^2)	Duration of maximum heat flux (seconds)
Dynamic high intensity (DHI)	600	10,236	40	120
Dynamic low intensity (DLI)	600	5540	19	120
Static high intensity (SHI)	255	10,200	40	255
Static low intensity (SLI)	291	5529	19	291
Static low intensity long duration (SLILD)	600	10,200	17	600

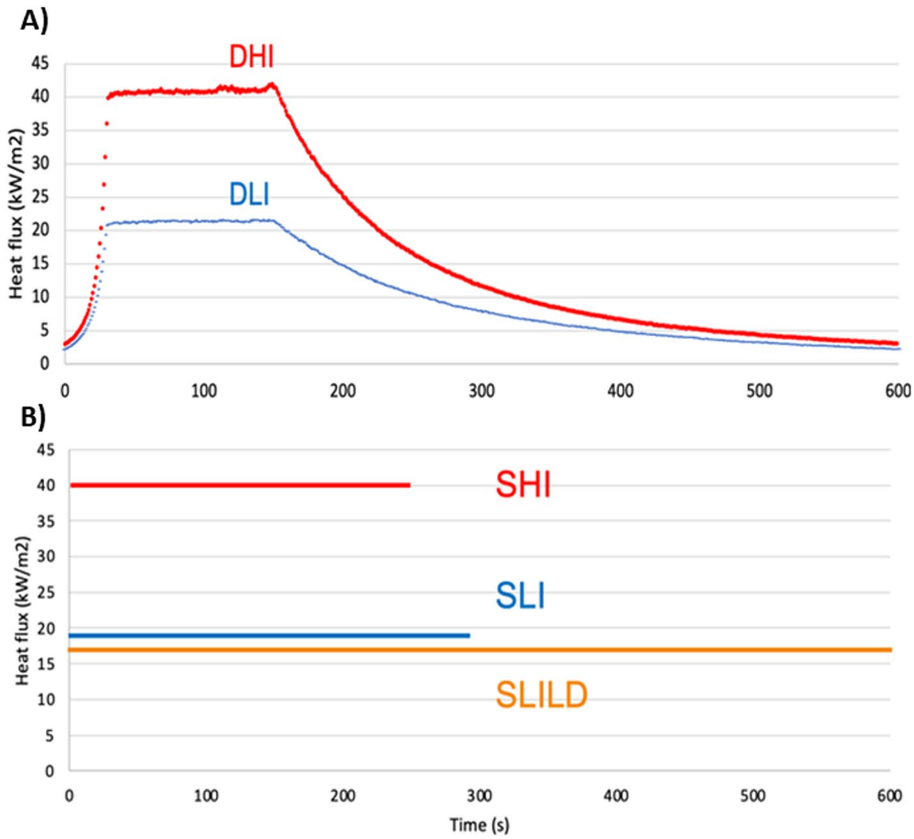

Fig. 2 Fire intensity treatments. The *x*-axis displays the time in seconds and the y-axis displays the radiative heat flux in kilowatts per square meter. **A** Dynamic heat treatments, displaying changes in heat flux over time. These include dynamic high intensity (DHI) and dynamic low intensity (DLI). **B** Static heat treatments, displaying a constant heat over time. These include static high intensity (SHI), static low intensity (SLI), and static low intensity long duration (SLILD)

established garden where they experienced comparable growing conditions, mitigating any possible substrate and climate effects. Both species are serotinous species in the *Proteaceae* family and are native to south-eastern Australia. They are tall shrubs; the mature heath-leaved banksia sampled was around 4.5 m in stature with a cone size of 10–20 cm long and the yellow hakeas around 2 m with a cone size of 2–3 cm. The two species are both obligate seeders, and thus individuals are fire-killed, but release and germinate their seeds post-fire (Falster et al. 2021). Yellow hakea cones commonly encapsulate two seeds, while heath-leaved banksia cones have a highly variable number of seeds (5–111 in the present study).

Cones were sampled at the University of Melbourne Creswick Campus, Creswick, Victoria, south-eastern Australia (−37.423°, 143.899°). Creswick experiences a temperate climate, with four distinct growing seasons. Individual plants form part of the garden beds, intentionally planted likely within the last 20 years. We sampled 120 mature canopy cones from across the form of the plant, from three randomly selected mature individuals of comparable height. This provided six replicate samples of 20 cones, one for each of the six treatment types including the control. Samples were collected immediately prior to heat treatments. This ensured cones would exhibit similar flammability characteristics as live plants in wildfire and prevented hakea cones from opening naturally during air-drying and thus compromising treatment effects.

Fire intensity treatments

We utilized the variable heat flux (VHFlux) apparatus to expose cones to heat treatments (Fig. 1). The VHFlux is a panel of 12 infrared short-wave lamps mounted to a 1.5-m linear stage, which produces a radiative heat flux (Miller et al. 2022). To deliver the target levels of radiative heat flux to samples, the panel's foremost position was determined using a water-cooled heat flux sensor SBG01–100 (Hukseflux Thermal Sensors B.V., Delft Netherlands). We controlled the position of the heat source relative to the samples using the SMC60WIN software via PCL601USB programmable stepper motor controller (Anaheim Automation, Inc., Anaheim USA). A remotely operated shutter positioned between the sample and the panel prevented the sample from receiving heat radiation prior to the treatment. Behind the shutter, a repurposed battery-powered rotisserie was installed vertically, to uniformly expose cones to heat (Fig. 1). To prevent any additional preheating during the test, the cones were placed on a calcium silicate insulation stage.

