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PRACTICE AND TECHNICAL ARTICLE

Overcoming germination constraints in seven grass species for seed-based restoration in the Australian monsoonal tropics

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The increasing reliance on native seeds for ecological restoration requires the understanding of seed traits across each species, and the testing of novel processing approaches to optimize germination outcomes. Knowledge regarding Australian native seeds is critical due to the high proportion of species manifesting some degree of seed dormancy. The evaluation of approaches to overcome dormancy and identify optimal conditions for promoting germination in native species has significant applications in the restoration of degraded ecosystems. Grasses are an important component of ecosystems in the Australian monsoonal tropics, a bioregion which covers much of northern Australia, yet they are often forgotten or poorly represented when used in restoration. We investigated the effect of seed processing technique and smoke-based stimulants on the germination of seven species from the Kimberley region, testing three different hypotheses: (1) florets germinate less than extracted caryopses; (2) acid digestion treatments with different exposure times can enhance germination; and (3) smoke-based treatments can increase both germination and germination speed. Floret removal was generally helpful in improving germination, whereas the response to acid and smoke-based treatments was varied. Brief acid exposure produced no to low germination improvements, whereas longer acid treatments showed contrasting results, with some species showing significant germination increase and others showing a severe reduction in germination rate. The only species showing a clear positive germination effect of smoke-based treatments was *Triodia bynoei*. These results are helpful for restoration practitioners to improve their potential use in current and future restoration programs in the Australian monsoonal tropics.

Key words: acid digestion, Kimberley, *Poaceae*, seed processing, smoke water

Implications for Practice

- Extracting the caryopses from grass florets increases germination whereas reducing bulk volume and improving handling.
- Acid treatments facilitate caryopsis extraction and enhance germination in some grass species, but need to be carefully evaluated for each species because it can, at times, negatively affect germination.
- *Triodia bynoei* seeds show higher germination if treated with smoke-based solutions.

Introduction

Using native seeds to restore degraded ecosystems has become more widespread in the last decades (Merritt & Dixon 2011; Erickson et al. 2017; Pedrini & Dixon 2020). Many organizations across the globe are launching ambitious restoration targets at global scales, such as the UN Decade on Ecosystem Restoration (https://www.decadeonrestoration.org/) and the Bonn Challenge (https://www.bonnchallenge.org/).

Australia is particularly rich in diverse ecosystems (Cresswell & Murphy 2017). Specifically, the Kimberley region, in the north of Western Australia, is one of the least impacted by human activities and therefore contains some of the most pristine areas of the continent. The region is mostly covered by tropical savannah but encompasses also deserts, tropical woodlands, and vine thickets. Yet, it faces critical threats to its ecosystem's health, specifically mining, overgrazing, inappropriate fire regimes, and invasion of alien plants and animals (Government of Western Australia 2011). Restoration of these degraded areas is necessary to manage and conserve the environment of the Kimberley. Nevertheless, due to the vastness of the region and scarcity of population, it is hard to quantify the scale and degree of degradation (Carwardine et al. 2011). However, there are easily visible,

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highly impacted areas, such as the site of the former Argyle Diamond Mine, which will require considerable restoration effort for the mining company to relinquish the site to the state and to the traditional owners after several decades of intense mining activity.

Effective seed-based restoration is currently limited by seed availability, low seed quality, loss of seed viability due to poor storage conditions, and lack of effective dormancy alleviation treatments. Also, the harvesting of locally sourced seeds could be onerous, seed quality variable and seed cleaning complex, thus new methods are needed to improve seed processing to meet the challenges and goals of large-scale restoration (Frischie et al. 2020). Restoration practitioners should thoroughly plan for seed needs, giving primary importance to knowledge of seed biology and ecology, seed purity and quality, and ways to effectively process seed batches to improve storability, usability, and germination performance (Erickson et al. 2017).

When required, native seed batches may need to undergo processing treatments to remove covering structures (such as awns and glumes), extracting viable seeds and alleviating dormancy to improve germination success (Frischie et al. 2020). Those treatments are species-specific due to the high variability in morphology and germination response among different taxonomic groups and in some instances, batch-specific to account for potential seed trait differences among populations of the same species (Merritt et al. 2007; Kildisheva et al. 2020; Martyn Yenson et al. 2021). For example, seeds with physiological dormancy require an environmental signal to overcome the physiological block inhibiting germination, such as through dry after-ripening, cool/warm stratification or wet/dry cycles (Baskin & Baskin 2004; Turner et al. 2013; Erickson et al. 2017; Kildisheva et al. 2020).

