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Germination of selected Australian native grass species, with potential for minesite rehabilitation

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Running heading: Seed Dormancy in Australian Grass Species

Abstract

Native grasses have become increasingly important in the post-mining landscape where land rehabilitators try to reconstruct vegetation communities similar to those present before land clearing. So as to include native grasses in these communities, there is a requirement to understand their germination biology, because in the past, many grasses have typically been hard to establish in the final community. The present study found that poor germination of 13 native grass species was due to (1) low percentage of seed fill, (2) low seed viability of filled seeds and/or (3) seed dormancy. Eight species had dormancy treatments investigated. Most were found to exhibit at least one form of dormancy that was either located in the hull structures immediately external to the caryopsis (i.e. the

lemma, palea and glumes), within the seed coat (i.e. testa and pericarp, tissues that are found inside the hull, but external to the embryo and endosperm) and/or within the embryo. Seven of the grass species tested were found to have a dormancy mechanism present in two or more locations of their dispersal unit. Germination of the selected native grass species could be improved by (1) processing seeds to enrich the percentage of seeds that are filled, (2) testing viability to ensure a high proportion of the seeds are likely to germinate or (3) using methods to help overcome dormancy and promote germination.

Additional keywords: seed dormancy, seed germination, Poaceae, mining, revegetation .

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Native grasses are key components for successful rehabilitation of most post-mining vegetation communities but germination is often low. We investigated 13 native grass species and found that poor germination of selected native grass species was due to (1) low percentage of seed fill, (2) low seed viability of filled seeds and/or (3) seed dormancy. Most of these species were found to exhibit at least one form of dormancy and half were found to have two dormancy mechanisms.

Introduction

Problems may arise in the post-mining rehabilitation program when certain endemic native species fail to establish (Bellairs *et al.* 1999; Bell 2001). Many of the plant communities needing to be re-established are required to contain components of native tree, shrub, forb and grass species. Native grasses are sometimes overlooked or are problematic because of their poor germination (Waters *et al.* 1997). This may be a result of the poor quality of the seed lot used, and this poor quality might be because of issues such as low seed fill and viability, or dormancy. Although some grasses produce seeds that are not dormant, many have non-deep physiological dormancy (Baskin and Baskin 1998). These issues have been identified in laboratory studies as common problems, resulting in poor germination of Australian native grass species (Jurado and Westoby 1992; Adkins and Bellairs 1996; Clarke and French 2005).

The mechanisms causing dormancy in grasses may be found in several locations within the seed (here used to describe the grass caryopsis dispersal unit; Simpson 1990). The structures immediately external to the caryopsis (i.e. the lemma, palea and glumes) are often referred to as the ‘hull’. There is considerable literature documenting the delay, or prevention of germination, of newly harvested grass seeds encased by the hull (Simpson 1990; Baskin and Baskin 1998; Loch *et al.* 2004). *Austrostipa bigeniculata* (Hughes) S.W.L.Jacobs & J.Everett. and *Themeda triandra* Forssk. provide examples of Australian native grasses where the hull can impose dormancy on the seeds (Hagon 1976). When embryo and seed-coat dormancy are absent, then the removal of these structures will allow germination to proceed.

There are examples of a stimulatory effect on grass-seed germination when the integrity of the tissues that are found inside the hull, but external to the embryo and endosperm (i.e. pericarp and testa, referred to as the seed coat) are disrupted. For example Harrington and Crocker (1923) identified a relatively impermeable layer (made up of the inner integument fused with the pericarp) enveloping

the whole caryopsis of *Sorghum halepense* (L.) Pers. that restricts water and oxygen uptake (Benech Arnold *et al.* 1992) and prevents germination. Disruption or scarification of this layer allows germination to occur. From these and similar studies, seed-coat dormancy is likely to be due to a balance of restricted imbibition, mechanical resistance, restricted oxygen uptake and inhibitors and other factors (smoke, light, temperature, nitrate) acting to stimulate or inhibit the physiology of the seed.