We exposed species to five intensity treatments using the VHFlux: three "static" treatments and two "dynamic" treatments. These included dynamic high intensity (DHI), dynamic low intensity (DLI), static high intensity (SHI), static low intensity (SLI), and static low intensity long duration (SLILD) (Table 1; Fig. 2). Static treatments had a fixed radiative heat flux for their duration (Table 1; Fig. 2B), comparable to current laboratory-based methods investigating intensity effects. In contrast, dynamic treatments had varying heat flux (Table 1; Fig. 2A), experiencing a rise in flux, a peak, and then a slow drop, more comparable to the stages of the fire front, namely the approaching stage, passing stage, and leaving stage. Such conditions were generated by changing the distance between the heating panel and the sample. Static and dynamic treatments varied in duration and maximum heat flux (Table 1; Fig. 2). We selected two levels of maximum heat fluxes—40 kW/m^2 (severe fire exposure) and 19 kW/m^2 (high fire exposure) and a maximum duration of 600 s. It is acknowledged that radiant heat profiles can differ between wildfires. The specified radiant heat exposure conditions for the static and dynamic treatments, including a rapid increase and a gradual decrease in radiant heat levels, peak heat flux values, and exposure durations, are considered conservative for wildfire exposures, as supported by several recent studies (Morandini et al. 2010; Mueller et al. 2018; Santoni et al. 2006) and AS 1530.8.1 (Standards Australia 2014).

The total radiant energy received by the sample during the 600 s of dynamic heating period is expressed as:

$$H_e = \int_0^{30} q_{r1}(t)dt + \int_{30}^{150} q_{r2}(t)dt + \int_{150}^{600} q_{r3}(t)dt,$$

where H_e is the total radiant exposure of a surface (J/m^2), t is time (seconds), q_{r1} is the radiative heat flux (W/m^2=J/s·m^2) in the approaching stage, q_{r2} is the radiative heat flux during the passing stage (40 kW/m^2 for DHI and 19 kW/m^2 for DLI), and q_{r3} is the radiative heat flux during the leaving stage. H_e was estimated to be 10,236 kJ/m^2 for DHI and 5540 kJ/m^2 for DLI (Table 1). In the static treatments, the 255 s of exposure at 40 kW/m^2 released 10,200 kJ/m^2 (SHI) and the 291 s of exposure at 19 kW/m^2 released 5529 kJ/m^2 (SLI). The third static heating regime (SLILD) was introduced to test the effect of a sustained heat at long duration on seed viability. For SLILD, the target total heat exposure of 10,200 kJ/m^2 was achieved by applying a constant 17 kW/m^2 flux across the 600-s duration (Table 1).

All seeds were stored in a drying oven at 30 °C for at least a week after treatment. As many serotinous cones do not naturally release seeds without intervention from heat, the control groups (which were not exposed to the VHFlux apparatus) were kept in a drying oven at 30 °C until they dehisced. Drying equated to 2 days for the yellow hakea control group. For heath-leaved banksia, there was no dehiscence at 30 °C after 16 days. The oven temperature was subsequently increased to 40 °C. After an additional 10 days, 50% of cones had released their seeds and were subsequently removed from the oven. The remaining cones were kept in the oven at an increased temperature of 50 °C until their follicles opened (up to 7 days). This was considered a plausible temperature range for the control treatment to extract seeds, while mimicking an extremely hot Australian summer day.

Seed viability tests

All seeds were extracted from cones, sterilized in a 1% sodium hypochlorite (NaOCl) solution, then rinsed with

Table 2 Summary statistics of viable and non-viable seeds by treatment type: dynamic high intensity (DHI), dynamic low intensity (DLI), static high intensity (SHI), static low intensity (SLI), static low intensity long duration (SLILD), and control (C)

	Hakea nodosa						*Banksia ericifolia*					
Treatment	**DHI**	**SHI**	**DLI**	**SLI**	**SLILD**	**C**	**DHI**	**SHI**	**DLI**	**SLI**	**SLILD**	**C**
Germinated	16	24	32	31	8	37	707	732	693	496	724	589
Viable at cut-test	12	4	1	3	1	0	14	72	0	1	72	6
Unviable at cut-test	12	12	7	6	31	3	1	11	2	7	15	2
Total seeds	40	40	40	40	40	40	722	815	695	504	811	597
Germination success rate (%)	70.0	70.0	82.5	85.0	22.5	92.5	99.9	98.7	99.7	98.6	98.2	99.7

