Felicity E. Charles[1*] 0000-0002-7241-2720

Patrick T. Moss[1,2] 0000-0003-1546-9242

Annabel L. Smith[1] 0000-0002-1201-8713

[1]School of the Environment, The University of Queensland, St Lucia, 4067, QLD, Australia

Present Address: [2]School of Earth and Atmospheric Sciences, Queensland University of Technology, Brisbane City, 4000, QLD, Australia

[*]Correspondence: f.charles@uq.edu.au

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Keywords: fire ecology; fire management; fire-cued germination; reproductive traits; demography; plant-animal interaction

Abstract

Aim

In fire-prone regions globally, plants have developed reproductive traits enabling population persistence under historical fire regimes. However, many common plant species are threatened by a mismatch between historical and contemporary fire regimes, which also threatens animal species relying on them for resource provision. We investigated how recent fire history affected reproductive trait variation in two congeneric food tree species (Casuarinaceae) for the threatened Glossy black-cockatoo (*Calyptorhynchus lathami*, Cacatuidae): *Allocasuarina littoralis* (an obligate seeder) and *A. torulosa* (a facultative resprouter).

Location

This study took place in southeast Queensland, Australia, within the distributional range of Glossy black-cockatoos, *A. littoralis* and *A. torulosa*.

Methods

Lab-based germination experiments measured germination responses of seeds exposed to heat shocks of 80° and 95°C, *Allocasuarina* smoke, and combinations of these treatments. Field-based surveys measured demographic structure and reproductive output.

Results

Heat and smoke treatments slowed germination in *A. torulosa* but had no effect on germination in *A. littoralis*. Proportion germination increased with seed weight but was unaffected by heat and smoke. Heavier seeds were associated with higher fire frequencies and greater temperature variability at seed collection sites. In *A. torulosa*, heavier seeds took longer to germinate, especially when seeds were collected from frequently burnt sites, possibly reflecting a resprouting-seed production trade-off. Fire history did not influence reproductive output or population demographic structure for either species.

Main conclusions

For restoration, heat and smoke treatments are unlikely to be necessary once seeds are released from cones. However, local fire history and seed weight should be considered when collecting seeds for restoration programs, especially for *A. torulosa*. Our study suggests seed germination is influenced by laboratory fire treatments and recent fire history at seed collection sites. Thus, variation in germination response to fire of *Allocasuarina* could influence a dietary specialist threatened cockatoo through differences in species post-fire establishment.

Keywords: fire ecology, fire management, fire-cued germination, reproductive traits, demography, plant-animal interaction

Introduction

Fire is an important driver of plant trait evolution, especially for reproductive traits which are closely associated with plant fitness (Keeley et al. 2011, Villellas et al. 2021, Campbell et al. 2022). In fire-prone ecosystems, post-fire reproductive modes can be divided broadly into resprouters, which survive through tissue structures below bark or soil (R+); or obligate seeders which are killed by fire and persist through propagules stored in soil or canopy seedbanks (P+) (Pausas et al. 2004, Pausas and Keeley 2014, Clarke et al. 2015). These strategies result in contrasting life histories: resprouters tend to be long-lived with low population turnover, whereas obligate seeders are short-lived with high population turnover (Pausas et al. 2004, Pausas and Keeley 2014). Compared with seeders, resprouters generally have lower seed production and seedling densities than seeders, and their higher investment in resprouting tissue production may slow maturation rates (Verdú 2000, Whelan et al. 2002,

Hunter 2003, Pausas et al. 2004, Pausas and Keeley 2014, Ojeda et al. 2016, Bendall et al. 2022). Thus, resprouters face a trade-off between investment in seed production and resprouting (Verdú 2000, Whelan et al. 2002, Hunter 2003, Pausas et al. 2004, Pausas and Keeley 2014, Ojeda et al. 2016, Bendall et al. 2022). Conversely, obligate seeders have high seed production and seedling densities, and usually have mass recruitment events post-fire (Keith et al. 2002, Hunter 2003, Pausas and Keeley 2014, Ojeda et al. 2016). Studying closely related species with differing post-fire reproductive modes can be useful because trait variation can be explained by ecology and environmental variation rather than phylogeny (Seglias et al. 2018, Cortés-Flores et al. 2020, Fenollosa et al. 2021, Zhao et al. 2021, Wang et al. 2022).

Since seed regeneration enables successful recolonisation after disturbance, many species from fire prone ecosystems show strong germination responses to fire-related cues of heat and smoke (linked to fire intensity and severity, Bellingham and Sparrow 2000, Kennard et al. 2002, Hanley et al. 2003, Gómez-González et al. 2008, Pausas and Keeley 2014, Le Breton et al. 2020). Selection on seed traits over evolutionary timescales is likely stronger in obligate seeders than resprouters due to their reliance on regeneration from seed (Bellingham and Sparrow 2000, Pausas and Keeley 2014, Bendall et al. 2022). Obligate seeders can also spread risk and increase reproductive output by producing smaller seeds under certain fire regimes (Verdú 2000). Heat from fire creates a selection pressure on seed size and how this plays out depends on the type of seedbank (Lamont et al. 2019). Serotinous canopy seedbanks, for example, lack the insulating properties of soil and rely on seed mass to protect the embryo, resulting in selection for larger seeds (Keeley 1977, Escudero et al. 2000, Hanley et al. 2003, Liyanage and Ooi 2017, Tangney et al. 2025). Understanding how recent fire history influences post-fire germination could help determine whether enough trait variability

exists for species to respond to contemporary and near-future fire regime changes. Integrating fire history information from seed collection sites has been done (e.g., Gómez-González et al. 2011, Vandvik et al. 2014, Gómez-González et al. 2016, Zaki et al. 2021, Kasel et al. 2024, Plumanns-Pouton et al. 2024) but most studies apply laboratory-based heat and smoke treatments without considering fire history variation at the seed collection site (e.g., Tangney et al. 2020). This is a problem because we might miss recent variation in responses driven by contemporary fire regimes (Gómez-González et al. 2016, Kelly et al. 2025).

Contemporary changes in fire regimes are causing misalignments between plant trait variability and fire regime characteristics (Moritz et al. 2012, Johnstone et al. 2016, Day et al. 2020, Canadell et al. 2021, Harvey and Enright 2022, Kelly et al. 2025). For example, some fire-adapted sclerophyllous species have failed to regenerate after fires that are too severe or too frequent (Bennett et al. 2016, Etchells et al. 2020, Sano et al. 2025). Declines in regeneration of primary producers could impact plant-animal interactions or food webs (Smith 2018, Carbone et al. 2019, Ellison 2019, Kelly et al. 2020, Rainsford et al. 2020, Ballarin et al. 2024). Specialist plant-animal interactions are most vulnerable to changes in fire regimes, yet are drastically understudied in fire ecology (Charles et al. 2025). Whether trees can adapt in situ is unclear, as fire regime changes are often accompanied by climatic changes which can also impact post-fire regeneration success (Stevens-Rumann et al. 2018, Young et al. 2019, Kelly et al. 2025). Understanding how plants respond to fire is especially important when those species form critical habitat for specialised plant-animal interactions (Talluto and Benkman 2014, Lybbert and St. Clair 2016, Charles et al. 2025).

After germination, individuals must be able to grow and recruit into the adult population, and the environmental conditions driving transitions among growth stages can change rapidly

post-fire (Keeley et al. 2011, Smith et al. 2016). Variation in post-fire recruitment rates can result in differing population demographic structure across fire history gradients (Taylor 2010, Pausas and Keeley 2014, Ojeda et al. 2016). In obligate seeders, short inter-fire intervals relative to their age at maturity cause immaturity risk, where two or more fires occur before a species can reach reproductive maturity (McCarthy et al. 1999, Turner et al. 2009, Taylor 2010, Pulsford et al. 2016). This situation reduces the ability of obligate seeders to replenish seedbanks and increases the risk of local extinction (Keith 1996, Agne et al. 2022, McColl-Gausden et al. 2022). Conversely, resprouters tend to survive exposure to repeated fire (Taylor 2010, Pausas and Keeley 2014), with shifts in demographic structure caused by age- and size-related variation in resprouting capacity or, in facultative resprouters, additional recruitment from seed (Gill and Catling 2002, Shibata et al. 2014, Clarke et al. 2015, Matula et al. 2019). Fire at appropriate intervals, therefore, is critical for both obligate seeders and resprouters to cue regeneration, promote seedling establishment, and stimulate flowering (McCarthy et al. 1999, Taylor 2010, Enright et al. 2011, Zirondi et al. 2021, Agne et al. 2022, Thomsen and Ooi 2022). Research examining population demographic structure in closely related species with contrasting reproductive modes (e.g., Ojeda et al. 2016, Schmidberger and Ladd 2020) can help untangle the relationship between post-fire reproductive mode and reproductive trait expression.