Grasses are the main understory herbaceous species in most Kimberley ecosystems, providing food and shelter for numerous native animals, contributing to soil stabilization and enhancing biodiversity (Bowman et al. 2010). The caryopsis of most grass species is enclosed within an indehiscent floret that greatly improves dispersal ability and, in some cases, improves seed burial in soil but can represent a barrier to water imbibition, oxygen permeation, and radicle emergence (Farley et al. 2013; Pedrini et al. 2019). The floret is, therefore often removed to allow better germination, though in many cases this is not easy to do (Farley et al. 2013; Pedrini et al. 2019). Moreover, many grass species in Australia show a degree of physiological dormancy (Merritt et al. 2007; Turner et al. 2013; Martyn Yenson et al. 2021), the alleviation of dormancy through specific treatments is often necessary to obtain satisfactory seedling establishment (Turner et al. 2013; Dayrell et al. 2016; Pedrini et al. 2019).

Knowledge of germination traits for each species is necessary for effective use in restoration programs (Hancock et al. 2020; Pedrini et al. 2020), applying the needed treatments to overcome specific constraints, based on understanding the seed biology. Data are already available in the literature for widespread species like *Heteropogon contortus* (e.g. Panchal et al. 2011; Baldos et al. 2014; Bellairs & Caswell 2016), whereas species with restricted distribution ranges are much less studied, yet, many of them are a high priority for use in restoration. For instance, relatively little literature is available about grass species typical of the Kimberley region of north-Western Australia, including species belonging to genera such as *Triodia*, *Eriachne* or *Cymbopogon* (Fesuk 2006; Bellairs & Caswell 2016; Erickson et al. 2016).

The cleaning of seeds from inert material and their removal from the florets is often essential also to reduce the bulk size of the batches, hence optimizing storage space, and allowing for easier delivery to site (Pedrini et al. 2019). Among several seed extraction methods, acid is particularly effective in reducing subsequent mechanical cleaning and processing, also acting as a scarifying agent for seeds with physiological dormancy (Stevens et al. 2015). Further germination promotion can be obtained by exposing the seed to germination stimulants such as smoke water (SW) or the smoke derived karrikinolide (KAR_1), known to have a positive effect on grass germination (Long et al. 2011; Erickson et al. 2016).

In this context, the present work aimed at defining the germination characteristics of seven grass species native to the east Kimberley region of Western Australia and optimizing seed processing and enhancement techniques to assist practitioners in their use during restoration programs. In particular, the following hypotheses were assessed: (1) extracted caryopsis germinate better than the whole floret; (2) acid digestion is a useful tool to remove the floret from the caryopsis and; (3) KAR_1 and SW enhance germination.

Methods

Species Selection and Seed Collection

This work focused on seven perennial grasses (*Poaceae*) native to the Kimberley region (Western Australia, Australia). The species were Silky oilgrass (*Cymbopogon bombycinus* [R.Br.] Domin), Lemon grass (*Cymbopogon procerus* [R.Br.] Domin), Pan Wandarrie grass (*Eriachne glauca* R.Br.), Northern Wandarrie grass (*Eriachne obtusa* R.Br.), Bunch speargrass (*Heteropogon contortus* [L.] Roem. & Schult), Curly spinifex (*Triodia bitextura* Lazarides), and Giant oat-eared spinifex (*Triodia bynoei* [C.E. Hubb.] Lazarides). Floret material from each species was collected within a 200 km zone of the former Argyle Diamond Mine and assessed in the field to confirm full floret maturity which was determined by the initial appearance (i.e. changed from green to brown) and visual inspection of the caryopsis within a small sample of representative florets. Floret material was harvested by Gelganyem Limited (https://gelganyem.com.au/) from December 2021 to April 2022, from across the greater Argyle region (16°42′45″S and 128°23′15″E) in the eastern Kimberley (Western Australia, Australia) which is a part of the Victoria Bonaparte and Ord Victoria Plain Interim Biogeographic Regionalisation for Australia classification system (Department of Climate Change, Energy, the Environment and Water 2022).

Upon collection, the floret material was laid out in large trays on metal tables and placed in a well-ventilated shed for several days during which time florets continued to naturally dehisce. The florets and remaining debris were then threshed to separate the remaining florets that were retained within the inflorescence.

