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Gamba grass (*Andropogon gayanus* Kunth.) seed persistence and germination temperature tolerance

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Abstract. Gamba grass (*Andropogon gayanus* Kunth.) is a highly invasive, naturalised Weed of National Significance in Australia due to its economic, environmental and social impacts. It outcompetes native pastures and fuels intense fires in northern Australian rangelands. To aid management of current infestations and to better understand its potential distribution, this study determined the germination response of gamba grass under a range of constant (13°C−48°C) and alternating (11/7°C–52/42°C) temperature regimes and quantified the potential longevity of soil seed banks. The effect of different soil types, levels of pasture cover and burial depths on seed longevity was investigated in the Dry Tropics of northern Queensland.

Germination of gamba grass occurred under a wide range of both constant (17°C−39°C) and alternating day/night temperatures (16/12°C–47/39°C), although the level of germination declined at the lower and higher temperature ranges. At the cooler temperatures, seed viability was not affected, but seeds went into a state of dormancy. The highest level of seed viability was recorded at the lowest constant temperature regime (13°C) and at the two lowest alternating temperatures (11/7°C and 16/12°C). A gradual but variable decline in viability occurred thereafter with increasing temperatures. At the higher temperature range (e.g. constant temperatures of 39°C−43°C and alternating temperatures of 47/39°C) both dormancy and loss of seed viability were occurring, but once alternating and constant temperatures reached above 47/39°C and 43°C all seeds were rendered unviable after 9 and 6 weeks respectively.

In the Dry Tropics of northern Queensland, viability of seeds was <1% after 12 months and nil after 24 months, irrespective of soil type or vegetation cover. However, burial depth had a significant effect, with surface located seeds exhibiting a faster rate of decline in germination and viability than seeds buried below ground (i.e. 2.5–10 cm). These findings have implications for the duration of control/eradication programs (i.e. seed persistence) and also suggest that gamba grass has the potential to greatly expand its current distribution into the relatively cooler southern latitude areas of Australia.

Additional keywords: burial depth, dormancy, soil type, temperature regimes, vegetation cover, viability.

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Introduction

Gamba grass (*Andropogon gayanus* Kunth) is native to tropical and sub-tropical African savannas with extended dry seasons (Fig. 1). In Australia it was introduced and planted as a high yielding pasture grass in the Northern Territory in 1931, Queensland in 1942 and Western Australia in 1952 and has now become naturalised (Csurhes 2005). Preliminary trials from 1946 at the Katherine Research Station in the Northern Territory resulted in the production of a cultivar in 1986, known as cv. Kent, which is now commonly known as gamba grass (Oram 1990; Northern Territory Government 2010; Australian Weeds Committee 2013; Tropical Forages 2017). This cultivar is referred to as gamba grass throughout the remainder of this paper. It was developed specifically for use as a cattle fodder in the Northern Territory by crossing two varieties and has been widely planted in the pastoral and agricultural areas of the Top End, northern Australia. Gamba grass can provide valuable feed for cattle, with young growth highly palatable and readily eaten throughout the year under moderate grazing pressure. However, if under-grazed, it becomes coarse, fibrous, and less palatable to cattle (Cook *et al*. 2005). Under such situations it has become invasive and has spread into non-grazed parcels of land, such as conservation areas, semi-urban residential blocks and mining leases (Csurhes and Hannan-Jones 2008; Department of the

Fig. 1. Clumps of mature flowering plants of gamba grass showing a tussocky growth habit.

Environment, Water, Heritage and the Arts 2010; Queensland Government 2016; Western Australia Government 2017).

Infestations of gamba grass contribute to ecosystem degradation, habitat loss and species decline (Rossiter *et al*. 2003; McIntyre *et al*. 2004; Flores *et al*. 2005; Grice and Martin 2005; Rossiter-Rachor *et al*. 2009; Brooks *et al*. 2010; Setterfield *et al*. 2010). Gamba grass not only outcompetes short native grasses but it grows profusely to produce a large biomass of highly flammable material. This has the potential to increase the frequency and intensity of late dry season wildfires, which can convert vast tracts of eucalypt woodland into almost treeless plains (Kean and Price 2003; Rossiter *et al*. 2003; Csurhes 2005; Flores *et al*. 2005; Brooks *et al*. 2010).