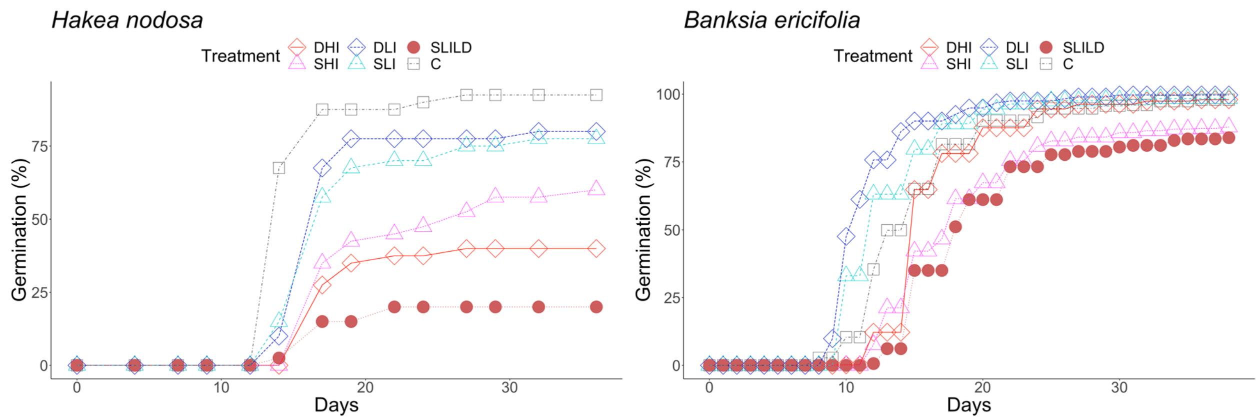

Fig. 3 Speed of germination for each species, differentiated by treatment types. Time to germination curves exclude seeds that were deemed viable during the cut test

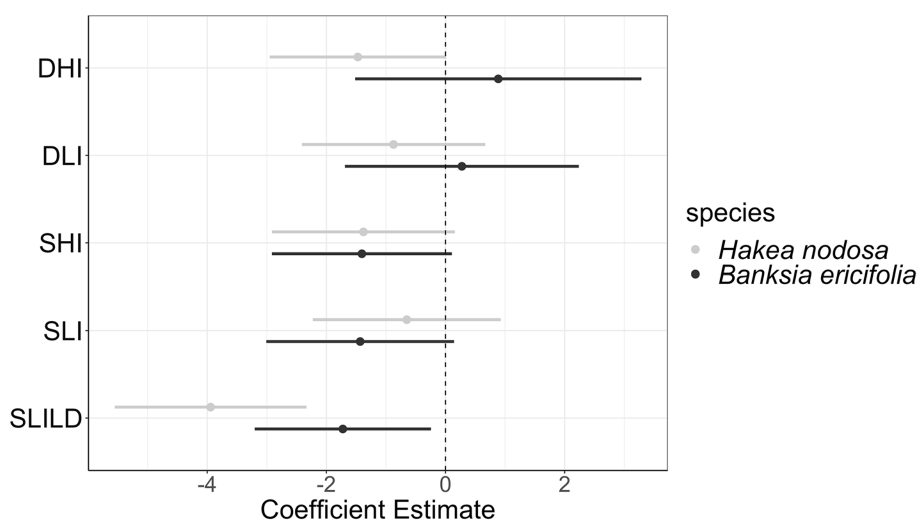

Fig. 4 Estimated effect and 95% confidence intervals of the different treatments on seed viability of yellow hakea (gray) and heath-leaved banksia (black). Treatments include TreatmentDHI—dynamic high intensity (short peak, high intensity), TreatmentDLI—dynamic low intensity (short peak and low intensity), TreatmentSHI—static high intensity (sustained but short high intensity), TreatmentSLI—static low intensity (sustained low intensity), and TreatmentSLILD—static, low intensity, long duration (sustained low intensity for long period). All treatments are compared to the control

distilled water (Abdul-Baki and Moore 1979). Seeds per cone were placed in 90 mm petri dishes on filter paper and moistened with 4 ml of distilled water. Petri dishes were then placed in a germination chamber set to 18 °C, on a light cycle of 12 h/12 h at 50% light/100% darkness. Seed were checked for germination every 2 to 4 days and remoistened as needed. Germination was determined by the evident emergence of the radicle. After an incubation period of 37 days, we tested the viability of non-germinated seeds using a cut-test. Seeds were considered viable if their embryo and endosperm tissues were bright and firm (Tangney et al. 2019).

Statistical analyses

We ran five univariate models per species, with the proportion of viable seeds (including the cut-test results) per cone as the response variable for all models. The first model included treatment as the categorical predictor variable. We then ran separate models with categorical predictors that represented each fire intensity component, including maximum heat flux (the highest heat flux exposed to), total duration (total duration of the treatment), duration of the maximum heat flux, and total heat (total radiant exposure) (Table 1). We grouped total radiant exposure into two categories: in the 5000 kJ/m^2 and in the 10,000 kJ/m^2.