Purified florets were then placed in a second temperature (approximately 20°C) and humidity (30–50% Relative Humidity) controlled room for several months in porous linen seed collection bags prior to shipment to Curtin University in June 2021.

Upon receipt by Curtin researchers, linen bags containing floret material were stored in an incubator at 15°C for several months. Dryland Australian *Poaceae* species often exhibit some degree of physiological dormancy, which is alleviated by dry-after ripening (Baskin & Baskin 2014). This was achieved by moving the seeds to a 25°C incubator from August until November 2022 in preparation for laboratory experimentation which commenced in late November 2022.

Seed Quality Test

A two-step (purity and viability) seed quality test was performed on each batch. The purity test was performed on a representative sample through manual separation and weighing of the florets (pure seed units [PSU]) and inert material in each batch. Assessment of seed-fill was carried out through an x-ray scanner (Faxitron MX-20 X-ray cabinet, Tucson, AZ, U.S.A.) on five replicates of 50 florets each. Purity and fill data were used to compute the values of PSU, viable seed units (VSU), and pure live seeds (PLS) as a proportion of the total number of florets assessed. The definition of PSU, VSU, and PLS follows Pedrini and Dixon (2020).

Seed Germination

Germination tests for each species and treatment were performed with four replicates of 25 florets or caryopses placed in a 30°C incubator. Only filled florets, according to the x-ray tests, were selected. Each replicate was placed on filter paper soaked with deionized water in a 90 mm Petri dish, which was sealed with cling wrap to avoid desiccation. Germination was defined as radicle emergence from the floret or the caryopsis coat, and was regularly (every 1–3 days) checked for up to 25 days, with a shorter frequency during the first week when most germination was observed.

Caryopses Extraction

The first test consisted in the comparison of germination response between caryopses enclosed in their florets and caryopses manually removed with the help of forceps to gently extract the caryopsis from the surrounding floret. For *H. contortus*, a scalpel was used, due to the relative difficulty of cleaning it without damaging the caryopses.

Sulfuric Acid Processing

Acid treatment was performed through the application of 0.5 g of 98% (w/v) sulfuric acid (H_2SO_4) for each gram of floret material. H_2SO_4 was poured over the florets and then stirred with a glass rod to ensure even distribution of the acid across all of the floret material. After the acid digestion, the resulting floret/acid slurry was neutralized with 8.4 g/L sodium bicarbonate ($NaHCO_3$) solution; the volume of $NaHCO_3$ solution varied according to the amount of digested seeds in order to entirely cover the digested mass. Florets were then rinsed under tap water for 2 minutes and then dried in a dehydrator at 35°C for 3.5 hours. After acid treatment and drying, the florets were mechanically removed by rubbing them between two rubber mats and the caryopses were cleaned from the inert material through air separation. The control underwent only mechanical removal of the floret with a rubber mat following the methodology described by Pedrini et al. (2019). Three acid treatments and the control were tested for germination with four replicates of 25 seeds. The treatments differed for the time of exposure to acid, namely: 2, 5, and 20 minutes. Some tests only had three replicates due to a lack of viable florets to perform the fourth replicate or because of microbial contamination, these were: 5 and 20 minutes in *C. procerus*, 2 and 5 minutes in *H. contortus*, 2 minutes in *T. bitextura*, and 20 minutes in *T. bynoei*.

Germination Promoters

The comparison among treatments for germination enhancement was performed on seeds cleaned through acid digestion choosing for each species the optimal exposure time that significantly maximized germination during the previous acid test. In absence of any significant difference between the best performing treatments, the longer exposure was chosen as it reduces subsequent mechanical cleaning. Thus, *Cymbopogon* spp. and *T. bitextura* were exposed to acid for 2 minutes, *E. obtusa* for 5 minutes, and the three remaining species for 20 minutes. The three treatments, that is water (control), 10% (v/v) SW, and 1 μM KAR_1 (3-methyl-*2H*-furo[2,3-*c*]pyran-2-one; KAR_1) solution (Flematti et al. 2004), were applied by soaking the germination paper with the respective solution. SW was produced by the method described by Dixon et al. (1995) with the same batch of SW used for all experiments, while KAR_1 was purchased from Bioaustralis (Smithfield, NSW, Australia).

Statistical Analysis

Germination data for each replicate and monitoring date were summed into cumulative values and fitted into dose response models with the function "drm" of the "DRC" package (Ritz et al. 2005, 2015) in the software R v. 3.6.2 (R Core Team 2022). Models were then used to estimate for each treatment and species the final germination, which was tested for significance through the comparison of the "compParm" function of the "DRC" package (Ritz et al. 2005, 2015).