Gamba grass is a C_4 plant, which means that it can perform photosynthesis particularly at elevated CO_2 levels, as is usual for tropical grasses (Harper 1977; Bhatt *et al*. 2007). Gamba grass inflorescence is a type of raceme which consists of a large, leafy, compound cluster of slender branches, which end in a pair of elongated fluffy flower clusters (racemes), each bearing pairs of very hairy flower spikelets. One spikelet of each pair is sessile, whereas the other is on a pedicel. The sessile spikelet is bisexual and fertile and produces the seed (7–9 mm long), which has a large, bent and twisted awn (1–4 cm long) (Fig. 2). The pedicellate spikelet is unisexual (male) and sterile. The sterile florets usually have a much smaller, straighter awn (1–10 mm long).

Gamba grass is a prolific seeder (up to 244 000 seeds/plant. year with 65% viability) (Flores *et al*. 2005; Queensland Government 2016; Northern Territory Government 2017) comparable with other naturalised perennial grasses such as buffel grass (*Cenchrus ciliaris* L.) and olive hymenachne [*Hymenachne amplexicaulis* (Rudge) Nees]. In Queensland, gamba grass flowers between March and May with seeds maturing in late May–June, whereas in Western Australia flowering and seeding occur mainly during autumn and winter (i.e. from April to August) (Rossiter *et al*. 2004; Western Australia Government 2017). However, gamba grass can also seed in October–November following early wet season storms (DSEWPC 2011).

Fig. 2. Feathery (hairy) gamba grass, stalkless (sessile) and bisexual seed with bent and twisted awn.

Information on the seed ecology of gamba grass is limited, but is critical for gaining an improved understanding of its potential distribution and to aid management decisions particularly those associated with the frequency and duration of control/eradication activities (Campbell and Grice 2000; Panetta 2004; Panetta *et al*. 2011; Dodd *et al*. 2015). The literature suggests that fresh seed viability can be highly variable ranging from as low as 10–20% up to 80% (Reid and Miller 1970; Barrow 1995; Gobius *et al*. 2001; Setterfield *et al*. 2004). Similarly, reports on dormancy range from nil (Bowden 1964; Felippe *et al*. 1983) to periods of three to nine months (Dieng *et al*. 1991). Seedling emergence studies in the Northern Territory confirm that most freshly produced seeds are likely to germinate on the first rains of the wet season with minimal seeds remaining in the seed bank (ranging from <1 to 2.3%) after 12 months (Barrow 1995; Setterfield *et al*. 2004; Flores *et al*. 2005).

According to Harper (1957, 1977) plant seeds may be of three categories: some may be born dormant (innate), some acquire dormancy (induced) and some have dormancy thrust on them (enforced). Although gamba grass appears to have limited innate dormancy to help prolong the longevity of soil seed banks and to enhance opportunities for seedling recruitment under favourable environmental conditions, it is not clear if it has the ability to display quiescence or enforced dormancy. This is a strategy used by some plant species to prevent germination from occurring until more favourable environmental conditions prevail (e.g. temperatures) (Baskin and Baskin 2001).

The present study investigated the germination and viability responses of gamba grass to both constant (Experiment 1a) and alternating temperatures (Experiment 1b) under controlled conditions in order to better understand its potential distribution. A seed persistence trial (Experiment 2) was also initiated in the dry tropics of northern Queensland to determine the time taken for seed banks exposed to a range of conditions (i.e. different soil types, levels of pasture cover and burial depths) to be completely exhausted. The findings are discussed in the context of implications for ecology and management of gamba grass.

Materials and methods

Seed collection

Seeds used for a preliminary seed test to determine an appropriate lighting regime (alternating light/dark or continuous dark conditions) for germination testing were sourced from ‘El Questro Station’ in Western Australia (15°57′S, 128°01′E) whereas seeds used in Experiment 1a, 1b and 2 were sourced from ‘Kalinga Station’ near Lakefield National Park in Queensland (15°2′S, 143°85′E), 340 km north-west of Cairns. Seeds were collected by either plucking them directly from flowering branches or collecting whole flower heads and manually threshing and cleaning the seeds afterwards. Seeds were then stored in glass jars at room temperature until required. All collections were undertaken in June 2010.

The preliminary test found that an alternating (12 h/12 h) light/dark regime provided higher germination (44%) than continuous dark conditions (22%) and was subsequently used for all experiments in this study.

Experiment 1a – seed germination under alternating day/night temperature regimes

This laboratory experiment commenced at the Tropical Weeds Research Centre on 17 September 2010 to determine the germination range of alternating temperatures under which gamba grass seeds germinate.