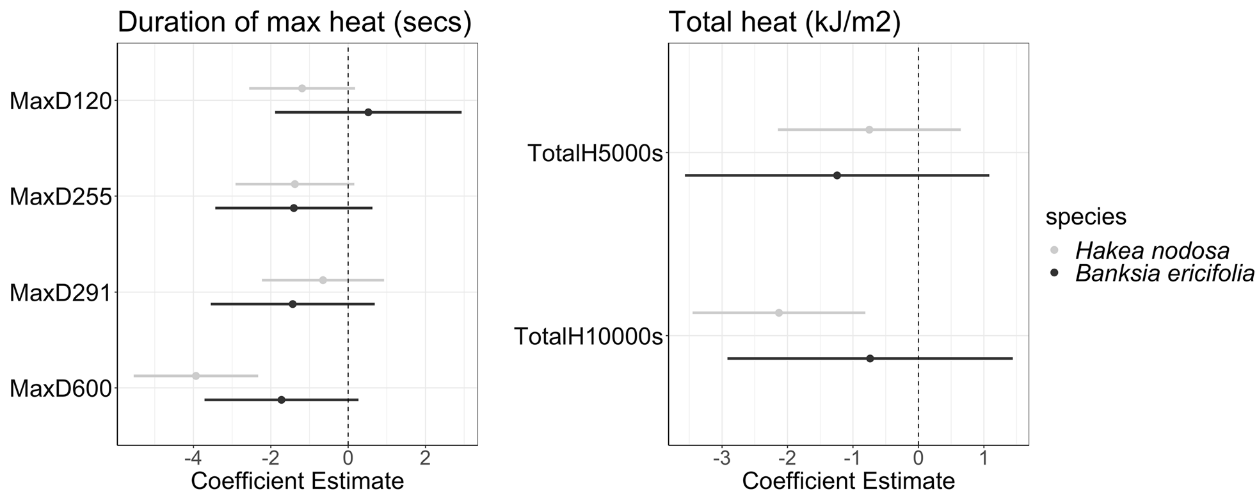

Fig. 5 Estimated effect and 95% confidence intervals of different intensity components on seed viability of yellow hakea (gray) and heath-leaved banksia (black). Intensity components displayed include: the duration of time exposed to the maximum heat flux (120, 255, 291, and 600 s), and the total amount of heat cones were exposed to (between 5000 and 6000 kJ/m^2 or between 10,000 and 11,000 kJ/m^2). All effects are compared to the control

We utilized ordinal logistic regression models for yellow hakea, as it has only two seeds per cone, and therefore only three possible germination outcomes. Analyses were conducted in the package Ordinal (Christensen 2022). For heath-leaved banksia, we used generalized linear models in a binomial link function, or a quasibinomial link function if overdispersed, using the package lme4 (Bates et al. 2015). We checked the residuals for overdispersion and normality using the package DHARMa (Hartig 2022). We obtained model outputs and then displayed model estimates and 95% confidence limits using the packages dotwhisker (Solt and Hu 2015) and ggplot2 (Wickham 2016). All analyses were performed using R programming language version 4.2.0 (R Core Team 2022) and RStudio version 2022.02.1 (Posit Team 2022).

Results

We observed varied tolerances to intensity treatments. High proportions of viable seeds were observed under the control treatment for both species (37/40 yellow hakea seeds and 595/597 heath-leaved banksia seeds) (Table 2). Fewer heath-leaved banksia seeds were counted in the control treatment in comparison to other treatments, due to difficulty in manual extraction of seeds from follicles without fire (Table 2), as is often observed in highly serotinous banksia species (Clarke et al. 2010). Both species germinated at similar rates, with yellow hakea reaching a plateau in cumulative germination slightly earlier than heath-leaved banksia (Fig. 3).

Overall, the application of heating treatments reduced seed survival from the control. For both species, seed viability was most reduced under the treatment SLILD, characterized by a low static and sustained heat for a long duration, and demonstrated by the greatest change in the coefficient estimate plots (Fig. 4; Supplementary Material Table 3). SLILD was the only treatment with strong evidence of an effect for both species (P-value < 0.001 for yellow hakea and < 0.02 for heath-leaved banksia). In contrast, seed survival was fairly consistent across treatments that were characteristic of more realistic wildfire scenarios.

SHI and DHI had comparable total radiant exposure to SLILD, but these two treatments did not have consistent effects across the species (Fig. 4; Supplementary Material Table 3). There was weak evidence that DHI reduced seed viability for yellow hakea (P-value 0.05) and weaker evidence for SHI (P-value 0.08). There was no evidence of an effect for remaining treatments for yellow hakea. For heath-leaved banksia, in addition to SLILD, there was weak evidence of reduced seed survival under SHI and SLI (P-value 0.07 for both), which were comparable to SLILD in that they had extended durations of their maximum heat. There was no evidence of an effect for remaining treatments for heath-leaved banksia.

Different intensity components had varied effects on the two species. For total radiant exposure (total heat), there was only evidence in yellow hakea (P-value < 0.002) that an exposure in the range of 10,000 kJ/m^2 reduced seed survival from the control (Fig. 5; Supplementary Material Table 4). Similarly, for total duration (at all heat levels), there was only evidence in yellow hakea that a duration of 600 s reduced seed survival from the control (P-value 0.004; Supplementary Material Table 4).

For the duration of the maximum heat flux, there was strong evidence in yellow hakea (P-value < 0.001) that a duration of 600 s reduced seed survival from the control and weak evidence in heath-leaved banksia (P-value 0.09; Fig. 5; Supplementary Material Table 4). For yellow hakea, there was reasonable evidence that higher maximum heat reduced the seed survival from the control (MaxH40 = < 0.05) and no evidence for heath-leaved banksia (Supplementary Material Table 4).