Many grass species that lose some dormancy when the hull or seed coat is disrupted, may also have an additional dormancy mechanism in their embryos (Simpson 1990). This dormancy mechanism could be overcome in *Avena fatua* L. by the application of appropriate plant-growth regulators such as gibberellic acid (GA), which presumably promote embryo development and radical growth, which in turn promote germination (Naylor and Simpson 1961). Embryo dormancy can also be overcome in the long term by exposure to certain biotic or abiotic conditions. Embryo dormancy is common to many grass species (Simpson 1990; Adkins and Bellairs 1996; Adkins *et al.* 2002).

Some grass species have more than one dormancy mechanism, for example Heteropogon contortus (L.) P.Beauv. ex Roem. & Schult. (Tothill 1977) and wild oats (Harrington and Crocker 1923; Naylor and Simpson 1961; Simpson 1990). In addition, the depth of dormancy and the kind of dormancy mechanisms present can differ among species, from location to location and from season to season within a species, depending on factors such as the seed-developmental conditions (Groves *et al.* 1982; Adkins and Bellairs 1996).

Previous studies have identified dormancy as an issue resulting in the initial low germination and explored some of the possible dormancy mechanisms that may be found in Australian native grass species (Cresswell and Nelson 1972; Mott 1974; Hagon 1976; Lodge and Whalley 1981; Brown 1982; Groves *et al.* 1982; Adkins and Bellairs 1996; Farley *et al.* 2000). Several other studies have investigated possible ways to overcome this dormancy (Martin 1975; Whitehorne and McIntyre 1975; Dixon *et al.* 1995; Roche *et al.* 1997; Clarke and French 2005). However, there is little in the literature describing to what extent low seed fill, and poor seed viability contribute to the observed low initial percentage germinability. Seed quality can be influenced by pre- or post-dehiscence factors and by intrinsic (within the plant and seed) and extrinsic (environmental and human influences) causes (Dixon 1996). A good example of this can be found with *Triodia* species, where the plants are observed to flower well, but seed set is often low and the viability is poor (Westoby *et al.* 1988), leading to low germination and plant establishment when it is used in revegetation work (Jacobs 1984, 1992).

In those species in which dormancy is identified as an issue, an understanding of the location and type of mechanism that is preventing germination will assist in the development of methods to overcome dormancy and germinate such seeds in revegetation programs (Adkins *et al.* 2002). The present study looks at the issues of seed viability and seed dormancy and how these influence the initial germination percentage of seed lots of selected native grass species.

Materials and methods

Seed handling

Mature seeds of 13 species were hand-collected at physiological maturity from natural populations of each species or purchased from seed collectors (Table 1). Hand-collected seed lots were posted by

surface mail to the laboratory within 7 days of collection. Once seed lots were received at The University of Queensland (UQ), they were air-dried in the air conditioned seed laboratory to approximately 5–10% moisture content and stored in brown paper bags in a darkened temperature-controlled room set at a continuous 23 ± 2°C, before being used for experimentation within 4 weeks of collection.

Seed-quality assessment

Seed-fill percentages were assessed by cutting four replicates of 25 seeds open with a scalpel blade under a magnifying lens, to look for the presence of an anatomically normal embryo.

Viability of all 13 seed lots after drying were assessed using the 2,3,5 triphyenyltetrazolium chloride (TZ) staining technique, following the procedure as outlined by the International Seed Testing Association (1999) and undertaken at the Seed Testing Laboratory of Australia Pty Ltd, Mansfield, Queensland. Seeds were considered viable if the embryo stained red. The percentage of viable seeds in the results was calculated as the percentage of total seeds, with unfilled seeds considered non-viable.

Seed germination was determined using four replicates of 25 seeds imbibed in 9-cm-diameter plastic Petri dishes containing two 8.4-cm-diameter seed filter papers (Whatman No. 1) soaked with 15 mL of deionised water containing a 0.15% Previcur® solution (Bayer CropScience, Hawthorn, Victoria, Australia) to prevent potential fungal growth. Germination was said to have occurred when the radicle became visible and was at least 3 mm in length. The Petri dishes were incubated in either a 15°C or 25 ± 2°C controlled-temperature germination cabinet, according to whether the species being tested was a winter (15°C), or a summer (25°C) germinant in the wild. (Only *Neurachne alopecuroides* was germinated at 15°C). A constant 24-h photoperiod was used in both cabinets and consisted of a white light (~142 ± 15 µmol m^{-2} s^{-1}) produced by four 30-W fluorescent tubes and six 15-W tungsten globes. Germination was scored daily for 21 days, with all germinants removed once scored. Deionised water was added as necessary to keep the filter papers moist and Petri dishes were randomly relocated within the controlled-temperature cabinets after each observation was completed.