Four replicate lots of 50 randomly selected seeds were placed in Petri dishes (9 cm diameter) containing two layers of Whatman no. 1 filter paper moistened with 10 mL of distilled water. Groups of four Petri dishes were then placed vertically on top of each other in plastic containers (11 cm × 17 cm × 7 cm) to help maintain a moist environment, with the lids perforated at the four corners to allow air circulation. Containers were individually placed into 10 temperature compartments within a multi-temperature incubator (Model: LMMT-10, Linder and May, Northgate, Qld, Australia). Seeds received 12 h of darkness and 12 h of light, with temperatures within each compartment measured on an hourly basis using type K steel encased thermocouples connected to a data logger (Data Electronics Pty Ltd, Brisbane, Qld, Australia). Across the 10 temperature compartments, seeds were exposed to day/night temperature ranges of 11/7°C to 52/42°C in 10 steps (see Table 1).

Germinated seeds from each Petri dish were counted and removed daily and when necessary, distilled water was added to keep the filter paper moistened. The positions of the Petri dishes within the plastic containers were re-randomised daily. Germination was considered to have ceased in a dish when no seeds germinated for two weeks. Any remaining seeds were then checked for viability using the tetrazolium method (Moore 1985).

Experiment 1b – seed germination under constant temperature regimes

This laboratory experiment commenced on 21 April 2011 and was similar to experiment 1a in all experimental details except that seeds were exposed to constant temperature throughout the day (12 h) and night (12 h) regimes. Across the 10 temperature compartments, seeds were exposed to a temperature range of 13°C–48°C (Table 1).

Experiment 2 – seed persistence

Site description

The experimental site (38 m × 36 m) was located at the Tropical Weeds Research Centre. The site was secured with a rabbit and kangaroo exclusion fence. It had been previously

Table 1. Day and night temperatures associated with each of the 10 compartments of the Linder and May multi-temperature incubator when set at constant or alternate temperature regimes

Compartment No.	Temperature (°C) (12 h light/12 h dark)				
	Constant		Alternate		
	Day	Night	Day	Night	Average
1	13	13	11	7	9.0
2	17	17	16	12	14.0
3	20	20	20	16	18.0
4	24	24	24	20	22.0
5	27	27	29	24	26.5
6	31	31	33	28	30.5
7	35	35	37	31	34.0
8	39	39	41	35	38.0
9	43	43	47	39	43.0
10	48	48	52	42	47.0

cleared of shrubs and trees, and originally comprised an open woodland. The ground cover vegetation included buffel grass, Indian couch [*Bothrichloa pertusa* (L.) A.Camus]; dark wiregrass (*Aristida calycina* R.Br.), purpletop chloris (*Chloris inflata* Link), red Natal grass (*Melinis repens* (Willd.) Zizka), feathertop Rhodes grass (*Chloris virgata* Sw.), sabi grass (*Urochloa mosambicensis* [Hack.] Dandy), budda pea (*Aeschynomene indica* L.) and siratro (*Macroptilium atropurpureum* (DC.) Urb.).

Long-term mean annual rainfall for Charters Towers is 658 mm with 54% of this occurring during the summer months (December–February) (BOM 2016). The mean summer maximum daily temperature is 37.6°C and the mean winter (June–August) maximum daily temperature is 28.2°C. Rainfall and ambient temperature at the field site were measured using an on-site automatic weather station at a distance of 2.5 m above ground (Campbell Scientific, Logan, UT, USA). Between 2010 and 2014 annual rainfall was 1148, 908, 750, 432 and 482 mm, respectively.

Experimental design

This experiment formed a part of a larger study established in 2008 to test the longevity of seeds of several weed species. It comprised a multi-factor, split-plot design with four replicate blocks. Factors consisted of two soil types (alluvial river loam and clay), two levels of pasture cover (pasture present or pasture excluded), four seed burial depths (0, 2.5, 10 and 20 cm) and nine retrieval times, which varied between species. For gamba grass, experimental units were 50 randomly selected seeds placed in 180-µm woven stainless wire mesh bags (7 cm × 7 cm). Burial of gamba grass seeds commenced in November 2010 with retrievals designated to occur 3, 6, 12, 18, 24, 30, 36, 42 and 60 months afterwards or until no viable seeds were recorded for two consecutive retrievals. A full description of the overall design and implementation of treatments is provided by Bebawi *et al.* (2015).