We investigated the influence of fire history on reproductive trait variation in two congeneric species with differing post-fire reproductive modes: the obligate seeder *Allocasuarina littoralis* and the facultative resprouter *Allocasuarina torulosa* (Casuarinaceae). These species are common across eastern Australia, where they form mixed stands with *Eucalyptus spp*. in swamps, woodlands, and forests (Neldner et al. 2019, Atlas of Living Australia 2021a, b). Both species are dioecious and store seeds in serotinous cones in the canopy. Fire

126 management guidelines are often based on the *Eucalyptus* species which co-occur with
127 Casuarinaceae, but eucalypts require different fire regimes than Casuarinaceae (Kellman
128 1986, Moss et al. 2011, Stewart and Moss 2015, Neldner et al. 2019). The *Allocasuarina*
129 species we studied are common and widespread, and their seeds are a primary food resource
130 for the threatened dietary specialist Glossy black-cockatoo, *Calyptorhynchus lathami*
131 (Cacatuidae) (listed nationally as Vulnerable, *EPBC* Act 1999). Glossy black-cockatoos have
132 one of the most specialised diets of all Australian birds, feeding on a subset of 12 of 78
133 Casuarinaceae species (Chapman 2007, Menkhorst et al. 2024), making them vulnerable to
134 fire regime changes which impact food resource availability and quality (Cameron et al.
135 2021, Delzoppo et al. 2021, Mooney et al. 2026). Glossy black-cockatoos are notoriously
136 cryptic, shifting their feeding locations in response to a range of unknown environmental cues
137 (similar to other nomadic bird species, Webb et al. 2014). Thus, understanding the fire
138 ecology of *Allocasuarina spp*. is fundamental to effective conservation for these cockatoos.
139
140 We first aimed to determine how contemporary fire frequency and post-fire reproductive
141 mode affected fire-cued germination responses (heat and smoke, as measures of fire intensity
142 and severity) and seed size. (**H1**) We expected that post-fire reproductive mode would
143 influence germination and seed investment, leading to heavier seeds and higher tolerances to
144 fire cues in *A. littoralis* (obligate seeder) than *A. torulosa* (facultative resprouter). Given the
145 trade-off between post-fire reproductive mode and seed size and number (Leishman 2001,
146 Pausas and Keeley 2014, Hodgson et al. 2020, Walsh et al. 2022, Li et al. 2025, Maleki et al.
147 2025), we expected *A. littoralis* to have (**H1a**) heavier seeds with increasing fire frequency;
148 and (**H1b**) increased germination rates in response to heat and smoke (Paula and Pausas
149 2008, Pausas and Keeley 2014). *Allocasuarina torulosa* was expected to have (**H1c**) lighter

150 seeds with increasing fire frequency; and **(H1d)** lower germination rates in response to heat
151 and smoke (Staden et al. 2000, Paula and Pausas 2008).
152
153 Second, we aimed to determine how fire frequency, time since fire, and post-fire reproductive
154 mode influenced population demographic structure and reproductive output (i.e., number of
155 cones on female individuals). We expected (**H2**) longer times since fire and low fire
156 frequencies would reduce the ratio of seedlings and saplings to mature individuals but
157 increase reproductive output. Due to immaturity risk, we expected (**H2a**) high fire frequency
158 and short time since fire would result in a lower ratio of seedlings or saplings to mature
159 individuals in *A. littoralis*, compared with *A. torulosa*. Because high-intensity or frequent fire
160 would reduce the capacity to reach reproductive maturity during inter-fire periods (Enright
161 and Lamont 1989, Pausas and Keeley 2014), we also expected (**H2b**) high fire frequency and
162 short times since fire would be related to lower reproductive output in both species.
163
164 Third, we aimed to investigate how environmental attributes relating to site productivity
165 (topographic wetness, water availability (Gallant and Austin 2012); foliage projective cover,
166 woody vegetation cover (Fisher et al. 2018)) and climate (latitude; precipitation seasonality
167 and temperature seasonality (Noce et al. 2020, Wang et al. 2024)) interacted with fire regimes
168 to influence reproductive trait variation. We expected (**H3a**) environments with low
169 productivity and high climate variability to be stressful for *Allocasuarina*, reducing
170 reproductive output, seed weight, and ratios of seedlings and saplings to mature individuals
171 (Enright et al. 2015, McColl-Gausden et al. 2022). Additionally, as lower latitudes are
172 associated with increased temperatures, growth and reproduction, we expected (**H3b**)
173 sampling locations at lower latitudes to have higher reproductive outputs, seed weight and

ratios of seedlings and saplings to mature individuals (Moles and Westoby 2003, Chamorro et al. 2018, Käber et al. 2021, Wang et al. 2023).

Methods

Study region

This study took place in southeast Queensland, Australia, within the distributional range of Glossy black-cockatoos, *Allocasuarina littoralis* and *A. torulosa*. Sampling sites (hereafter 'sites') included public land (i.e., national parks, state forests, and conservation parks) and private properties (i.e., Hidden Vale Nature Refuge, Gillies Ridge Nature Refuge, Bartopia Nature Refuge, and Bulimbah Nature Refuge) (Fig. 1). The region has a subtropical climate with mean maximum temperatures in summer ranging from 25°C to 32°C, and in winter from 17°C to 21°C. Mean annual rainfall in the region ranges from 688 mm to 1584 mm. In our inland study region in southeast Queensland, *A. torulosa* is more common than *A. littoralis* (Atlas of Living Australia 2021a, b). Dominant vegetation at sampling locations included eucalypt woodland to open forest and, for some *A. torulosa* sampling locations, wet eucalypt forest (Neldner et al. 2019). At these sampling locations, the dominant soil orders included tenosols, sodosols and dermosols and soil types included volcanics; red soils; sandstone; and igneous, Cainozoic and sedimentary rocks (Neldner et al. 2019).

Allocasuarina littoralis and *A. torulosa* are dioecious trees growing 5 to 15 m and 5 to 30 m tall, respectively (Australian Biological Resources Study. Advisory Committee 1989, Spencer 1995). *Allocasuarina littoralis* has a more coastal distribution on sandy, heavy clay, or stony soils (Australian Biological Resources Study. Advisory Committee 1989, Foreman and Walsh

199 1993) while *Allocasuarina torulosa* is distributed widely from coastal to inland regions in
200 forests on fertile soils (Stanley et al. 1983, Australian Biological Resources Study. Advisory
201 Committee 1989). *Allocasuarina littoralis* lives, on average, 40-70 years (with a potential
202 lifespan up to 100 years), while *A. torulosa* can typically live for 50-100 years as individuals
203 can resprout following fire (Kattge et al. 2020, Falster et al. 2021). Reproductive maturity can
204 be reached in five years for both species, but *A. littoralis* is more likely to take 10 years
205 (Kattge et al. 2020, Falster et al. 2021). Both species gradually release seed from serotinous
206 cones as they dry (Crowley 1986, Kattge et al. 2020, Falster et al. 2021). A number of studies
207 have considered post-fire recruitment mode of *A. littoralis* and *A. torulosa*. Some have
208 reported *A. littoralis* to be an obligate seeder (R-P+) which is fire killed and germinates from
209 canopy-stored seed (Burley et al. 2007, Williams et al. 2012), while others suggest it is a
210 facultative resprouter (R+P+) (Schmidt and Stewart 1997, Knox and Clarke 2005, Clarke et
211 al. 2010, Clarke et al. 2015, Paul et al. 2017, Kattge et al. 2020). It is unclear from these
212 studies whether *A. littoralis* was classified as a resprouter following the convention of
213 resprouting after 100% scorch or stem death (a condition required for categorisation as R+,
214 Pausas et al. 2004). *Allocasuarina torulosa* is generally considered to be a resprouter (Kubiak
215 2009, Williams et al. 2012, Benwell 2024), with some evidence of inter-fire seed regeneration
216 where canopy seedbanks are available (R+P+, facultative resprouter) (Clarke et al. 2015,
217 Kattge et al. 2020).
218
219 Both tree species lack seed dormancy, with seed protection and germination timing mediated
220 by storage in serotinous cones (Turnbull and Martensz 1982, Crowley 1986). Germination
221 occurs across a range of incubation temperatures between 17-37°C (Turnbull and Martensz
222 1982). There has been limited research on fire-cued germination in *A. littoralis* and *A.*
223 *torulosa* (but see, Crowley 1986, Clarke et al. 2000). In other Casuarinaceae, seeds have been

reported to survive heat shock of up to 120°C (Hanley and Lamont 2000, Callister et al. 2018). Temperature in *Allocasuarina* canopies during wildfire is unknown but flame temperature in eucalypt forests, where *Allocasuarina* commonly occur, can reach 300° to 1100°C (Huss et al. 2019), and *Allocasuarina* leaf litter can burn at high temperatures (e.g., soil temperatures of 60° to 111°C at 1 cm depth, Tangney *et al.* 2020). Storage of *Allocasuarina* seeds in woody cones provides some insulation from fire, reducing extremes of temperature exposure but potentially exposing seeds to temperatures above 100°C during fire (Huss et al. 2019).