Seed treatments

Experiment 1 investigated all 13 species. The percentage of filled seeds per sample was determined as a proportion of the total number of seeds per replicate. The percentage of viable seeds per replicate was determined from the TZ results. Germination percentage was determined from the number of germinants counted per replicate. For determining seed dormancy, germination percentage was corrected to the proportion of viable seeds by using the average number of viable seeds. The proportion of dormant seeds was then expressed as 100 minus the germination percentage of viable seeds.

In Experiment 2, only eight of the initial species were studied. Some species were excluded because of the lack of dormant seeds (*C. truncata, D. sericeum*) or because of the lack of availability of sufficient numbers of viable seeds (*A. lappacea, A. pectinata, N alopecuroides*). Seed-dormancy mechanism(s) present were studied with the view that mechanisms could be in one (or more) of three different locations, namely the hull around the caryopsis (glumes, palea and lemma), the seed coat (pericarp and testa) and/or the embryo.

Once the seeds had been air-dried, several treatments were applied to the species under study, including the following:

(1) The removal of the hull with forceps, taking particular care not to damage the seed coat and other tissues of the caryopsis.

(2) Scarification, with a scalpel blade, of the seed coat (pericarp and testa), after the removal of the hull by carefully cutting away part of these tissues from over the endosperm away from the embryo.

(3) Application of the plant-growth regulator, gibberellic acid (GA3). After the removal of the hull and the scarification of the seed coat, caryopses were placed onto filter papers soaked in a GA_3 potassium salt solution (2.9 mM; Mott 1978; Sigma-Aldrich, Sydney, Australia). Seeds were monitored each day for germination, and germinants were removed. Deionised water alone was added as necessary to keep the filter papers moist.

Experimental design

For all studies, the experimental design was a complete randomised block design with three treatments, each with four replicate batches of 25 seeds. Results for each treatment were compared using the final germination percentage and data for each were analysed for statistical significance.

Statistical analysis was performed using an analysis of variance (ANOVA) in GENSTAT (Version 8.0). Percentage data was arc-sine transformed to normalise data before analysis, so as to meet the assumptions of the ANOVA test. Significance is reported at the 5% level.

Results

Experiment 1

Initial germination tests on intact (with the hull in place) seeds of 13 species indicated that 10 species gave <30% germination, whereas three species had no germination (Fig. 1).

Seed-fill results indicated that although most species had filled seeds, there were four species that had <50% filled seeds (Fig. 1). Seed viability was assessed soon after harvest using the TZ test. Eleven of the species tested contained <80% viable seeds, with three species demonstrating a very low viability of <30% (Fig. 1).

It was clear that seed dormancy was present in 12 of the species studied (Fig. 1). Ten species contained >50% dormant seeds, with three species having 100% of viable seeds dormant. *Chloris truncata* contained no dormant seeds, *Dichanthium sericeum* had <20% dormant seeds and *Astrebla lappacea* had <50% dormant seeds.

Experiment 2

Hull-imposed dormancy occurred commonly. All of the eight species tested (*Brachyachne convergens* ($P < 0.001$), *Enneapogon nigricans* ($P = 0.001$), *Astrebla squarrosa* ($P < 0.05$), *Triodia longiceps* ($P < 0.001$), *Themeda triandra* ($P < 0.001$), *Sorghum intrans* ($P < 0.001$), *S. timorense* ($P < 0.001$) and *S. stipoideum* ($P < 0.005$)) demonstrated a significant increase in their ability to germinate when the hull was removed from around the seed (Fig. 2a). Three species (*B. convergens, T. longiceps* and *S. timorense*) could not germinate at all without the removal of the hull, with final germination values increasing from 0 to 53 ± 4%, from 0 to 4 ± 1% and from 0 to 30 ± 7%, respectively. This indicated that 53%, 4% and 30% of the individual seeds within these populations had hull-imposed dormancy alone.