Germination and viability testing

Germination and viability testing was undertaken on 64 lots of 50 seeds at commencement of the trial to determine initial germinability and viability, and then on seeds removed from packets at the designated retrievals. Seeds were placed in Petri dishes (9 cm diameter) containing two layers of Whatman no. 1 filter paper moistened with 10 mL of distilled water. These dishes were then put into a growth cabinet set at 30°C/20°C day/night with alternating 12/12 h of light/dark. Additional distilled water was added when necessary to keep the filter papers moist. Seeds that germinated (identified by plumule emergence) were counted and removed daily until no germination has occurred for 10 days. Ungerminated seeds were checked for dormancy and viability as described for Experiment 1a.

Germination was calculated as a percentage of the number of seeds that germinated out of the original 50 seeds buried in individual packets. Viability included those seeds that initially germinated in the Petri dishes plus those that tested positive when exposed to the tetrazolium test.

Data analysis

GENSTAT was used for all statistical analyses (GENSTAT 16, VSN International, Hemel Hempstead, Hertfordshire, UK) and Fisher's protected least significant differences test was used to determine differences between treatments whenever analysis showed treatment effects to be statistically significant ($P < 0.05$). Split-plot ANOVA were carried out according to the actual statistical designs described previously. All statistical analyses of percentage seed germination and viability were undertaken on arcsine-transformed data, which were later back-transformed for display. In all ANOVA the statistical assumptions of normality and equality of variance were checked by inspecting the patterns in the residuals in data values from the fitted models.

Results

Experiment 1a – seed germination and viability under alternating day/night temperature regimes

A significant difference ($P < 0.001$) in seed germination was detected between alternating temperature regimes (Fig. 3*a*). At the lowest (11/7°C) temperature regime, nil germination was recorded. Germination commenced (<1%) at 16/12°C then rose steadily with increasing temperatures before peaking (average of 19%) between 37/31°C and 41/35°C. A decline in germination was observed as temperatures increased further, until nil occurred at 52/42°C.

Seed viability also differed significantly ($P < 0.001$) between alternating temperature regimes (Fig. 3*a*). Viability was highest (average 54%) at relatively cooler temperatures of 11/7°C and 16/12°C but then exhibited a gradual but variable decline uptil 47/39°C. It then dropped rapidly with nil viability recorded at 52/42°C. The differential response between viability and germination rates indicates that under all temperature regimes a portion of viable seeds exhibited dormancy. The proportion of dormant seeds was generally lower (11–31% of total seeds) under temperatures closer to the optimum for germination (between 29/24°C and 41/35°C) and higher (32–54% of total seeds) at the cooler and warmer temperature regimes (between 11/7°C to 24/20°C and 47/39°C).

Experiment 1b – seed germination and viability under constant temperature regimes

Overall, much lower germination and viability were recorded in the constant temperature experiment (Fig. 3*b*) compared with the alternating temperature experiment at the same mean temperatures (Fig. 3*a*). However, as for alternating temperatures, constant temperature regimes significantly affected ($P < 0.001$) germination of gamba grass seed (Fig. 3*b*). Although maximum germination (average 8.5%) occurred at a constant temperature of 24°C, there was no significant difference ($P < 0.05$) in germination between 17°C and 35°C. Outside of these temperatures, the level of germination was reduced significantly. At the lowest constant temperature of 13°C and temperatures >39°C, no germination was recorded.

Seed viability was highest (15%) at the lowest constant temperature of 13°C (Fig. 3*b*), before exhibiting a general decline with increasing temperatures thereafter. No viable seeds remained after 6 weeks once temperatures reached 43°C. As for alternating temperatures, a proportion of seeds remained