Discussion

Fire intensity directly impacts serotinous seed survival. Our study demonstrates that variation in heat flux and exposure duration have distinct impacts on serotinous seed survival. Results from the study demonstrate most support for hypothesis B that static levels of heat, akin to the fire "passing" stage, causes seed death at long durations. The sustained static heat that cones were exposed to in the SLILD treatment was the only combination of fire intensity dynamics that had significant effects on seed death for both species. This is despite other treatments having comparable total radiant exposure to the SLILD treatment and higher maximum heat exposure. These results demonstrate a remarkable capacity of serotinous cones, and the seeds within them, to tolerate the dynamic heat of a fire front.

The distinct impacts of heat flux, exposure duration, and their combination, regardless of total radiant exposure, demonstrate the relationship between fire intensity and serotinous seed death is mechanistic. For example, DHI, SHI, and SLILD had comparable total radiant exposure. Nevertheless, SLILD, a sustained heat flux at long duration, was the only treatment to demonstrate a significant reduction in seed survival for both species (Fig. 4, Supplementary Material Table 3). This shows that different combinations of fire intensity—in heat flux and duration—trigger specific effects. The larger impact of "duration of the maximum heat flux" in comparison to other intensity components suggests that the duration of the second stage of the fire front, the "passing" time, has the most importance in determining seed survival, as per hypothesis B. A greater importance of passing time is consistent with other studies that show that prolonged exposure to high temperature reduces seed survival (Milich et al. 2012). We suggest this could be related to cones opening under a certain heat flux, leaving seeds exposed to the sustained "passing" stage without protection from their woody fruit structures (Clarke et al. 2010). However, we have no formal quantification of this from the present study.

We observed species-specific responses to the intensity treatments: heath-leaved banksia appeared more tolerant to high-intensity fire than yellow hakea. Heath-leaved banksia had higher proportions of surviving seeds per cone and higher tolerance to higher maximum heat and total radiant exposure than yellow hakea. Previous studies have also demonstrated the ability of seeds of various Banksia species to withstand high fire temperatures, attributed to their low moisture content (Tangney et al. 2019, 2020). Seeds with low moisture content are more likely to tolerate high temperatures due to the highly viscous state of the water within seeds (Tangney et al. 2019). However, moisture content has not been found to be an important factor in seed survival of other serotinous and non-serotinous species from the genus *Pinus* (Greene et al. 2024). Difference in survivability could also be related to seed mass, or seed coat thickness, which we did not measure. Studies in soil-stored seed have found larger seeds had greater tolerance to heat shock (Ribeiro et al. 2015). However, from qualitative observation, yellow hakea and heath-leaved banksia had comparable seed sizes, so this may not be a plausible explanation. The most convincing explanation for species differences are related to the shape and size of the cone and the seed arrangement within cones (Greene et al. 2024). Banksia species are likely able to retain seeds in follicles for longer periods and at high temperatures (Enright and Lamont 1989), because the genus Banksia utilizes a complex cone structure and seed arrangement to protect seeds (Huss et al. 2019), whereas the Hakea genus appears more simplistic. For example, in the control group, the yellow hakea opened cones readily after air drying, while heath-leaved banksia required oven treatment to open follicles, suggesting the serotiny mechanism is much stronger in the Banksia species studied.

This experiment has demonstrated that the study species have a large capacity to survive brief high-intensity fires and long dynamic fires with a contained "passing" time. This is likely due to a prolonged evolutionary history of serotinous species tied to crown fires (He et al. 2016; Keeley et al. 2011; Lamont et al. 2019; Pausas 2015). Most yellow hakea seeds and the great majority of heath-leaved banksia seeds survived other treatments than SLILD. If a high level of heat flux is applied at long duration without mimicking the "leaving" stage of a fire, species may appear less tolerant to high level of heat flux than they are. Testing fire intensity effects with only static heat treatments may therefore distort interpretations of fire intensity effects on serotinous species, although this is a common practice (Cochrane 2017; Emery et al. 2011). We suggest that future fire intensity experiments conducted in laboratory settings should incorporate the three stages of the fire front, to test true tolerances of fire exposure, analogous to the response within an actual fire event.

In this study, we contributed knowledge of how fire intensity affects the survival of serotinous seeds, and we now outline directions for future work to advance this knowledge to support biodiversity. First, our study focuses solely on modeling the effects of radiation, which represents scenarios where fire burns at some distance from trees or where radiation serves as the dominant heat transfer mechanism. However, in some cases, convective heat and direct flame contact also play a significant role in seed mortality. For example, this applies when the fire front directly touches trees or when convective heat from surface fires affects cones in crowns. In our study, we were unable to account for convection and direct flame contact due to technical restrictions in our experimental design. However, including direct flame contact and convective heat along with radiative heat will increase our understanding of the combined effects of fire front exposure. Second, understanding how fire intensity effects may interact with climatic conditions post-fire, such as water limitation, or high temperatures, may reveal new fire-seed relationships (Davis et al. 2018), such as in post-fire conditions critical to recruitment success (Mackenzie et al. 2021). Third, it is essential to understand fire intensity effects on seed survival in field environments. Plant architecture, cone arrangement, and interactions with surrounding vegetation are likely to influence how fire intensity drives seed mortality. A better understanding of seed-fire interactions is important for the conservation of fire-prone plants facing altered fire regimes and climates.