Seed-coat dormancy occurred in five species that demonstrated a significant increase in final germination (*Astrebla squarrosa* ($P < 0.001$), *Brachyachne convergens* ($P < 0.001$), *Sorghum intrans* ($P < 0.005$), *S. stipoideum* ($P < 0.001$) and *S. timorense* ($P < 0.001$)) after having the seed coat scarified (Fig. 2b).

Embryo dormancy was also present. Five of the grass species tested (*Brachyachne convergens* ($P < 0.001$), *Sorghum stipoideum* ($P < 0.001$), *S. timorense* ($P < 0.05$), *Themeda triandra* ($P < 0.001$) and *Triodia longiceps* ($P < 0.001$)) demonstrated significant increases in final germination in response to the application of GA_3 (Fig. 2c). Gibberellic acid increased the germination percentage for *S. stipoideum* from 69 ± 4% to 100%, *T. triandra* from 56 ± 4% to 88 ± 4% and *T. longiceps* from 14 ± 8% to 38 ± 6%.

Most of the species had several dormancy mechanisms. Seven of the eight species tested (*Astrebla squarrosa, Brachyachne convergens, Sorghum intrans, S. stipoideum, S. timorense, Themeda triandra* and *Triodia longiceps*) demonstrated an increase in final germination after more than one treatment had been applied, indicating the presence of more than one dormancy mechanism within the seeds (Table 2).

Discussion

The low germination percentages in 10 of the 13 species investigated would equate to significant problems if these species were to be used, without further investigation, in land-rehabilitation work. The use of such seed lots could result in certain species not being represented in the final vegetation community and lack of achievement of rehabilitation goals.

Poor seed fill was an issue for *Neurachne alopecuroides, Sorghum timorense, Themeda triandra* and *Triodia longiceps*. Seed fill can be influenced by pre- or post-dehiscence factors and causes may be intrinsic (within the plant and seed) and/or extrinsic (environmental and human influences). Intrinsic factors include genetic factors and biological characteristics of the plant, such as different ripening times, the allocation of moisture or nutrients within the plant and infertile or decoy seeds (Dixon 1996). Extrinsic factors such as disease, predation of the plants and handling of seeds once collected can also affect the quality of the seed lot (Wulff 1986; Gutterman 1992; Bewley and Black 1994; Dixon 1996; Smith *et al.* 2003; Cole and Johnston 2006).

An understanding of the intrinsic and extrinsic factors that can be used to manipulate seed fill in native grass species would help in the planning of future seed collection. In the field, a simple cut test (Way 2003) needs to be performed on a representative sample of seeds before harvesting large quantities, to avoid collecting seeds that are of low seed fill. This will enable a collector to avoid particular populations with a low seed-fill percentage, or adjust the amount of seeds collected so that the poor seed-fill percentage can be accounted for when the seed lots are to be used.

Even when seed fill is high, the seed lot can contain many dead seeds. The TZ test identified that for four of the study species, more than 50% of the filled seeds were dead, and for three species, more than 70% of seeds were dead. Thus, the cut test does not always give sufficient information and such a high proportion of dead seeds in the seed lots would cause significant problems when they are used in rehabilitation projects. Low seed viability may be a result of seed being stressed when it is being formed on the plant (Cole and Johnston 2006) or it may due to an inherent low viability that is genetically pre-determined for that species. To avoid the collection of seeds that are dead, a cut test

will give some indication of seed health, but a viability test such as the TZ will give a better indication of seed viability before harvest. Before seeds are to be used in rehabilitation projects, testing for viability and seed quality should be undertaken. In this way, expense can be saved by not buying or collecting large amounts of seeds and broadcasting seeds that are of poor quality. One species, *Chloris truncata*, had a notably higher germination percentage than the viability indicated by the TZ test, possibly because of variation associated with the sample size and the difficulty in assessing viability of these seeds. Some seeds that showed only slight staining may have been incorrectly assessed as non-viable because standard test information is not available for this species.