Field surveys

We established 40 sampling locations to cover a range of fire histories within the distribution of the Glossy black-cockatoo, *A. littoralis*, and *A. torulosa*. Our primary goal was to sample each tree species across a range of fire histories (**H2**) and environments (**H3**). Thus, we used occurrence records from Atlas of Living Australia to locate areas where *A. littoralis* and *A. torulosa* had been observed within our study region. We then randomly selected occurrence records for each species across a range of fire frequencies. We conducted reconnaissance field surveys at these locations to verify occurrences. Where no *Allocasuarina* were found, we moved to another location with a similar fire frequency until a range of sampling locations was identified. Reconnaissance surveys identified that *A. littoralis* and *A. torulosa* generally occurred in areas with low fire frequency (unburnt or 1-3 fires from 1987-2023) with fewer occurrences (<20 records) in frequently burned areas (4-7 fires from 1987-2023) (Atlas of Living Australia 2021a, b, The Global Biodiversity Information Facility 2022a, b). As such, we established more sampling locations in areas with low fire frequency (0-3 fires from 1987-2023; 32 sampling locations) than high fire frequency (4-7 fires from 1987-2023; six

sampling locations). Furthermore, high fire frequency sampling locations were in areas where *A. torulosa* was found (26 sampling locations), but not *A. littoralis*, limiting the fire frequency analysis for *A. littoralis*. *Allocasuarina littoralis* might have been excluded from high fire frequency areas due to inappropriate fire regimes, climate, or soil conditions.

Once 40 sampling locations had been identified, a 50 m × 4 m transect was established, beginning at a randomly identified individual tree, and oriented towards other individuals. Within locations where multiple transects were sampled (e.g., 2-7 transects), transects were spaced at least 140 m apart (range = 140 m – 14 km). Multiple individuals were sampled within transects (mean = 27.2 individuals; and range = 7 – 123 individuals). This hierarchical sampling structure was accounted for in the analysis. For each individual tree on a transect, we measured: demographic class (described below); diameter at breast height (DBH, cm), recruitment type (e.g., basal resprout, trunk resprout, seedling, or none); condition (e.g., dead or alive, burnt or unburnt); and height in metres using a Suunto PM5/360 PC Clinometer (Vantaa, Finland) or Nikon Forestry Pro II Laser Rangefinder (Tokyo, Japan). Following another *Allocasuarina* study (Schmidberger and Ladd 2020), we used demographic class categories to investigate the influence of fire history on population demographic structure (**H2**). These categories were defined as: mature = height >1 m, DBH >3 cm; sapling = height >1 m, DBH <3 cm; and seedling = height <1 m. For female trees, the total number of cones were counted as a measure of reproductive output (**H2b**). Where more than 100 cones were present on a single female tree, we recorded average estimates based on counts from two observers into equal-width intervals of 50 cones (e.g., 100-150, 150-200, 200-250, 250-300, etc.).

Biological material was collected under scientific permits from the Queensland Government (P-PTC-100230959; P-PTUKI-100230962-2; P-PTUKI-100395507-2). Cones were collected from up to six individuals per transect, with fewer individuals sampled if no cones were available or cones were not within *ca.* 5 m of the ground. Females bearing cones were randomly selected around transects for cone collection, with at least 20 m between individuals (range within sampling locations 20 m – 130 m). On each cone collection tree, we sampled a minimum of two visually mature cones (i.e., brown to grey-brown in colour with closed valves) to maximise the chance that seed was fully developed but not yet released. To increase sample size for the germination experiment, more cones were collected where available, without removing all cones from an individual (up to 73 cones with an average of 12 cones per individual). Cones were stored in paper bags in a warm, dry environment until seeds were shed. Unshed seeds were manually extracted from cones using tweezers. Seeds were then stored for eight to 24 months in an air-conditioned laboratory inside an airtight container to minimise ambient temperature fluctuations prior to the germination experiment.

Germination experiment

Germination experimental overview

We conducted a full factorial, replicated germination experiment, to test the hypothesis that post-fire reproductive mode and variation in fire frequency influenced fire-cued germination in *Allocasuarina* (**H1**). Three separate rounds of seed germination were conducted, with individuals exposed to the same treatment(s) in each replicate. Before conducting this experiment, we ran a series of optimisation trials on seed from both species to determine optimal incubation temperatures; heat shock temperatures and duration; aerosol smoke

exposure duration; and smoke material (Appendix S1: Section 1). Incubation temperature tests determined optimal germination temperature and baseline germination rate using thermal gradient bars (Appendix S1: Section 1, Fig. S1). Heat shock and smoke trials determined (1) upper thresholds for heat tolerance and (2) the level at which seeds showed germination variability. This latter property was considered important to indicate levels of heat and smoke that could drive selection (Kelly et al. 2025) (Appendix S1: Section 1, Fig. S2, S3).

After establishing optimal conditions, we began the full factorial experiment. For this experiment, the main response variables were (1) proportion of seeds germinated, as a measure of an individual's resilience to seed treatments (**H1b**, **H1d**); (2) time to 50% germination, as a measure of an individual's competitiveness (**H1b**, **H1d**); and (3) seed weight, as a proxy measure of seed size (**H1a**, **H1c**) (seed weight and size are strongly correlated and relate to investment in sexual reproduction Eriksson 1999, Verdú 2000, Gnan et al. 2014). A 'seed lot' was defined as the whole collection of seeds from an individual while a 'seed sample' was defined as 20 seeds from a seed lot used in the germination experiments. Seed weight was measured in two ways: first as the seed lot and, second, as a 10-seed fraction to estimate the total number of seeds in the seed lot. The estimated total number of seeds was used to estimate the average seed weight per seed in a seed lot.

For all germination experiments, seed samples were placed in plastic 90 mm petri dishes lined with Whatman no. 1 filter paper moistened with distilled water and sealed with parafilm to reduce water loss. Seeds exposed to aerosol smoke were plated on new sterile petri dishes prior to germination to reduce exposure to accumulated smoke residues. Seeds exposed to a combination of heat shock and smoke treatments were heat shocked prior to aerosol smoke

exposure. Seeds in all experiments (excluding incubation temperature optimisation) were germinated in illuminated refrigerated incubators (TRIL495-1-SD, Thermoline Scientific, Wetherhill Park, New South Wales, Australia) with a 12-hour photoperiod provided by Grolux fluorescent lighting (36W) and temperatures set to 17°C for *A. littoralis* and 20°C for *A. torulosa* (see Appendix S1: Fig. S1). Germination was considered to have occurred upon emergence of the radicle from the testa. After emergence, the germinant was recorded and removed from the petri dish to allow space for other seeds to germinate. Germination trials ran for a minimum of 29 days and stopped when no new seeds had germinated in a 7-day period. This means there was no upper time limit for the germination trial; we continued counting germinates until there was zero germination over a 7-day period.