Conclusions

It is important to understand the capacity of fire persistence traits such as serotiny to withstand fire intensity, as fire becomes more frequent and intense. This research has demonstrated the importance of accounting for the distinct and combined impacts of different fire regimes and intensity components, namely heat flux, exposure duration, and their dynamics. We found that the long exposure durations of the "passing" stage of the fire is most likely to cause seed death. We also found both species' seeds had very good capacity to tolerate dynamic high-intensity fires, if the "sustained" heat of the passing stage remains within certain limits. Future research should consider dynamic heating regimes when evaluating the effects of fire intensity on plants under experimental conditions. This will allow better replication of realistic wildfire scenarios, providing a more accurate understanding of plant responses under different fire conditions.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00295-7.

Supplementary Material 1: Table S3. Effects of treatments on the viability of seeds. Effect estimates, *P*-value, and confidence limits are reported for each treatment, for each species. All treatments are compared to the Control. We used an ordinal model for *Hakea nodosa*, for the limited range of potential germination (0,1,2). We used a generalized linear model with a binomial link function for *Banksia ericifolia*, to examine the proportion of viable seeds. *P*-value<0.05 = *, *P*-value <0.01**, *P*-value <0.001***. Table S4. Influence of different components of fire intensity tested on seed viability. The AIC, direction of effect, *P*-value and upper and lower confidence limits are displayed for each categorical predictor for each species. *Hakea nodosa* are run as ordinal models. *Banksia ericifolia* are run as generalized linear models in the quasibinomial link function. *P*-value<0.05 = *, *P*-value <0.01**, *P*-value <0.001***.

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Authors' contributions
CT, EPP, AF, and TP conceived the ideas, hypotheses, and designed the methodology; CT led the data collection with assistance from AF and EPP; CT and EPP conducted the statistical analysis of the data; all authors contributed to interpreting results; EPP and CT led the writing of the manuscript and AF and TP contributed critically to the drafts. All authors gave final approval for publication. CT and EPP are joint first authors of this manuscript.

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Availability of data and materials
The datasets generated and analyzed during the current study are available in the Figshare repository. This will be made available upon publication.

Declarations

Competing interests
The authors declare that they have no competing interests.

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References

Abdul-Baki, Aref. A., and Granville M. Moore. 1979. "Seed disinfection with hypochlorites: a selected literature review of hypochlorite chemistry and definition of terms. *Journal of Seed Technology* 4(1):43–56.

Agne, Michelle C., Joseph B. Fontaine, Neal J. Enright, and Brian J. Harvey. 2022. Fire interval and post-fire climate effects on serotinous forest resilience. *Fire Ecology* 18 (1): 22. https://doi.org/10.1186/s42408-022-00145-4.

Ayan, Sezgin, Cihan Erkan, Esra Nurten Yer Çelik, Orhan Gulseven, Şeyma Selin Akin, and Ergin Yilmaz. 2020. "Effects of high temperature shocks applications on seed viability and germination in some Anatolian black pine [Pinus Nigra J.F. Arnold Ssp. Pallasiana (Lamb.) Holmboe] populations." *Turkish Journal of Forestry* 106–12. https://doi.org/10.18182/tjf.677339.

Bates, Douglas, Martin Mächler, Benjamin M. Bolker, and Steven C. Walker. 2015. "Fitting linear mixed-effects models using Lme4." *Journal of Statistical Software* 67 (1). https://doi.org/10.18637/jss.v067.i01.

Bell, David T., and Deanne S. Williams. 1998. Tolerance of thermal shock in seeds. *Australian Journal of Botany* 46 (2): 221–233. https://doi.org/10.1071/bt97010.

Bowman, David M J S, Grant J Williamson, Rebecca K Gibson, Ross A Bradstock, and Rodney J Keenan. 2021. "The severity and extent of the Australia 2019–20 Eucalyptus forest fires are not the legacy of forest management." *Nature Ecology & Evolution* 1003–10. https://doi.org/10.1038/s41559-021-01464-6.

Bowman, David M.J.S.., Brett P. Murphy, Dominic L.J.. Neyland, Grant J. Williamson, and Lynda D. Prior. 2014. Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Global Change Biology* 20 (3): 1008–1015. https://doi.org/10.1111/gcb.12433.

Bradstock, R.A., A.M. Gill, S.M. Hastinga, and P.H.R. Moore. 1994. Survival of serotinous seedbanks during bushfires: Comparative studies of hakea species from southeastern Australia. *Australian Journal of Ecology* 19 (3): 276–282. https://doi.org/10.1111/j.1442-9993.1994.tb00490.x.

Causley, Casey Lee, William M. Fowler, Byron B. Lamont, and Tianhua He. 2016. Fitness benefits of serotiny in fire- and drought-prone environments. *Plant Ecology* 217 (6): 773–779. https://doi.org/10.1007/s11258-015-0552-y.

Christensen, RHB. 2022. *Ordinal—regression models for ordinal data* (version R package version 2022.11–16.). https://CRAN.R-project.org/package=ordinal.