Results

Seed Quality Test

The purity of the seed batches was observed to be highly variable among species (Table S1). The genera *Cymbopogon* and *Triodia* tended to have higher purity, reaching PSU values ranging from 89.3 to 98.1%. Conversely, *Heteropogon contortus* was found to have the lowest PSU of 16.1%.

Seed fill (VSU) of *Triodia* spp. and *Cymbopogon* spp., which had the highest PSU%, tended to be the lowest, ranging from

5.9% in *Triodia bynoei* to 25.2% in *Cymbopogon bombycinus*. The highest VSU were observed in *Eriachne* spp., with *Eriachne glauca* having the highest (64.8%).

Overall, the lowest PLS were found in *T. bynoei* and *H. contortus* having a PLS of only 5.2 and 3.8%, respectively. Batches of the genus *Eriachne* and *C. bombycinus* had the highest quality, with PLS values above 20% (Table S1).

Caryopsis Extraction

Germination was significantly improved by extracting the caryopses from the florets, with results varying among the studied species. *Cymbopogon procerus*, *E. glauca* and *Eriachne obtusa* showed a significant separation between florets and caryopses ($p < 0.001$; Fig. 1). The highest difference was that of *E. glauca*, for which only 32.8 ± 2.14% of the florets germinated against 82.8 ± 1.13% of caryopses. Germination of *Triodia bitextura* and *T. bynoei* occurred only for extracted caryopses; therefore no statistical comparison could be made between germination of caryopses and florets (Fig. 1E & 1F). These two species also had the lowest germination of the cleaned caryopses, 27.0 ± 0.58 and 14.3 ± 2.24%, respectively. *C. bombycinus* and *H. contortus* did not show any significant difference ($p > 0.05$) between florets and caryopses, which reached about 90 and 40% in both treatments, respectively (Fig. 1A & 1G).

Germination speed, as well as treatments was also different across species. *Cymbopogon* spp. and *Eriachne* spp. had slower germination within the floret, with a delay of the germination peak ranging from 1 to 5 days compared to the caryopses. Caryopses were slower than the florets only in *H. contortus*, reaching the same percentage of germination of the florets only after 4 weeks (Fig. 1).

Sulfuric Acid Processing

The effect of applying sulfuric acid varied among species and with treatment duration (Fig. 2). Both *Cymbopogon* species were negatively impacted by the acid (Fig. 2A & 2B), and could germinate only at the shortest exposure with a proportional reduction in germination rate with increasing exposure time. In comparison, *E. glauca* and *T. bynoei* improved their germination proportionally to the exposure time, reaching their maximum germination following 20-minute acid treatment (Fig. 2C & 2F). *E. obtusa* (Fig. 2D) showed a non-proportional effect of acid exposure, indeed control and 20-minute treatments did not show significant differences ($p > 0.05$), whereas 2- and 5-minute treatments had a significantly lower and higher germination, respectively ($p < 0.001$). *T. bitextura* had only one treatment significantly different from the others, 2-minute exposure increased germination to 16.0 ± 0.52%, which was slightly more than three-fold compared to all other treatments ($p < 0.001$; Fig. 2E). *H. contortus* (Fig. 2G) did not show differences among exposure times ($p > 0.05$), but all acid treatments had significantly higher emergence than the control seeds, with up to five times more germination.

Germination Promoters

The effect of applying germination promoters varied among species and with the type of promoter used. Application of KAR_1 had no significant effect on germination of *H. contortus*, *T. bitextura*, and *T. bynoei* ($p > 0.05$; Fig. 3E–G), but significantly improved the germination of *C. procerus*, *E. glauca*, and *E. obtusa* ($p < 0.01$; Fig. 3B–D). *C. bombycinus* instead showed a slightly significant decrease compared to the control ($p < 0.05$; Fig. 3A). Application of SW had no significant effect on germination of *C. procerus*, *E. obtusa*, and *T. bitextura* ($p > 0.05$; Fig. 3B, 3D, & 3E), but significantly improved germination of *T. bynoei* ($p < 0.01$; Fig. 3F) and reduced germination of *C. bombycinus*, *E. glauca*, and *H. contortus* ($p < 0.01$, $p < 0.01$ and $p < 0.05$, respectively; Fig. 3A, 3C, & 3G).