The common occurrence of seed dormancy found in the present study suggests that dormancy is indeed a common characteristic of Australian native grass species. At an appropriate germination temperature and continuous light, most species had >50% of their viable seeds dormant, and for three species, 100% were dormant. Seed dormancy is an ecological adaptation that allows both the temporal and spatial distribution of seeds, thus helping ensure the survival of the species through time (Bewley and Black 1994). Bellairs *et al.* (1999) found that of the 23 native grass species tested, most of them exhibited some degree of dormancy. This common occurrence of dormancy in Australian native grass species is most probably because of the unpredictable or extreme climate that exists in many parts of Australia. Several of the grass species studied (*Astrebla* spp., *Themeda triandra* and *Triodia longiceps*) are all known to possess dormancy when freshly harvested (Whalley and Davidson 1969; Groves *et al.* 1982; Davidson and Adkins 1997) and, therefore, their failure to provide high germination results was possibly due to dormancy. Of the three species that were found to have low dormancy in the present study, a lack of dormancy in *D. sericeum* has been noted before (Read and Bellairs 1999), whereas *T. triodia*, *D. sericeum* and *C. truncata* have all been reported to have dormant seeds in other studies (Jacobsen 1981; Lodge and Whalley 1981).

Once seed dormancy is identified as important, the next step is to identify the location of these mechanism(s) so that effective methods may be used to overcome this dormancy and so promote germination in revegetation programs. In many species, the embryo has the capacity to germinate, but dormancy is imposed by one or more of the tissues that surround it and act as permeability barriers, restricting the uptake of water or oxygen, and as a source of germination-inhibiting chemicals (Vose 1956; Wareing and Foda 1957; Black and Wareing 1959; Simpson and Naylor 1962; Fendall and Carter 1965; Adkins and Bellairs 1996; Xu *et al.* 2005; Li *et al.* 2010), or as mechanical barriers preventing embryo expansion (Ma *et al.* 2010; Duclos *et al.* 2013). These studies have shown that dormancy caused by the hull structures is affected by the interaction of several factors that depend on the species but can include the light regime, temperature regime, physical structure of the hull, water uptake, mechanical resistance and quantity of inhibitors. Such dormancy can often be overcome by removal, weakening and/or breakdown of the hull and/or seed-coat tissues of the seed (Adkins *et al.* 2002).

All species in the present study demonstrated significant improvements in germination after the removal of the hull and, for three of these species, removal of the hull was required for any germination to occur. Such results, and other studies that have looked at smaller groups of species (Mott 1974; Tothill 1977; Brown 1982), suggest that hull-imposed dormancy is common in Australian native grasses. Practical methods to overcome dormancy, on a large scale, need to be developed to ensure maximum germination of these seed lots.

Treatment of the seed coat also affected dormancy and increased germination in five of the eight species (*A. squarrosa*, *B. convergens*, *S. intrans*, *S. stipoideum* and *S. timorense*). These included species that had also responded to the removal of the hull. Scarification of grass seeds can be difficult

for rehabilitators to use. For many species, seeds can be threshed or shaken after drying. Although scarification can increase germination, it may also make seeds more susceptible to disease or dehydration in the field. Another problem may come when the application of scarification is attempted on a large scale by tumbling of the seeds within an abrasive medium or use of a chemical agent such as sodium hypochlorite solution. A balance between sufficient scarification to promote germination and not excessive scarification that damages the embryo needs to be achieved. Protocols to be used for treatment of large seed lots for these species need to be developed.