Clarke, Peter J., Kirsten J.E.. Knox, and Damian Butler. 2010. Fire intensity, serotiny and seed release in 19 woody species: Evidence for risk spreading among wind-dispersed and resprouting syndromes. *Australian Journal of Botany* 58 (8): 629–636. https://doi.org/10.1071/BT10193.

Cochrane, Anne. 2017. Are we underestimating the impact of rising summer temperatures on dormancy loss in hard-seeded species? *Australian Journal of Botany* 65 (3): 248–256. https://doi.org/10.1071/BT16244.

Collins, Luke, Hamish Clarke, Michael F. Clarke, Sarah C. McColl, Rachael H. Gausden, Trent D. Nolan, and Penman, and Ross Bradstock. 2022. Warmer and drier conditions have increased the potential for large and severe fire seasons across south-eastern Australia. *Global Ecology and Biogeography* 31 (10): 1933–1948. https://doi.org/10.1111/geb.13514.

Davis, Kimberley T., Philip E. Higuera, and Anna Sala. 2018. Anticipating fire-mediated impacts of climate change using a demographic framework. *Functional Ecology* 32 (7): 1729–1745. https://doi.org/10.1111/1365-2435.13132.

Emery, Sarah M., Joy Uwimbabazi, and S. Luke Flory. 2011. Fire intensity effects on seed germination of native and invasive eastern deciduous forest understory plants. *Forest Ecology and Management* 261 (8): 1401–1408. https://doi.org/10.1016/j.foreco.2011.01.024.

Enright, Neal J., and Byron B. Lamont. 1989. Fire temperatures and follicle-opening requirements in 10 Banksia species. *Australian Journal of Ecology* 14 (1): 107–113. https://doi.org/10.1111/j.1442-9993.1989.tb01012.x.

Falster, D., G. Gallagher, and E. Wenk. 2021. AusTraits, a curated plant trait database for the Australian flora. *Scientific Data* 8: 254.

Fernández-García, Víctor., Peter Z. Fulé, Elena Marcos, and Leonor Calvo. 2019. The role of fire frequency and severity on the regeneration of Mediterranean serotinous pines under different environmental conditions. *Forest Ecology and Management* 444 (July): 59–68. https://doi.org/10.1016/j.foreco.2019.04.040.

Gill, Nathan S., Tyler J. Hoecker, and Monica G. Turner. 2021. The propagule doesn't fall far from the tree, especially after short-interval, high-severity fire. *Ecology* 102 (1): e03194. https://doi.org/10.1002/ecy.3194.

Greene, D.F., J.M. Kane, E. Pounden, and S.T. Michaletz. 2024. Cone allometry and seed protection from fire are similar in serotinous and nonserotinous conifers. *New Phytologist* 242: 93–106. https://doi.org/10.1111/nph.19578.

Habrouk, Abdessamad, Javier Retana, and Josep Maria Espelta. 1999. Role of heat tolerance and cone protection of seeds in the response of three pine species to wildfires. *Plant Ecology* 145 (1): 91–99. https://doi.org/10.1023/A:1009851614885.

Hanley, Mick E., and Byron B. Lamont. 2000. Heat pre-treatment and the germination of soil- and canopy-stored seeds of south-western Australian species. *Acta Oecologica* 21 (6): 315–321. https://doi.org/10.1016/S1146-609X(00)01087-0.

Hartig, Florian. 2022. *DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. Package Version 0.4.6.* http://florianhartig.github.io/DHARMa/.

He, Tianhua, Claire M. Belcher, Byron B. Lamont, and Sim L. Lim. 2016. A 350-million-year legacy of fire adaptation among conifers. *Journal of Ecology* 104 (2): 352–363. https://doi.org/10.1111/1365-2745.12513.

Huss, Jessica C., Peter Fratzl, John W.C. Dunlop, David J. Merritt, Ben P. Miller, and Michaela Eder. 2019. "protecting offspring against fire: lessons from Banksia seed pods." *Frontiers in Plant Science* 10 (March). https://doi.org/10.3389/fpls.2019.00283.

Keeley, Jon E., Juli G. Pausas, Philip W. Rundel, William J. Bond, and Ross A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16 (8): 406–411. https://doi.org/10.1016/j.tplants.2011.04.002.

Lamont, Byron B., Tianhua He, and Zhaogui Yan. 2019. evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biological Reviews* 94 (3): 903–928. https://doi.org/10.1111/brv.12483.

Lamont, Byron B., Juli G. Pausas, Ed.T.F. Tianhua He, and Witkowski, and Mick E. Hanley. 2020. Fire as a selective agent for both serotiny and nonserotiny over space and time. *Critical Reviews in Plant Sciences* 39 (2): 140–172. https://doi.org/10.1080/07352689.2020.1768465.

Mackenzie, B.D., T.D. Auld, D.A. Keith, and M.K. Ooi. 2021. Fire seasonality, seasonal temperature cues, dormancy cycling, and moisture availability mediate post-fire germination of species with physiological dormancy. *Frontiers in Plant Science* 12: 795711.

Maia, Paula, Juli G. Pausas, Ana Vasques, and Jan Jacob Keizer. 2012. Fire severity as a key factor in post-fire regeneration of Pinus pinaster (Ait.) in Central Portugal. *Annals of Forest Science* 69 (4): 489–498. https://doi.org/10.1007/s13595-012-0203-6.