Seed viability measurements

Seed viability was measured using two methods: (1) non-destructive x-ray prior to germination experiments to estimate pre-treatment viability without reducing the number of seeds for the experiment; and (2) destructive post-experiment tetrazolium tests to determine whether seeds which remained ungerminated at the end of the trial were viable (Peters 2000). X-rays were taken on a Faxitron MX-20 Imaging system (Lincolnshire, IL, USA), on *ca*. 100 seeds from a seed lot with four replicates of 25 seeds at 28 kV for 6.55 seconds. X-ray images were examined to determine seed fill, a metric related to the amount of seed embryo and endosperm which is correlated with viability (Gagliardi and Marcos-Filho 2011, Tausch et al. 2024). Unfilled seeds were considered unviable but seeds with partial filling were classed as viable as there was potential for germination. X-ray viability data were summarised as the proportion of viable x-ray imaged seeds for analysis. Tetrazolium tests used a 1% 2,3-5 triphenyl tetrazolium chloride (TTC) solution with seeds cut laterally through the distal end

348 of cotyledons and incubated in solution for 18 hours at 30°C in darkness (Peters 2000). After
349 incubation, seeds were observed under a dissection microscope and seeds were classed as
350 viable if the radicle and cotyledons were completely stained pink (Peters 2000). Any TTC
351 staining inconsistencies or lack of staining was considered to indicate unviable seeds (Peters
352 2000).
353
354 Full factorial germination experiment
355
356 The full factorial experiment included six treatments: (1) control; (2) 80°C heat shock for 5
357 min; (3) 95°C heat shock for 5 min; (4) 20 min smoke exposure; (5) 80°C heat shock for 5
358 min + 20 min smoke exposure; and (6) 95°C heat shock for 5 min + 20 min smoke exposure
359 (see Appendix S1: Section 1, Fig. S2, S3 for optimisation). Three replicates for each
360 treatment combination were conducted, with each replicate staggered by 14 days to account
361 for potential starting condition biases. Seed germination was recorded on the first day after
362 plating then every second to third day until germination ceased. For calculation of
363 germination metrics, the germination period length (in days) had to be standardised across all
364 replicates. Germination period lengths varied across replicates; thus, the germination period
365 length was assigned a value of 46 days which was the longest germination period in the
366 dataset. For replicates with germination periods shorter than this, a value of zero was
367 assigned to each day beyond the germination period end date.
368
369 To test the hypothesis that variation in post-fire reproductive mode influenced fire-cued
370 germination (**H1b**, **H1d**) and seed size (**H1a**, **H1c**), species were considered separately for
371 analysis. Seed lots for *A. torulosa* were assigned to a fire frequency category based on that at
372 the collection site (i.e., low fire frequency = 0-3 fires, and high fire frequency = 4-7 fires

from 1987-2023). Due to seed limitations, we were unable to assign each individual tree to all six treatments (e.g., an individual with only 120 seeds could only be assigned to 3 treatments). Thus, we used the `arrangements` R package version 1.1.9 (Lai 2019) in R version 4.3.1 (R Core Team 2018) to randomly assign the six treatments to seed lots, with six separate rounds of assignment. We subsequently reduced treatment assignments on a case-by-case basis such that only three treatments were assigned to a seed lot with 120 seeds. During this case-by-case treatment assignment, we ensured 15 individual seed lots were included for all six treatments. Thus, each germination experiment replicate included six treatments with 300 seeds from 15 seeds lots, totalling 1800 seeds for *A. littoralis*, 1800 seeds for *A. torulosa* low fire frequency, and 1800 seeds for *A. torulosa* high fire frequency.

Spatial data compilation

Fire frequency data from was obtained from Queensland Parks and Wildlife Service (Table 1) and subset temporally (i.e., 1987-2023) to match the temporal resolution of modelled estimates of fire frequency from satellite-derived data (see Charles et al. 2026). Year of last fire was obtained from Queensland Parks and Wildlife fire history data and satellite-derived fire history data. Areas that were unburnt between 1987-2023 were assigned a year of last fire as 1986. Time since fire was calculated by subtracting year of last fire from the sampling year. We obtained data on temperature and precipitation seasonality (Fick and Hijmans 2017), Topographic Wetness Index (TWI) (Gallant and Austin 2012), and Foliage Projective Cover (FPC) (Department of Environment 2020, 2024) (Table 1). Spatial data requiring resolution adjustments were rescaled to 30 m resolution (Table 1) using the `gdalUtilities` R package version 1.2.5 (O'Brien 2023) and nearest neighbour resampling. Foliage Projective Cover (FPC) data was obtained as 0-100% foliage cover, but data from 2014 were on a

398 different scale. Therefore, 2014 FPC data were reclassified to align with other years. Foliage
399 projective cover was then rescaled to 30 m, prior to calculation of the average FPC (Table 1).
400
401 *Analysis*
402
403 Analyses of reproductive trait data were conducted in R version 4.3.1 (R Core Team 2023)
404 using generalised linear mixed models in the `lme4` R package version 1.1-34 (Bates et al.
405 2015). We used the same model structure for each response variable but modified the model
406 family (error structure) as appropriate for each type of response variable. Models were fit
407 separately for each species to account for biological differences related to their post-fire
408 reproductive modes and other biological factors. Prior to modelling, continuous numeric
409 predictors were scaled by dividing values by the series-wide standard deviation. To
410 investigate the influence of fire and (**H1**, **H2**) environmental variation (**H3**) on reproductive
411 trait variation, we fit models with and without a main effect for fire frequency, time since fire,
412 or another environmental variable. For each response variable, a null model was fit with no
413 variation, against which to compare the other models. Model selection was performed by
414 ranking models based on Akaike's Information Criterion corrected for small sample sizes
415 (AIC_c) in the `AICcmodavg` R package version 2.3-3 (Mazerolle 2020). The best model in
416 the candidate set was chosen as the model which (1) had the lowest AIC_c and (2) improved
417 model fit over the null model by $\Delta AIC_c > |2|$ (Arnold 2010, Leroux 2019). Where two or
418 more models were ranked within 2 AIC_c units of the top model and included one additional
419 parameter, we considered the additional parameter to be supported by the data if (1) the
420 additional parameter improved log likelihood over that of the top-ranked model; (2)
421 confidence intervals did not overlap zero (Arnold 2010, Leroux 2019). For top-ranked models
422 which included factorial predictor variables with multiple levels, we calculated least-squares

means contrasts to determine differences between levels within the factor. For example, if the top-ranked model included germination treatment, we used least-squares means contrasts to determine if germination rate differed in seed exposed to 95°C and control seeds.

Germination experiment

Cumulative proportion germination for each individual was calculated by dividing the cumulative sum of germination by the total number of seeds germinated at the end of the experiment. First and last germination day and time to 50% germination were calculated by adapting functions from the `germinationmetrics` R package version 0.1.8 (Aaravind et al. 2022). To analyse the effect of seed treatment and fire frequency on fire-cued germination (**H1b**, **H1d**) we fit seven models each for proportion of seeds germinated and time to 50% germination: a null model; three univariate models with main effects for treatment, fire frequency, and seed weight; and three multivariate models investigating interactions between treatment, fire frequency and seed weight. To account for individual-level similarities in responses and potential effects of replicates, we included a random effect for replicate and individual in each model. To analyse the effect of fire frequency and environment on seed weight (**H1a**, **H1c**, **H3a**, **H3b**), we used the calculated average weight of a singular seed (hereafter 'seed weight') as the response variable. We fit twelve models with a random effect for individual: a null model; six univariate main effect models for fire frequency and environmental attributes; and five multivariate models investigating interactions between fire frequency and environmental attributes.

Population demographic structure surveys

To analyse the effect of fire history on population demographic structure, we first calculated the ratio of seedlings, saplings, and recruits (i.e., grouped seedlings and saplings) to mature individuals plus individuals from that demographic class. For example, proportion of seedlings was calculated as $\frac{Number\ seedlings}{Number\ mature+seedlings}$. To analyse the effect of fire (**H2**) and environment (**H3a**, **H3b**) on population demographic structure, we fit twelve models: a null model; six univariate main effect models for the focal fire metric (i.e., fire frequency or time since fire) and environmental attributes; and five multivariate models investigating interactions between the focal fire metric and environmental attributes. We did not fit multivariate models including interactions for *A. littoralis* as there were too few transects which would lead to overfitting. To analyse the effect of fire (**H2b**) and environment (**H3a**, **H3b**) on reproductive output (i.e., cone number), we fit eight models: a null model and seven univariate models for fire frequency, time since fire, and environmental attributes. We did not fit multivariate models for reproductive output as there were too few individuals with cones which led to overfitting. For population demographic structure and reproductive output, we included 'transect' nested within 'site' as a random effect in each model, to account for the hierarchical structure of data.

Results

Overview

We sampled eight *A. littoralis* and 32 *A. torulosa* transects across the study region (Fig. 1). Seeds from 115 individuals, comprising 40 *A. littoralis* and 75 *A. torulosa* individuals were

sampled at these transects (Fig. 1). Seven individuals with less than 60 seeds were excluded from the germination experiment, resulting in 108 individuals (37 *A. littoralis* and 71 *A. torulosa*). Estimated fire frequency ranged from zero to four (*A. littoralis*) and zero to seven (*A torulosa*) fires at sampling locations over a 36-year time period. Time since fire at sampling locations for both species ranged from at least 36 years (i.e., those sites where the time since last fire was unknown) to two-years post-fire.