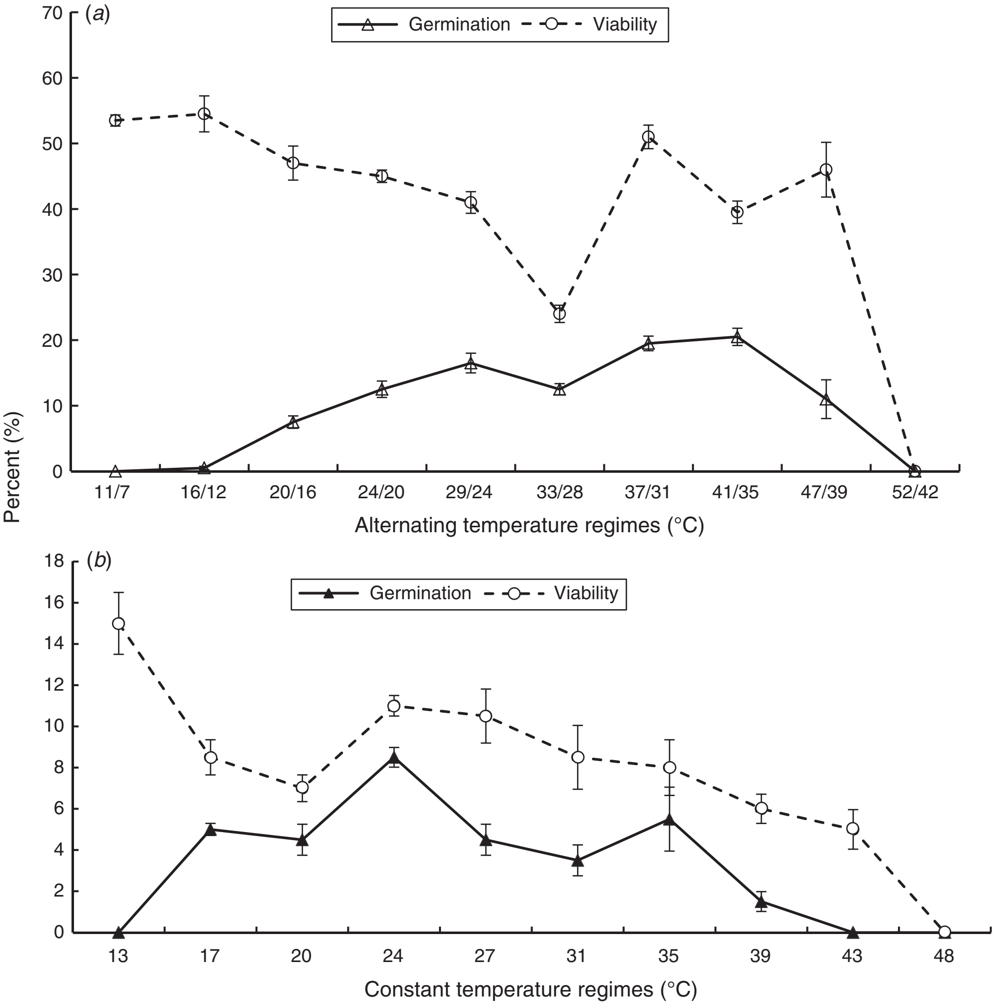

Fig. 3. Germination and viability response of gamba grass seed to (*a*) alternating and (*b*) constant temperature regimes. Vertical bars indicate the s.e. of the means.

dormant at all temperatures regimes, but more so at the cooler (13°C) and higher regimes (43°C) where 100% dormancy of viable seeds was recorded.

Experiment 2 – seed persistence

Seed germination

Initial seed germination averaged 58.6 ± 1.1% (Fig. 4*a*). Following burial, a significant interaction ($P < 0.05$) in germination was detected between burial depth and burial duration (Fig. 4*a*). Germination declined rapidly over the first three months across all treatments, but a greater proportion germinated after three months when buried at 10- and 20-cm depth (average of 11.5%) compared with those located on the soil surface or buried only 2.5 cm below ground (average of 3.5%). Thereafter germination remained low (<4% germination) at all burial depths until no germination was recorded at 30 months after burial.

Soil type also had a significant effect ($P < 0.001$), with germination slightly lower in clay soil (average of 8.9%) compared with river loam (average of 10.3%) when averaged across all burial durations, burial depths and levels of pasture cover. Pasture cover did not have a significant influence ($P < 0.05$) on germination.

Seed viability

Initial seed viability (percent of total seed number) averaged 64.3 ± 1.0% (Fig. 4*b*). Following burial, viability was significantly affected by burial duration ($P < 0.001$) (Fig. 4*b*) and burial depth ($P < 0.05$) (Fig. 5), with a significant soil type × level of pasture cover interaction ($P < 0.05$) also occurring (Fig. 6).