Discussion

The high heterogeneity of seed traits among native Australian grasses was confirmed by the results of this study (Read & Bellairs 1999; Farley et al. 2013). The amount of viable seeds in each batch varied from a few percentage points to over 25%. Most of the material in the batches was inert non-seed material or empty florets, with the worst species, *Heteropogon contortus*, found to have only 3.8% of the batch mass composed of PSU. Therefore, cleaning is recommended, especially if the seeds need to be stored for the medium to long term in expensive humidity and temperature-controlled facilities to ensure that seed viability is maintained during storage (Pedrini et al. 2022; Turner et al. 2022). Separation of PSU from inert material was challenging and time-consuming. The florets of both *Cymbopogon* species possess fluffy hairs that tend to become woolly during mechanical processing, thus limiting the efficacy of air separation. The florets of the other species had prominent awns, which greatly complicated the cleaning process, as noted in other studies (Stevens et al. 2015; Guzzomi et al. 2016; Pedrini et al. 2019).

As hypothesized, manually extracted caryopses germinated better than intact florets for most species but not all. The results following acid treatments were remarkably different among the species assessed. Although acid digestion always simplified the subsequent cleaning process, it also greatly affected the germination performances of some species. The rubbing motion required to complete the cleaning after the acid digestion could have damaged some of the seeds because the lateral position of the embryo in the *Poaceae* makes it vulnerable to mechanical damage. This may explain the generally lower germination rate of caryopses treated with acid compared to those extracted from florets manually. Nevertheless, the longer the exposure time to acid, the easier and faster was the rubber mat processing and the relatively less vigour needed to remove the remaining floret, reducing the severity of damage to the caryopsis.

Our results will be of use to guide practitioners in restoration of degraded ecosystems in the Kimberley region toward effective utilization of the seeds from these species. Thus, we recommend the following for each species.