Germination experiment

Seed viability was high across all experimental replicates and seed treatments for *A. littoralis* (mean = 0.813-0.854) and *A. torulosa* (mean = 0.767-0.880) (Appendix S1: Fig. S4, S5). Viability assessed by the x-ray and tetrazolium methods were correlated for both species (*A. litoralis* $r > 0.71$, $p < 0.001$; *A. torulosa* $r > 0.74$, $p < 0.001$) and there were no noticeable differences in viability among experimental replicates or seed treatments (Appendix S1: Fig. S4, S5). Germination rates were not strongly influenced by heat shock or smoke in either species, with null models ranked higher than models including seed treatments (Table 2, Appendix S1: Fig. S6). Seed weight influenced germination rate for *A. littoralis* (ΔAIC_c relative to null model = 3.07; Table 2, Fig. 2). For germination rate in *A. torulosa*, there was an interaction between seed weight and fire frequency (ΔAIC_c relative to null model = 10.97; Table 2, Fig. 2). In both species, heavier seeds were generally associated with greater germination rates (Table 2, Fig. 2). The *A. torulosa* model with an interaction term showed that, for individuals exposed to high fire frequencies, germination rates decreased with increasing seed weight and were highly variable (20-90% proportion of seeds germinated, Fig 2b).

For *A. littoralis*, there was little support for a seed treatment effect on time to 50% germination as the null model was equivalent to the treatment only model ($\Delta AIC_c = 0.81$; Table 3). The data from *A. torulosa* supported three models: seed treatment only (the top ranked model, ΔAIC_c relative to null model = 108.77); an interaction between seed treatment and seed weight (ΔAIC_c relative to the top ranked model = 0.11); and an interaction between seed treatment and fire frequency (ΔAIC_c relative to the top ranked model = 0.67) (Table 3, Appendix S1: Fig. S7, S8). Time to 50% germination increased for all treatments compared to controls, except for the 80°C treatment (Fig. 3a, Appendix S1: Fig. S7a). Thus, heat and smoke generally slowed germination in *A. torulosa*. In the seed weight interaction model, heavier seeds were typically faster to germinate, an effect which was most pronounced for individuals exposed to the smoke treatment (Fig. 3b, Appendix S1: Fig. S7b, S8a-c). In the fire frequency interaction model, seed from more frequently burned transects had slower germination for 95°C; smoke; and 80°C + smoke treatments (Fig. 3c, Appendix S1: Fig. S7c, S8d-f). However, this pattern was reversed for individuals exposed to the 95°C + smoke treatment, suggesting faster germination for individuals exposed to more frequent fire (Fig. 3c, Appendix S1: Fig. S7c, S8d-f).

Seed weight was influenced by an interaction between fire frequency and temperature seasonality in *A. littoralis*, and an interaction between fire frequency and latitude in *A. torulosa* (Table 4, Fig. 4). There was no evidence of any other environmental variables influencing seed weight in either species ($\Delta AIC_c > 5$, Table 4). For *A. littoralis*, seed weight increased with temperature seasonality for seeds collected at frequently burned transects (4 fires over 36 years, Fig. 4a). At low to intermediate fire frequencies (0-1 fire over 36 years) there was no relationship between seed weight and temperature seasonality (Fig. 4a). For *A. torulosa*, seed weight increased with decreasing latitude for frequently burned transects (6

fires over 36 years) and decreased with decreasing latitude for infrequently burned transects (0 fires over 36 years) (Fig. 4b). There was no relationship between latitude and seed weight for intermediate fire frequencies (3 fires over 36 years, Fig. 4b). In other words, at southern sampling locations seeds were heavier when collected at transects which had experienced frequent fire, compared to relatively unburnt transects. At northern sampling locations, there were no differences in seed weight related to fire history (Fig. 4b).

Reproductive output and population demographic structure

Reproductive output (number of cones per female tree) was not influenced by fire frequency or time since fire (Appendix S1: Table S1). There was a positive effect of foliage projective cover on number of cones in *A. littoralis* (Intercept = -1.793 [standard error (SE) = 1.081], FPC = 0.066 [SE = 1.175], Appendix S1: Table S1) and *A. torulosa* (Intercept = -3.409 [SE = 1.1336], FPC = 2.105 [SE = 1.303], Appendix S1: Table S1).

Population demographic structure in *A. littoralis* was not influenced by fire frequency, time since fire, or environmental variability, with the null model being top ranked for all analyses (Appendix S1: Table S2). In *A. torulosa*, foliage projective cover influenced the proportion of seedings within the total population (Intercept = -3.409 [SE = 1.336]; FPC = 2.105 [SE = 1.303], Appendix S1: Table S3). Increasing temperature seasonality reduced the proportion of saplings within the total population (Intercept = -1.040 [SE = 0.482], temperature seasonality = -1.136 [SE = 0.481], Appendix S1: Table S3) and recruits within the total population (Intercept = -0.919 [SE = -1.833]), temperature seasonality = -1.642 [SE = 0.535], Appendix S1: Table S3). The interaction between temperature seasonality and time since fire on the proportion of *A. torulosa* recruits within the total population was ranked within $\Delta AIC_c < 2$ of

546 the top-ranked model, but confidence intervals of the interaction term overlapped zero
547 (Appendix S1: Fig. S9). Thus, fire history did not strongly influence reproductive output or
548 population demographic structure in *A. littoralis* or *A. torulosa*, with environmental
549 variability being more important in constraining recruitment processes (Appendix S1: Table
550 S1, S2, S3).
551

552 **Discussion**

553

554 This study showed that seed responses to fire history and fire-related germination cues varied
555 in two closely related tree species with differing post-fire reproductive modes. Fire frequency
556 from seed collection locations was found to influence variation in laboratory-based
557 germination experiments. This is important because it indicates that reproduction in plant
558 species from fire-prone ecosystems is influenced not only by fire-related germination cues,
559 but also the recent fire history to which they have been exposed. Variation in germination
560 response to fire of these two closely related tree species could influence a dietary specialist
561 threatened cockatoo through differences in species post-fire establishment success and
562 competitiveness, driving food resource availability (Delzoppo et al. 2021, Menkhorst et al.
563 2024). Although we did not study the cockatoo distribution directly, the cockatoos are such
564 specialist feeders and so cryptic and difficult to study that the results from our study can
565 inform food tree conservation and restoration actions (Chapman 2007). Thus, investigating
566 how fire drives selection on reproductive traits and controls population demographic structure
567 is vital for conservation and restoration actions to mitigate the effects of future fire regime
568 changes.
569

570 Fast germination provides individuals with a competitive advantage (Hodges et al. 2021);
571 therefore, overall germination and germination speed can be promoted by fire-related cues,
572 especially in obligate seeders adapted for post-fire germination (Ramos et al. 2019, Tangney
573 et al. 2020, Hodges et al. 2021, Pausas and Lamont 2022). Results from this study ran
574 contrary to this general prediction: exposure of seeds to heat and smoke did not enhance
575 germination rate and speed of the obligate seeder *A. littoralis* (**H1b**) while it slowed
576 germination rate in the facultative resprouter *A. torulosa* (**H1d**). Reduced germination speed
577 with temperature increase may be related to lethal temperature thresholds which lower seed
578 viability. This was supported by the reduction in germination speed being stronger in *A.*
579 *torulosa* (lethal temperature threshold *ca.* 100°C) than *A. littoralis* (lethal temperature
580 threshold *ca.* 110°C) (Hanley et al. 2003, Emery et al. 2011). Nevertheless, *Allocasuarina*
581 seeds were generally resilient to heat shocks up to 95°C with little loss in seed viability. This
582 was not unexpected as temperatures inside cone follicles of other serotinous species during
583 fire can reach 100°C (Huss et al. 2019) and fire triggers seed release in serotinous species
584 such as *Allocasuarina* to coincide with favourable post-fire conditions (Lamont et al. 2019,
585 Lamont et al. 2020). However, obligate seeders are more likely to have increased post-fire
586 germination speed due to their greater investment in seeds than congeneric resprouters
587 (Zammit and Westoby 1987, Pausas and Keeley 2014, Tangney et al. 2020), and our study
588 supported this prediction (**H1b**). For the facultative resprouter, fire-cues inhibited
589 germination, to some extent, with inhibition especially extreme in individuals not pre-adapted
590 to fire or exposed to high fire frequencies.
591
592 A trade-off between reproductive output and resprouting capacity is often seen in plants from
593 fire-prone ecosystems, whereby greater seed production is usually associated with lower
594 resprouting capacity (Bellingham and Sparrow 2000). This trade-off might have influenced