Application of GA_3 increased germination of five of the eight species (*B. convergens, S. stipoideum, S. timorense, T. triandra* and *T. longiceps*), indicating a dormancy mechanism residing within the embryo. The dormancy mechanisms that reside within the embryo of grasses may involve the expression of certain genes, the levels of certain plant-growth regulators, the activity of important respiratory pathways or the mobilisation of seed-storage proteins (Graeber *et al.* 2012). In addition, some embryos may be too immature to germinate immediately and have to undergo a further growth phase before their germination is possible (Adkins *et al.* 2002). We note that two species (*Themeda triandra* and *Triodia longiceps*) did not achieve 100% germination of viable seeds. *Themeda* and *Triodia* have both been reported to respond to smoke (Davidson and Adkins 1997; Read and Bellairs 1999) and the application of smoke water, butenolide or other embryo treatments could further overcome embryo dormancy in these species. In the hands of a land rehabilitator, GA_3 solution (and smoke solution where necessary) could be applied to seeds just before they are sown, by spraying or soaking the seeds in GA_3, then drying the seeds back down to a level that allows storage. A priming approach could be used to prepare seeds for sowing, several months before they are actually sown (Wagner *et al.* 2011); however, this technique would need further investigation for native grasses.

Some native grass species may contain a combination of hull, seed-coat or embryo dormancy mechanisms (Adkins and Bellairs 1996). Seven of eight species tested in the present study were shown to have more than one dormancy mechanism present in different parts of the dispersal unit. The presence of more than one dormancy mechanism in the dispersal unit is not unexpected; however, it will have significant implications on the use of seeds of these species in rehabilitation projects. Seeds may require more than one dormancy-breaking treatment before they will achieve suitably high germination levels in the field. This not only helps rehabilitators make efficient use of native seeds, but allows such species to become represented in the final plant communities established. This is particularly important to help stabilise soil and stop erosion from wind and water, especially on slopes, and grasses are typically used for this purpose (Bell 2001).

It is important to recognise that dormancy does play an important role in the long-term survival of a species and seeds in the soil seed bank. It is important to understand and be able to break dormancy, to get germination of sown seeds; however, sometimes it may be important not to overcome all dormancy in the seed lot being sown, so that if conditions become unfavourable, some seeds will remain in the soil seed bank until a later date. Dormancy is an evolutionary trait that ensures a species survivability over time, by allowing it to persist through adverse conditions. By using a seed lot that still has a percentage of dormant seeds the species will have more chance of success in the long term if adverse environmental conditions occur after the seeds are sown.

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Table 1. Collection method and geographic location of the 13 species used in the present study

Collections were made in December 2000

Species	Nearest town to collection site (State)	Species	Nearest town to collection site (State)
Astrebla lappacea (Lindl.) Domin	Cannington (Qld)	*Neurachne alopecuroides* R.Br.	Jarradale (WA)
Astrebla pectinata (Lindl.) F.Muell. ex Benth	Cannington (Qld)	*Sorghum intrans* F.Muell. ex Benth.	Katherine (NT)
Astrebla squarrosa C.E.Hubb.	Cannington (Qld)	*Sorghum stipoideum* (Ewart & Jean White) C.A.Gardner & C.E.Hubb. ex C.E.Hubb.	Katherine (NT)
Brachyachne convergens (F.Muell.) Stapf.	Katherine (NT)	*Sorghum timorense* (Kunth) Buse.	Katherine (NT)
Chloris truncata R.Br.	Roma (Qld)	*Themeda triandra* Forssk.	Gympie (Qld)
Dichanthium sericeum (R.Br.) A.Camus	Murrumba Downs (Qld)	*Triodia longiceps* J.M.Black.	Cannington (Qld)
Enneapogon nigricans (R.Br.) P.Beauv.	Armidale (NSW)		

Table 2. Location of dormancy mechanism(s) present in each of the native grass species studied as assessed by the final germination (●)

Species	Hull	Seed coat	Embryo
Astrebla squarrosa	●	●	
Brachyachne convergens	●	●	●
Enneapogon nigricans	●		
Sorghum intrans	●	●	
Sorghum stipoideum	●	●	●
Sorghum timorense	●	●	●
Themeda triandra	●		●
Triodia longiceps	●		●