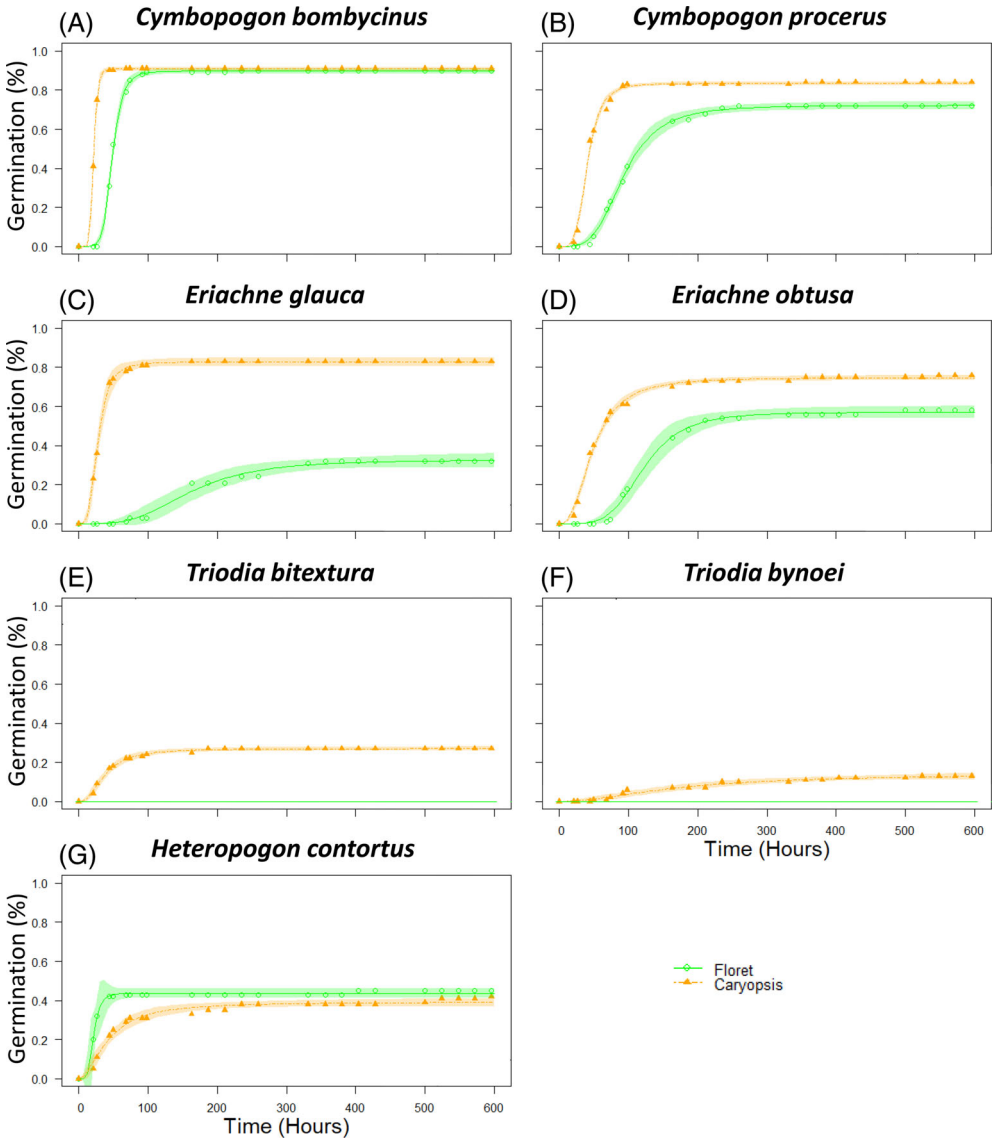

Figure 1. Cumulative germination of florets compared to manually extracted caryopses for seven Australian grass species ($n = 4$).

Cymbopogon bombycinus does not need the removal of the floret to improve germination because florets and cleaned caryopses have similar germination (about 90%). The mechanical removal of the floret and the acid treatments generally led to damage to the caryopses, followed by a reduction in germination. However, if processing is needed to reduce bulk volume and improve the flow through mechanized seed sowing equipment, a 2-minute exposure to acid is recommended.

In *Cymbopogon procerus,* floret removal improved germination from 70 to 80%. The mechanical cleaning that followed acid treatments probably caused the reduction to about 60% germination in the control and 2-minute acid treatment, but longer acid exposures further reduced germination. These results suggest that *C. procerus* is quite sensitive to mechanical damage, and more gentle methods need to be tested for effective caryopses extraction.

The removal of the floret in *Eriachne glauca* improved germination from 30 to 80%. Acid treatments proved to be effective in removing the floret without damaging the caryopsis, with 20-minute exposure leading to a value comparable to that of manually cleaned caryopses.

E. obtusa germinates quite easily, surpassing 70% germination and keeping above 50% within the floret. Acid treatment followed by mechanical removal of the floret drastically reduced germination, which remained above 65% only with the 5-minute exposure, which simplifies the cleaning without excessively damaging the caryopses.

H. contortus behaved with patterns that were often difficult to interpret. The cleaned caryopses had a slower germination than the florets, reaching a similar value only after the fourth week; hence the removal of the floret is probably not necessary. This could also be due to the high heterogeneity in germination