fire frequency effects on overall germination and germination speed in this study. As expected, (**H1d**) the facultative resprouting tree, *A. torulosa* had greater reductions in germination speed when seed were collected from frequently burnt environments compared with those from lower fire frequencies. This might reflect a higher investment in resprouting from bud banks than in seed production, trading off seed germination performance in individuals exposed to frequent fire (Bellingham and Sparrow 2000, Verdú 2000, Pausas and Keeley 2014, Bendall et al. 2022). However, the facultative resprouter produced heavier seeds with increasing fire frequency, contrary to expectations (**H1c**). Nevertheless, heavier *A. torulosa* seeds from collection sites exposed to frequent fire had slower germination speed, indicating lower competitiveness compared to the obligate seeder (**H1**). Thus, production of heavier seeds in *A. torulosa* could have reflected lower investment in seeds (i.e., fewer seeds produced as seed weight increased) in frequently burnt environments (Hodgson et al. 2020, Li et al. 2025, Maleki et al. 2025). An alternative explanation is that delayed germination occurred as a response to heat induced stress and seed tissue repair prior to germination (Visscher et al. 2021) and further research on this is warranted.

Selection on seed traits may also be driven by environmental variation, with strongly seasonal environments generally favouring heavier seeds that have greater energy reserves (Leishman et al. 2000, Muller-Landau 2010). This was reflected in our experiment where seeds collected from areas with variable climate conditions and high fire frequency (i.e., 4 fires over 36 years) had greater seed weight for the obligate seeder, *A. littoralis*, than the facultative resprouter, *A. torulosa* (**H3a**, **H3b**). In the facultative resprouter, *A. torulosa*, seed investment was more likely driven by exposure to recurrent fire as seed weight decreased in the absence of fire even under more seasonal climates. However, *A. torulosa* had high germination variability when seeds were heavier, possibly because seed reproductive effort was traded-off

620 with resource allocation to resprouting (Bellingham and Sparrow 2000). Where species show
621 plasticity in regeneration modes, high fire frequency could result in more resources being
622 allocated to resprouting capabilities than production of viable seeds (Bellingham and Sparrow
623 2000, Verdú 2000). Thus, exposure to fire was likely important for maintaining fire-cued
624 germination in *A. torulosa*.
625
626 Our results indicate that reproductive effort and population demographic structure appear to
627 be independent of fire history for both *Allocasuarina* species at later life stages (**H2**). In *A.*
628 *torulosa*, higher woody foliage cover increased reproduction, which might be related to
629 higher photosynthetic potential in these environments (**H3a**) (Wheelwright and Logan 2004).
630 Population demographic structure in *A. torulosa* might have been more strongly driven by
631 annual climate variability as stressful environments impose limitations on growth (**H3a**), with
632 more variable climates likely to increase the trade-off between survival, growth, and
633 reproduction (Zhang et al. 2020, Hamann et al. 2021). Conversely, for *A. littoralis* the lack of
634 effect of fire, climate, or environmental attributes on reproduction or population demographic
635 structure may be linked to these attributes already limiting establishment of *A. littoralis* in our
636 inland study region (**H3a**, **H3b**) (Australian Biological Resources Study. Advisory
637 Committee 1989, Foreman and Walsh 1993). For both species, the lack of effect of recent fire
638 activity on reproductive output was likely due to most sampling occurring in areas two or
639 more years post-fire, sufficient time for cone production (**H2b**) (Plumanns-Pouton et al.
640 2024). However, more extreme fire frequencies than sampled here (i.e., up to seven fires over
641 36 years) are likely to filter populations meaning that frequent fire could compromise
642 seedling establishment and resprouting or reproduction abilities (Christensen et al. 1981, Gill
643 and Catling 2002, Clarke et al. 2015, McColl-Gausden et al. 2022). Thus, further

644 experimental research is needed to better understand fire history effects on reproduction and
645 population demographic structure in *Allocasuarina*.
646
647 *Conservation implications*
648
649 Our results have important implications for Glossy black-cockatoo conservation and food tree
650 restoration actions. For restoration of food trees, seed collections should contain a range of
651 seed weights. Heavier seeds which provide a greater competitive advantage (i.e., reduced
652 time to reach 50% germination) are likely to aid restoration success and secure future food
653 resources for Glossy black-cockatoos. Restoration programs might also consider fire history
654 at seed collection sites. For *A. littoralis*, we recommend collecting seeds from individuals
655 exposed to high fire frequencies (e.g., four or more fires in recent decades) and from areas
656 with high annual temperature variability, as these had the greatest germination outcomes.
657 Conversely *A. torulosa* seeds from individuals exposed to high fire frequencies (e.g., six or
658 more fires in recent decades) might result in heavier seeds for restoration, but our data show
659 that overall germination could be more variable. For *A. torulosa*, we recommend collecting
660 seeds from individuals exposed to intermediate fire frequencies (e.g., three fires in recent
661 decades), as more moderate fire regimes showed stronger fire-cued germination responses in
662 *A. torulosa*.
663
664 Current fire histories appear to be suitable for persistence of *A. littoralis* and *A. torulosa* in
665 our study region (i.e., up to four and seven fires in 36 years, respectively). However, climate
666 change projections in many regions are associated with fire regime changes, including
667 increasing frequency, intensity, severity and extent of fire (Di Virgilio et al. 2019, Hantson et
668 al. 2024, Oliveira and Gil Martins 2026). Such changes could threaten the persistence of

669 *Allocasuarina* populations under future fire regimes, especially obligate seeders, and, thus,
670 food resource availability for Glossy black-cockatoos. For restoration of food trees, we
671 recommend targeting areas with higher annual temperature variability and low woody
672 vegetation cover as *Allocasuarina* might otherwise decline under high environmental stress
673 with low population turnover. These areas are also likely to be lower quality foraging for
674 Glossy black-cockatoos which generally show preferences for *Allocasuarina* stands burnt in
675 the last 10-60 years (Delzoppo et al. 2021, Menkhorst et al. 2024), further supporting
676 requirement for food tree restoration. Trends toward warmer annual temperatures are also
677 occurring, increasing evapotranspiration (Hughes 2003), which could further limit growth
678 and reproduction processes in these species (Gallagher et al. 2019, Zhang et al. 2020,
679 Hamann et al. 2021), and alter Glossy black-cockatoo food resource availability. In our study
680 region, restoration is likely to be most successful for *A. torulosa* due to their widespread
681 distribution and higher likelihood of persistence under projected higher fire activity (Hantson
682 et al. 2016, Di Virgilio et al. 2019, Dowdy et al. 2019). Nevertheless, restoring other food tree
683 species would provide a range of food resources for Glossy black-cockatoos, with *A. torulosa*
684 buffering against high fire frequencies and immaturity risk in *A. littoralis* or other obligate
685 seeding food trees.
686
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705
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707
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709 FEC. Analysis was performed by FEC and supported by ALS. The first draft of the
710 manuscript was written by FEC, with guidance from ALS. All authors commented on
711 previous versions of the manuscript. All authors read and approved the final manuscript.
712
713 **Conflict of interest statement**
714
715 The authors declare no conflicts of interest.
716

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Tables

Table 1 Spatial fire, climate, and environment variables used to investigate reproductive trait variability in *Allocasuarina littoralis* and *A. torulosa* in southeast Queensland, Australia.

Variable	Raw resolution	Resampled resolution	Temporal resolution	Data source
Fire history – Queensland Parks and Wildlife Service	1 m	30 m	1930-2023	Queensland Parks and Wildlife Service 2023
Annual Fire Scars – Landsat, QLD DES algorithm	30 m	Unchanged	1987-2016	Collett 2021
Sentinel-2 fire scars – QLD DES algorithm, annual	10 m	30 m	2017-2023	van den Berg 2021
Temperature seasonality	1 km	30 m	1970-2000	Fick and Hijmans 2017
Precipitation seasonality	1 km	30 m	1970-2000	Fick and Hijmans 2017
Topographic wetness index	30 m	Unchanged	2000	Gallant and Austin 2012
Foliage projective cover	30 m	Unchanged	1998-2014	Department of Environment 2020
- Landsat 2014				
- Statewide Landcover and Trees Study Sentinel-2	10 m, 30 m	30 m, Unchanged	2018, 2019, 2020, 2021	Department of Environment 2024

QLD = Queensland, DES = Department of Environment and Science.;

Table 2 Models used to examine the influence of fire frequency and seed treatment on proportion germination in *Allocasuarina littoralis* and *A. torulosa* from southeast Queensland, Australia. Models for each species are ranked from lowest to highest AIC_c and the top-ranked models are indicated in bold.