McColl-Gausden, Sarah C., Lauren T. Bennett, Dan A. Ababei, Hamish G. Clarke, and Trent D. Penman. 2022. Future fire regimes increase risks to obligate-seeder forests. *Diversity and Distributions* 28 (3): 542–558. https://doi.org/10.1111/ddi.13417.

Milich, Kate L., John D. Stuart, J. Morgan Varner, and Kyle E. Merriam. 2012. Seed viability and fire-related temperature treatments in serotinous california native Hesperocyparis species. *Fire Ecology* 8 (2): 107–124. https://doi.org/10.4996/fireecology.0802107.

Miller, Timothy S., Alexander I. Filkov, Trent D. Penman. 2022. "Improved laboratory method to test flammability metrics of live plants under dynamic conditions and future implications. "*International Journal of Wildland Fire* https://doi.org/10.1071/WF21172.

Morandini, Frédéric., and Xavier Silvani. 2010. Experimental investigation of the physical mechanisms governing the spread of wildfires. *International Journal of Wildland Fire* 19 (5): 570–582.

Mueller, Eric V., Nicholas Skowronski, Jan C. Thomas, Kenneth Clark, Michael R. Gallagher, Rory Hadden, William Mell, and Albert Simeoni. 2018. Local measurements of wildland fire dynamics in a field-scale experiment. *Combustion and Flame* 194: 452–463.

Ooi, Mark K.J.., Andrew J. Denham, Victor M. Santana, and Tony D. Auld. 2014. Temperature thresholds of physically dormant seeds and plant functional response to fire: Variation among species and relative impact of climate change. *Ecology and Evolution* 4 (5): 656–671. https://doi.org/10.1002/ece3.973.

Pausas, Juli G. 2015. Evolutionary fire ecology: Lessons learned from pines. *Trends in Plant Science* 20 (5): 318–324. https://doi.org/10.1016/j.tplants.2015.03.001.

Posit Team. 2022. *R Studio: integrated development environment for R. Posit Software* (version 1.4.1717). Boston, MA. http://www.rstudio.com/.

R Core Team. 2022. *R: a language and environment for statistical computing. R Foundation for Statistical Computing,*. Vienna, Austria: R Core Team. http://www.R-project.org/.

Ribeiro, Leandro C., Eduardo R. M. Barbosa, Frank van Langevelde, and Fabian Borghetti. 2015. The importance of seed mass for the tolerance to heat shocks of savanna and forest tree species. *Journal of Vegetation Science* 26 (6): 1102–1111. https://doi.org/10.1111/jvs.12314.

Rossi, Jean Louis, François Joseph Chatelon, and Thierry Marcelli. 2018. "Fire intensity." In *Encyclopedia of Wildfires and Wildland-Urban Interface (WUI) Fires*, edited by Samuel L. Manzello, 1–6. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-51727-8_51-1.

Santoni, P.A., A. Simeoni, J.L. Rossi, F. Bosseur, F. Morandini, X. Silvani, J.H. Balbi, D. Cancellieri, and L. Rossi. 2006. Instrumentation of wildland fire: Characterisation of a fire spreading through a Mediterranean shrub. *Fire Safety Journal* 41 (3): 171–184.

Solt, Frederick, and Yue Hu. 2015. *Dotwhisker: dot-and-whisker plots of regression results. Available at The Comprehensive R Archive Network (CRAN).* http://CRAN.R-project.org/package=dotwhisker.
Standards Australia. 2014. "Methods for fire tests on building materials, components and structures: Part 4 – Fire resistance tests of elements of building construction (AS 1530.4:2014)." SAI Global. https://www-saiglobal.com.
Tangney, Ryan, David J. Merritt, J. Nikolaus Callow, Joseph B. Fontaine, and Ben P. Miller. 2020. Seed traits determine species' responses to fire under varying soil heating scenarios. *Edited by Colleen Seymour. Functional Ecology* 34 (9): 1967–1978. https://doi.org/10.1111/1365-2435.13623.
Tangney, Ryan, David J. Merritt, Joseph B. Fontaine, and Ben P. Miller. 2019. Seed moisture content as a primary trait regulating the lethal temperature thresholds of seeds. *Journal of Ecology* 107 (3): 1093–1105. https://doi.org/10.1111/1365-2745.13095.
Torres, O., L. Calvo, and L. Valbuena. 2006. Influence of high temperatures on seed germination of a special Pinus pinaster stand adapted to frequent fires. *Plant Ecology* 186 (1): 129–136. https://doi.org/10.1007/s11258-006-9117-4.
Turner, Monica G., Kristin H. Braziunas, Winslow D. Hansen, and Brian J. Harvey. 2019. "Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. "*Proceedings of the National Academy of Sciences* 116 (23). *National Academy of Sciences* 11319–28. https://doi.org/10.1073/pnas.1902841116.
Whelan, Robert J., and David J. Ayre. 2022. High adult mortality and failure of recruitment in a population of Banksia spinulosa following high-intensity fire. *Austral Ecology* 47 (6): 1162–1167. https://doi.org/10.1111/aec.13208.
Wickham, Hadley. 2016. *Ggplot2, elegant graphics for data analysis*. New York: Springer-Verlag.

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