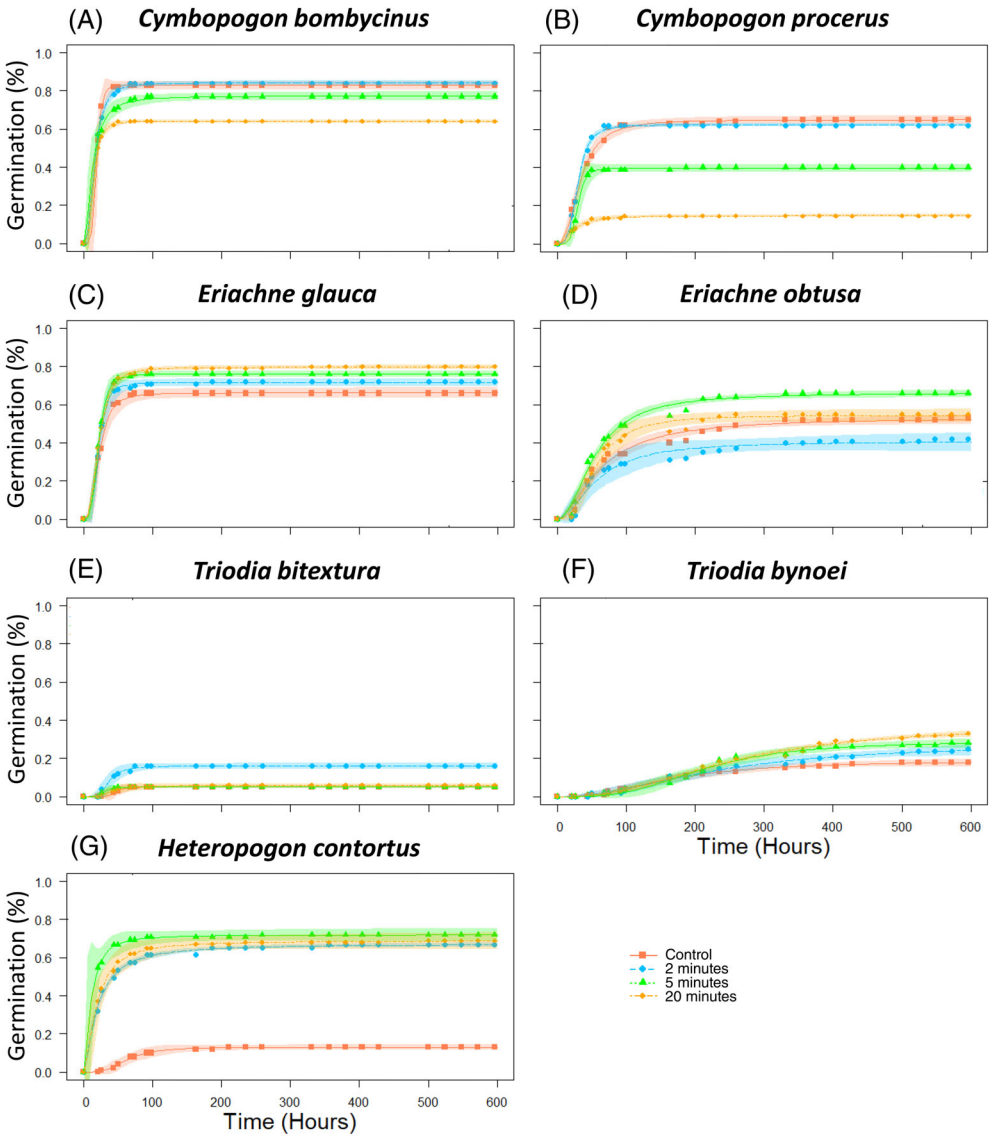

Figure 2. Cumulative germination of seven Australian grass species following treatment of florets with sulfuric acid for 0, 2, 5, or 20 minutes and mechanical extraction of caryopses ($n = 3$–4).

response of the seeds of this species, which had the highest variability among replicates in all treatments. All acid treatments were useful to enhance germination, increasing it to around 70%, nearly a five-fold increase in germination. This is an especially meaningful result considering that this species was the most complex to clean mechanically. The 20-minute exposure greatly weakened the floret structural integrity, reducing the amount of time and effort required for cleaning, allowing much easier removal of the caryopsis from the lemmas and entangled awns, though it was noted that some of these were damaged as a result of the cleaning process. Nevertheless, broken caryopses were observed to germinate for this species, but further observations on the subsequent survival of those seedlings should be carried out in the future. Overall, the low germination with smoke compounds confirmed that *H. contortus* is not directly affected by fire dynamics in Australia (Tothill 1977). Interestingly, SW-treated *H. contortus* seeds actually showed a significantly lower germination, possibly indicating that some compounds present in the SW could have an inhibitory effect on its seeds in some circumstances.

Triodia bitextura showed a sharp difference between caryopses, which reached 27% germination, and florets, which did not germinate at all. Seed cleaning is therefore necessary for this species. Interestingly, the use of acid, followed by rubber mat cleaning, resulted in a reduction in germination (dropped to about 5%) due to mechanical damage to the caryopsis and fungal contamination. Only the treatment with 2-minute exposure reduced this loss, improving germination to 16%. *T. bitextura* seeds were delicate; thus, cleaning processes that have little to no impact on the caryopsis should be tested.