Species	Model structure	Number of parameters	AIC_c	ΔAIC_c	Log Likelihood
Allocasuarina littoralis	**Seed weight**	**3**	**129.07**	**0.00**	**-60.46**
	Null model	3	132.14	3.07	-63.03
	Seed weight × fire frequency	4	132.81	3.74	-60.25
	Fire frequency	3	133.42	4.34	-62.63
	Treatment	3	136.27	7.20	-59.86
	Treatment × seed weight	4	140.94	11.86	-55.65
	Treatment × fire frequency	4	144.84	15.76	-57.59
Allocasuarina torulosa	**Seed weight × fire frequency**	**4**	**404.26**	**0.00**	**-196.05**
	Seed weight	3	408.31	4.05	-200.12
	Null model	3	415.23	10.97	-204.59
	Fire frequency	3	416.75	12.49	-204.34
	Treatment	3	421.81	17.55	-202.77
	Treatment × seed weight	4	422.75	18.49	-196.97
	Treatment × fire frequency	4	430.50	26.24	-200.85

AIC_c = Akaike's Information Criterion corrected for small sample sizes; Δ = change in.

Table 3 Models used to examine the influence of fire frequency, seed weight, and seed treatment on time to reach 50% germination in *Allocasuarina littoralis* and *A. torulosa* from southeast Queensland Australia. Models for each species are ranked from lowest to highest AIC_c and the top-ranked models are indicated in bold.

Species	Model structure	Number of parameters	AIC_c	ΔAIC_c	Log Likelihood
Allocasuarina littoralis	**Treatment**	**3**	**1284.18**	**0.00**	**-633.81**
	Null model	**3**	**1284.99**	**0.81**	**-639.45**
	Seed weight	3	1286.36	2.18	-639.10
	Fire frequency	3	1286.82	2.64	-639.34
	Seed weight × fire frequency	4	1289.69	5.51	-639.69
	Treatment × seed weight	4	1292.97	8.79	-631.66
	Treatment × fire frequency	4	1295.10	10.92	-632.72
Allocasuarina torulosa	**Treatment**	**3**	**2579.61**	**0.00**	**-1281.67**
	Treatment × seed weight	**4**	**2579.72**	**0.11**	**-1275.46**
	Treatment × fire frequency	**4**	**2580.28**	**0.67**	**-1275.74**
	Seed weight	3	2680.38	100.77	-1336.15
	Seed weight × fire frequency	4	2682.91	103.30	-1335.38
	Null model	3	2688.38	108.77	-1341.17
	Fire frequency	3	2690.24	110.63	-1341.08

AIC_c = Akaike's Information Criterion corrected for small sample sizes; Δ = change in.

Table 4 Models used examine the influence of fire frequency and environmental variation on seed weight in *Allocasuarina littoralis* and *A. torulosa* from southeast Queensland, Australia. Models for each species are ranked from lowest to highest AIC_c and the top-ranked models are indicated in bold.

Species	Model structure	Number of parameters	AIC_c	ΔAIC_c	Log Likelihood
Allocasuarina littoralis	**Fire frequency × temperatures seasonality**	**4**	**-8418.33**	**0.00**	**4215.33**
	Null model	3	-8376.10	42.23	4191.10
	Temperature seasonality	3	-8347.75	70.58	4177.95
	Precipitation seasonality	3	-8330.16	88.17	4169.16
	Latitude	3	-8329.41	88.92	4168.78
	Fire frequency	3	-8317.17	101.16	4162.66
	Fire frequency × latitude	4	-8263.94	154.40	4138.13
	Fire frequency × precipitation seasonality	4	-8235.42	182.91	4123.87
	Fire frequency × topographic wetness	4	-8224.59	193.75	4118.45
	Topographic wetness	3	-8215.94	202.40	4112.04
	Foliage projective cover	3	-7533.58	884.75	3770.88
	Fire frequency × foliage projective cover	4	-7521.56	896.77	3766.96
Allocasuarina torulosa	**Fire frequency × latitude**	**4**	**-16303.73**	**0.00**	**8157.95**
	Fire frequency × topographic wetness	4	-16297.98	5.75	8155.07
	Topographic wetness	3	-16170.19	133.54	8089.13
	Null model	3	-16126.40	177.33	8066.22
	Precipitation seasonality	3	-16112.83	190.90	8060.45
	Temperature seasonality	3	-16112.83	190.90	8060.45
	Fire frequency	3	-16044.97	258.76	8026.52
	Fire frequency × precipitation seasonality	4	-16034.15	269.59	8023.15
	Fire frequency × temperature seasonality	4	-16034.15	269.59	8023.15
	Latitude	3	-16004.08	299.34	8006.08
	Fire frequency × foliage projective cover	4	-15192.60	1111.13	7602.39
	Foliage projective cover	3	-15158.09	1145.65	7583.08

AIC_c = Akaike's Information Criterion corrected for small sample sizes; Δ = change in.

Figures

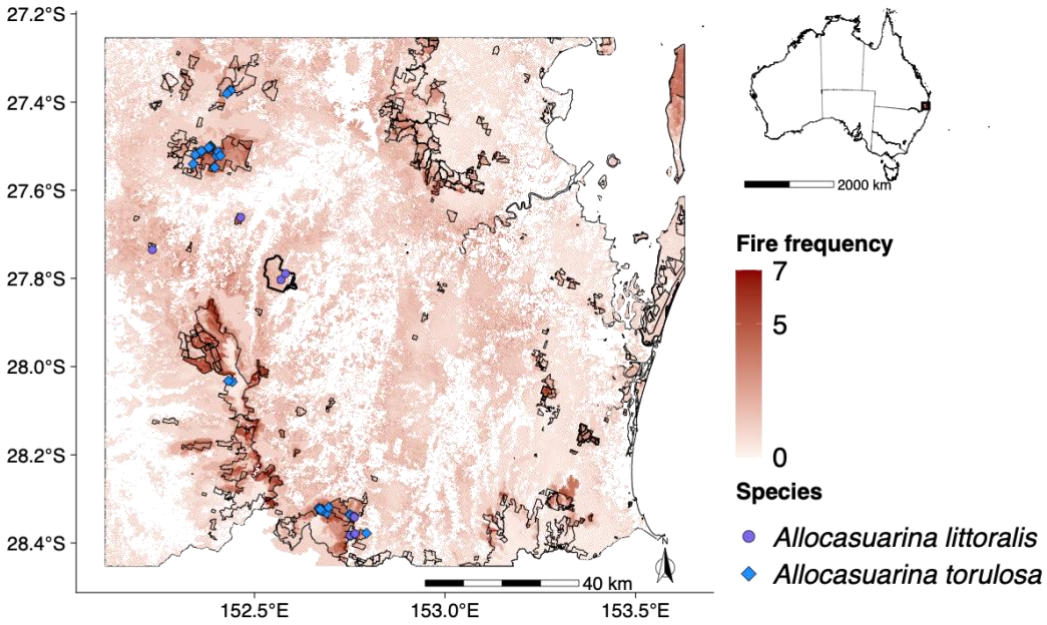

Figure 1 Sampling locations of *Allocasuarina littoralis* (n = 385 individuals from 8 transects) and *A. torulosa* (n = 703 individual from 32 transects) in southeast Queensland, Australia. Protected areas are displayed with black outlines including public land (conservation parks, state forests and national parks) and privately managed nature refuges. Fire frequency between 1987-2023 is show in red shading and was derived from integrating fire history records from Queensland Parks and Wildlife service and satellite imagery (Charles et al. 2026). Fire frequency ranged from 0 to 11 fires in the past 36 years for the study region, with white representing areas mapped as unburnt. To aid visualisation of fire frequency variation among transects, fire frequency was rescaled, so areas burnt 7 or more times are represented by the darkest shade of red.