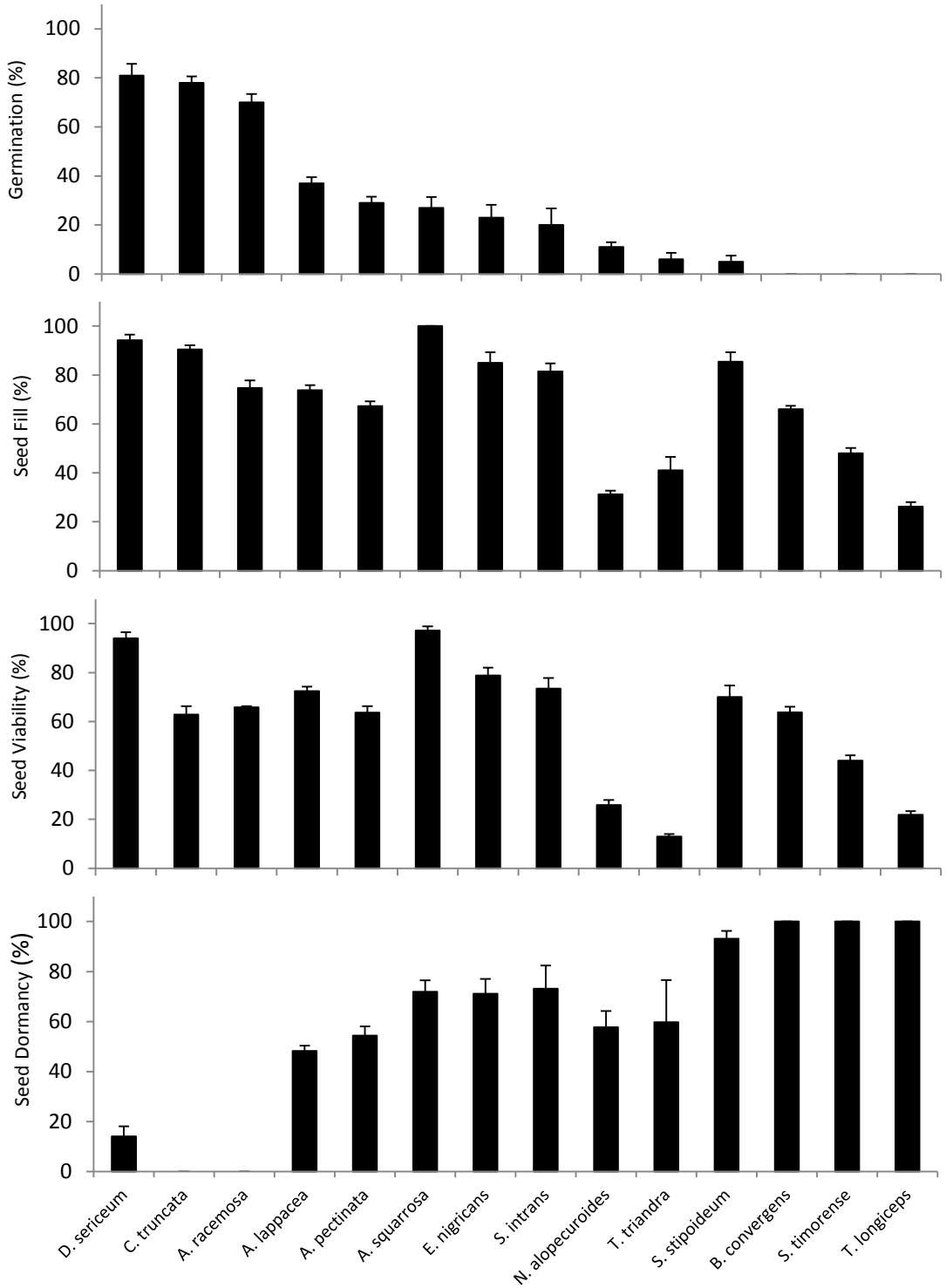

Fig. 1. Germination, seed fill, seed viability and dormant seed rates of 13 native grass species. *Neurachne alopecuroides* was germinated at 15 ± 2°C, whereas all other species were germinated at 25 ± 2°C, under continuous light. Data are the mean ± s.e.m. of four replicates of 25 seeds.