Seed viability rapidly declined with the duration of burial, averaging 10.7% after 3 months and was fully exhausted at the 30-month retrieval. Similar to germination, seeds located in the top 2.5 cm displayed significantly lower viability (average 9.7%) compared with seeds buried 10–20 cm below ground (average 13.5%) (Fig. 5). The level of pasture cover did not have a significant effect ($P < 0.05$) on seed viability in the river loam soil but in the clay soil viability was significantly ($P < 0.05$) reduced if pasture was excluded (average of 9.3%) compared with a full grass canopy (average of 13.4%) (Fig. 6).

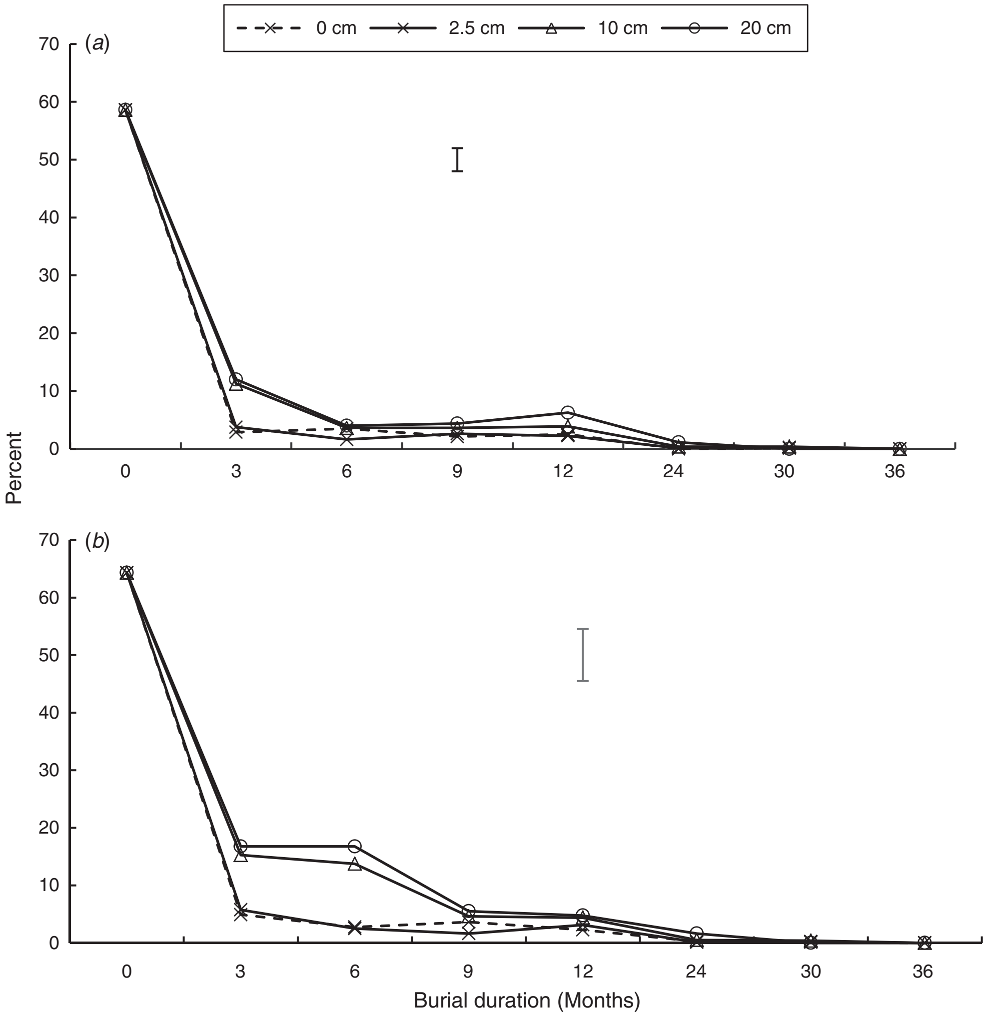

Fig. 4. (*a*) Germination and (*b*) viability response of gamba grass seed to burial duration and burial depth. Vertical bars indicate the l.s.d. at $P = 0.05$.

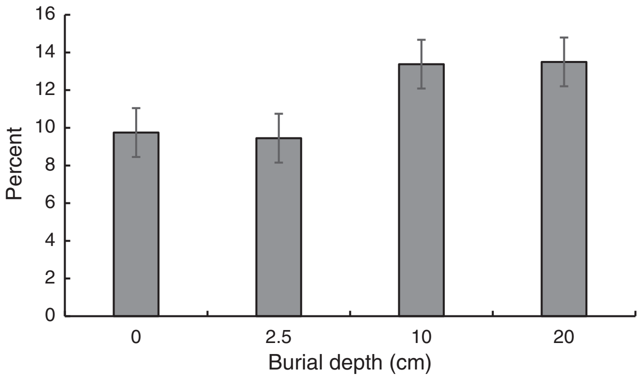

Fig. 5. Effect of burial depth on viability of gamba grass seed across all soil types, levels of pasture cover and burial duration. Vertical bars indicate the l.s.d. at $P = 0.05$.