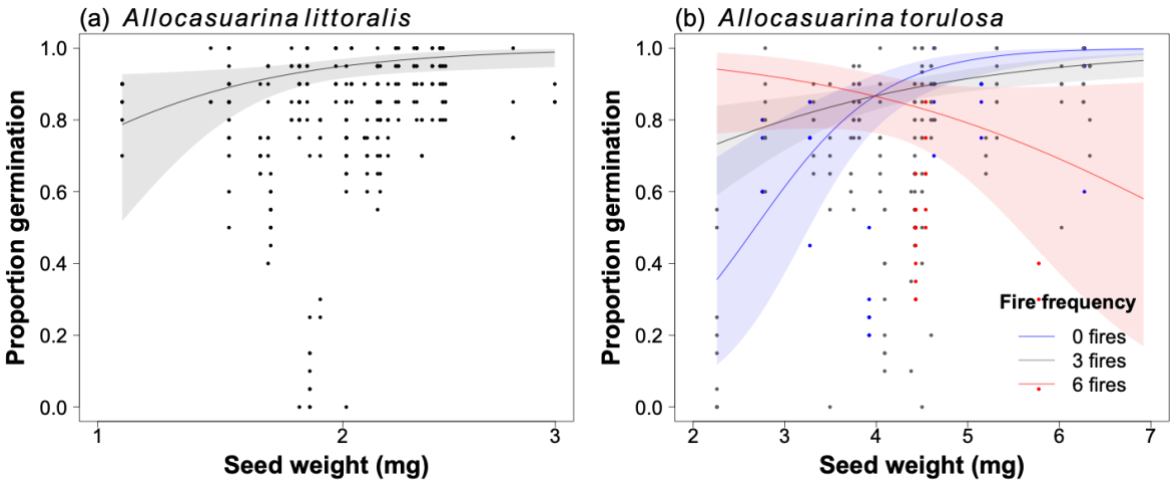

Figure 2 The estimated effect (and 95% confidence intervals) of seed weight on proportion germination in (a) *Allocasuarina littoralis* and (b) *A. torulosa* from the top-ranked models for each species. The model for *A. torulosa* included an interaction between seed weight and fire frequency.

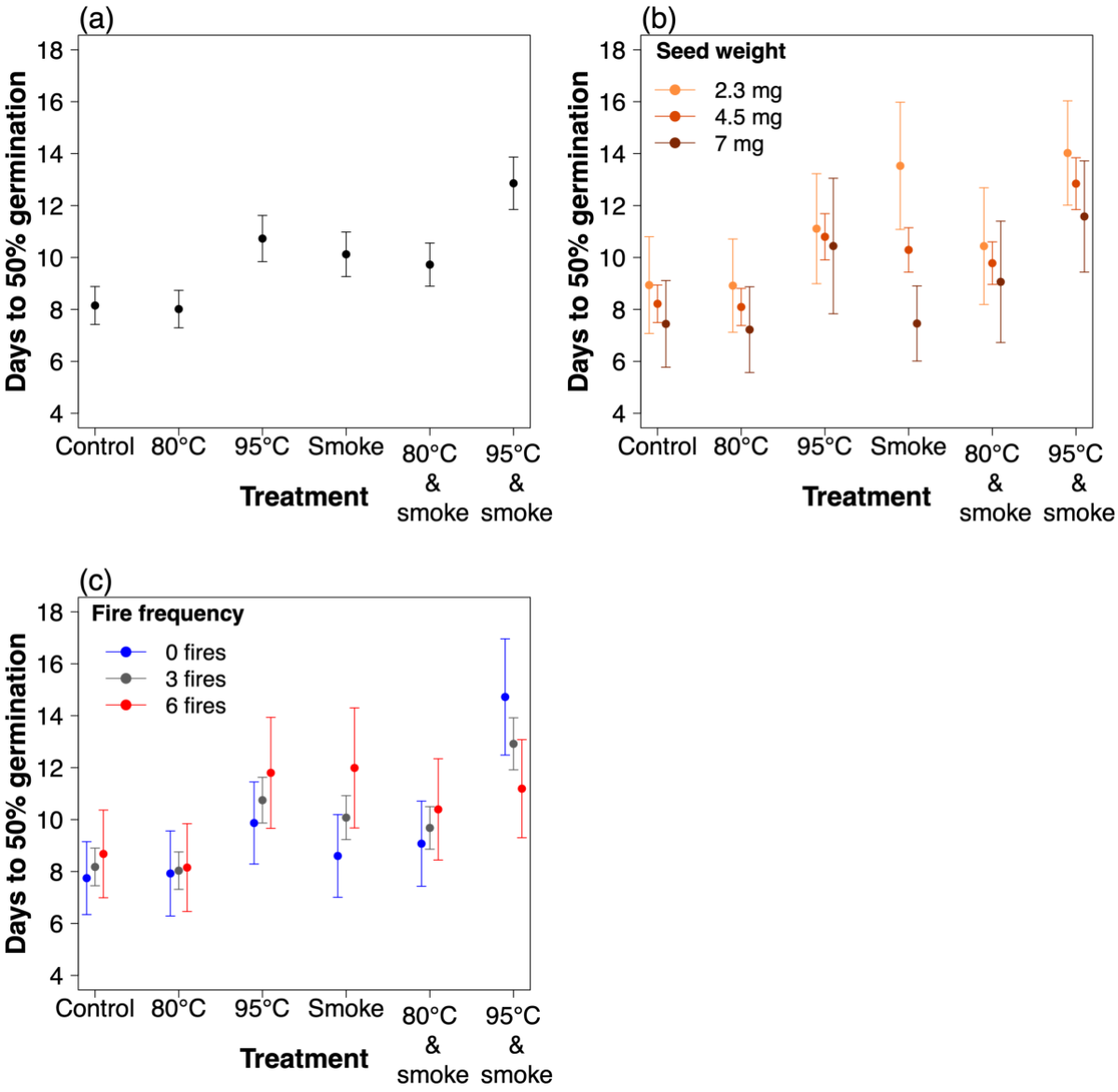

Figure 3 The estimated effect (and 95% confidence intervals) of seed treatment on time to 50% germination (days) from the three top-ranked models for *A. torulosa* (ΔAIC_c <2), (a) top-ranked model with a treatment effect; (b) second ranked model with an interaction between treatment and seed weight; and (c) third-ranked model with an interaction between treatment and fire frequency. For A. littoralis, there was little evidence of treatment effects on time to 50% germination (see Table 3).

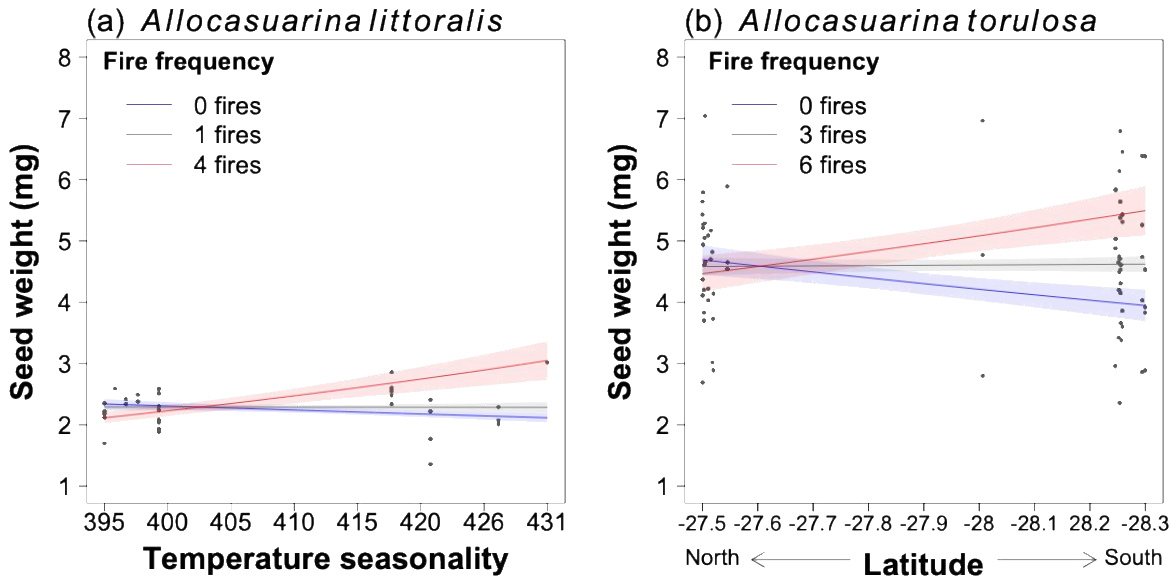

Figure 4 The estimated effect (and 95% confidence intervals) of fire frequency on seed weight in (a) *Allocasuarina littoralis* and (b) *A. torulosa*. (a) In *Allocasuarina littoralis*, seed weight was influenced by an interaction between fire frequency and temperature seasonality. (b) In *Allocasuarina torulosa*, seed weight was influenced by an interaction between fire frequency and latitude.