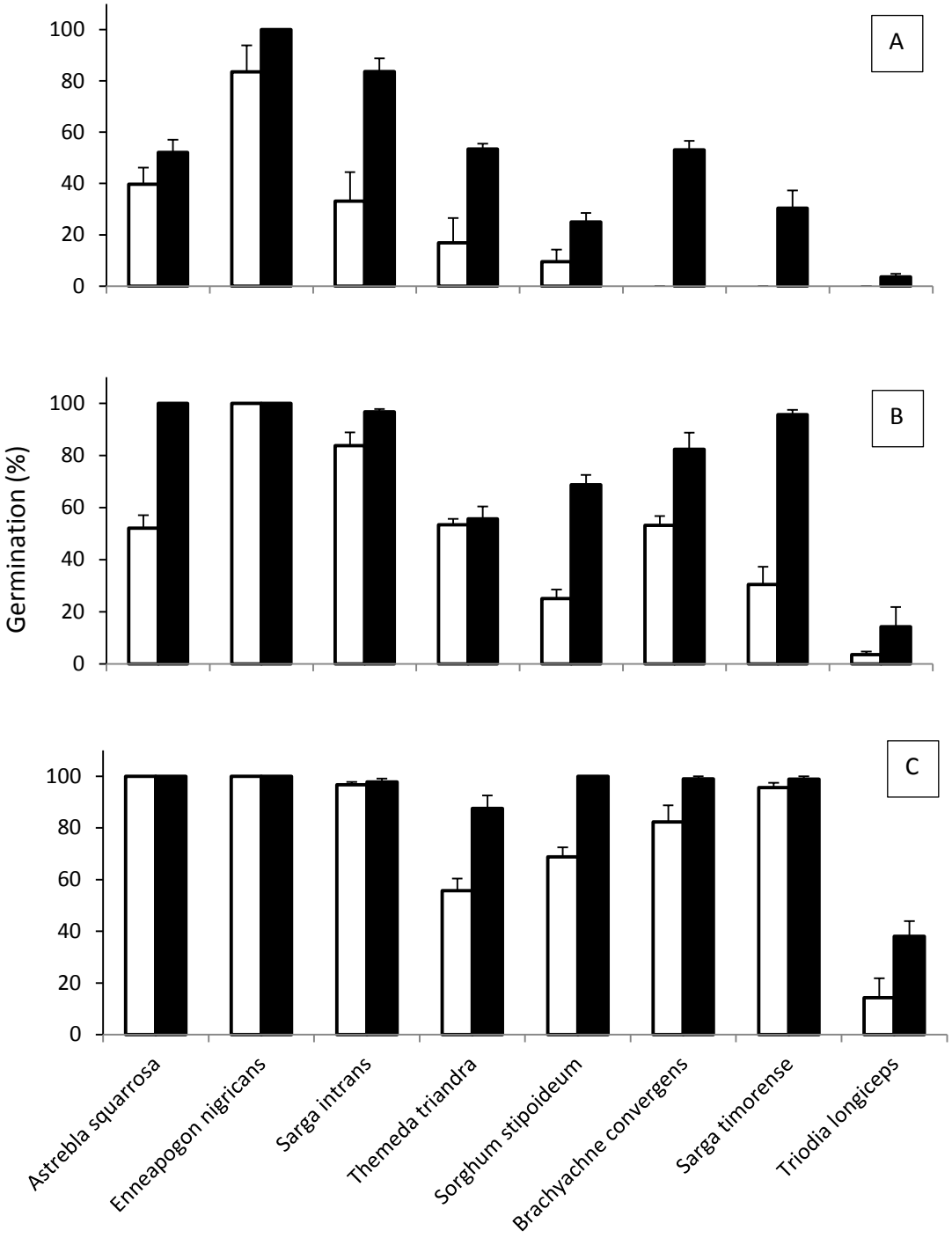

Fig. 2. Germination for eight species of native grass after treatments to increase germination. Treatments included (*a*) + Hull (□) or –Hull (■), (*b*) –Hull (□) or – Hull + Scarification (■) and (*c*) – Hull + Scarification (□) or –Hull + Scarification + 1.0 mM gibberellic acid (■). All seeds were incubated at 25 ± 2°C in continuous light. Data are the mean ± s.e.m. of four replicates of 25 seeds per treatment.