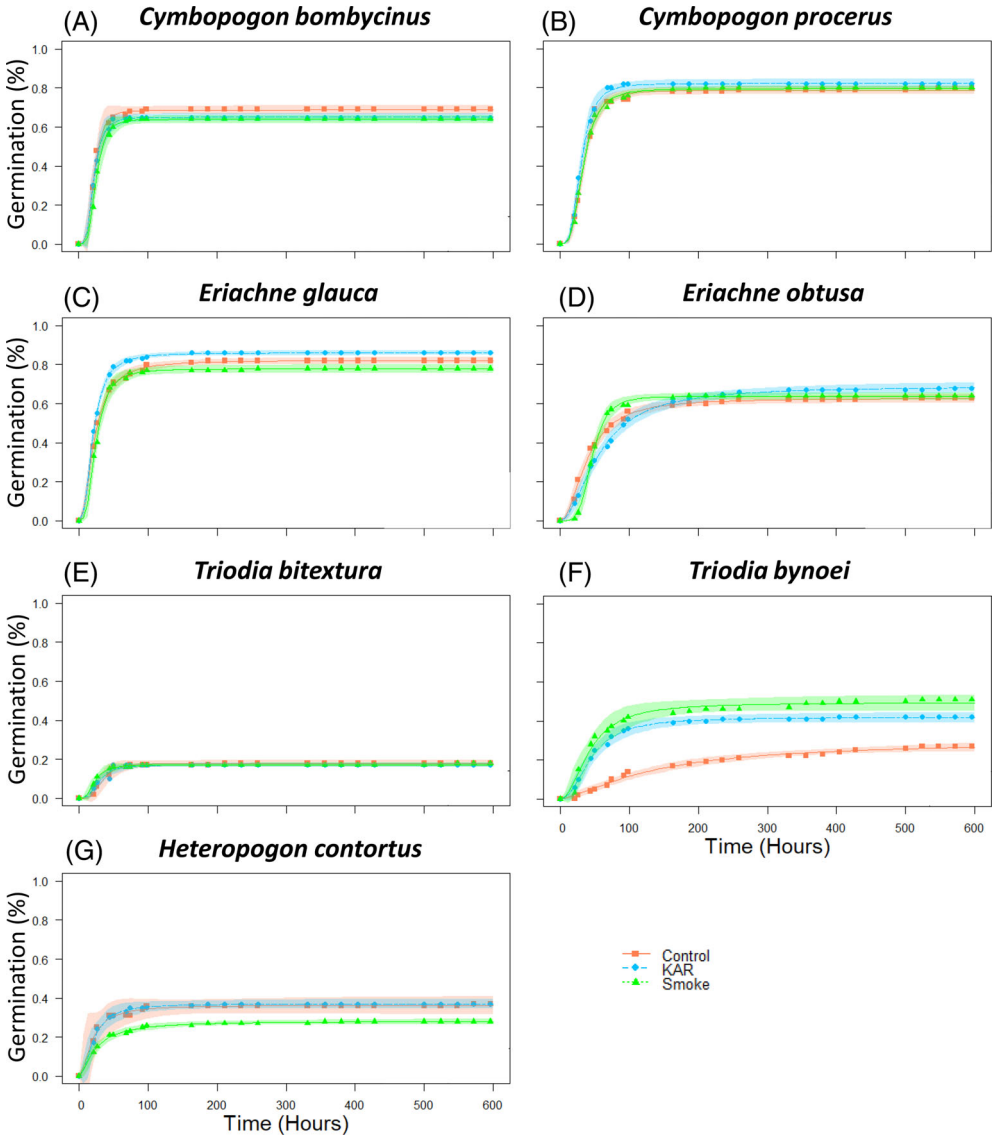

Figure 3. Cumulative germination of seven Australian grass species following cleaning with sulfuric acid for 2–20 minutes (species dependent), mechanical extraction of caryopses, then germination on filter paper soaked with water (control), 10% (v/v) smoke water (smoke) or 1 μM karrikinolide (KAR_1; $n = 4$).

The removal of the florets is essential in *Triodia bynoei,* as germination from the florets was not observed whatsoever. Moreover, it was the species with the slowest and lowest emergence, reaching only 14% in the manually cleaned caryopses. The acid test confirmed the low control values, but it is interesting to notice a gradual increase in germination proportional to the exposure to acid. Indeed, the best emergence was that of the 20-minute acid treatment, reaching 37%. More satisfactory values were reached thanks to the KAR_1 and SW treatments, which brought the emergence rate to 41 and 49%, respectively.

The high diversity of seed traits and germination responses among the grass species examined confirmed the results of previous experiments (e.g. Pedrini et al. 2019; Lewandrowski et al. 2021) and highlights the overall complexity of this globally important family. The often low germination is unsurprising as many studies (e.g. Erickson et al. 2016, 2017; Lewandrowski et al. 2017) have highlighted the seed dormancy and germination complexity inherent in this large cosmopolitan family for which more research is needed in order to better understand their underlying seed biology and consequently maximize their effectiveness for restoration given their overall importance and dominance in many Australian semiarid ecosystems.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Distribution, seed and plant traits of the seven native grass species used in this study.

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