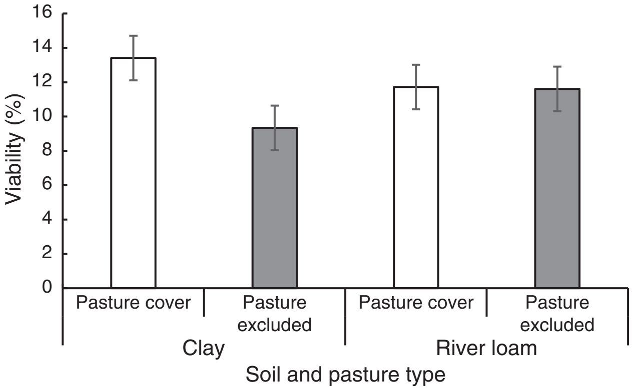

Fig. 6. Viability of gamba grass seed associated with soil type and pasture cover across all burial depth and burial duration. Vertical bars indicate the l.s.d. at $P = 0.05$.

Initial seed dormancy (viable less germinable) averaged 6%, but following burial the proportion of dormant seeds was 3-fold greater when seeds were buried deeper (10–20 cm) compared with surface located seeds.

Discussion

Gamba grass seeds remained viable and germinated across a broad temperature range, but under suboptimal temperatures a proportion lost viability or exhibited dormancy. The longevity of viable soil seed banks is affected by burial depth, with soil seed reserves fully depleted after 24 months in the Dry Tropics of northern Queensland.

Seed germination and viability

Fresh seed lots of gamba grass that were collected for the experiments in the present study exhibited moderate germination (44–58%) and viability (64–72%), the difference being the portion of seeds that were dormant. In general, these initial germination results concur with those of Harrison (1987) (40–70%). High germination has been reported for gamba seed in Thailand (average 73%) at 4–6 months post-harvest, which was attributed to high seed purity (Gobius *et al*. 2001). In terms of seed viability, in the Northern Territory Barrow (1995) reported 40–67% viability for seeds sourced from three locations, whereas Setterfield *et al*. (2004) reported 80% viability.

Fresh seeds of other perennial tropical and sub-tropical grasses including black spear grass [*Heteropogon contortus* (L.) P. Beauv. Ex Roem and Schult. and *H. triticeus* (R. Br. Stapf] showed similar seed viabilities (65 ± 3.6% and 70.0 ± 3.4%) to gamba grass but much lower germinability (1%) (McIvor and Reid 2011). Another Australian perennial grass, kangaroo grass (*Themeda triandra* Forssk.), also recorded greater seed viability (93 ± 1.3%) and relatively lower germinability (39 ± 3.5%) than gamba grass (McIvor and Reid 2011). Initial germination of other exotic perennial grasses including buffel grass, Indian bluegrass [*Bothriochloa pertusa* (L.) A. Camus] and red Natal grass [*Melinis repens* (Willd.) Zizka] were relatively lower (average 0%, 1% and 37%, respectively) than gamba grass whereas their viability was considerably higher (average 88%, 90% and 75%, respectively) (McIvor and Reid 2011). These species and gamba grass, along with several other perennial grasses such as giant rat's tail grass (*Sporobolus pyramidalis* Beauv.) and slender rat's tail grass (*S. elongatus* R.Br.) appear to have dormancy mechanisms that prevent all seeds germinating in one event. This provides multiple opportunities for germination to occur, ideally during the wet season and maximises seedling survival and establishment (Mott 1978; Lodge and Whalley 1981; Groves *et al*. 1982; Campbell 1995; Vogler and Bahnisch 2002, 2006; McIvor and Reid 2011). Seeds with low dormancy levels rely on frequent seed input rather than persistent soil seed banks for long-term survival (Keir and Vogler 2006).

In terms of germination temperature tolerance, the present study showed that gamba grass seeds have the potential to germinate across a wide range of constant (17°C–39°C) and alternating temperatures (16/12°C up to 47/39°C), although the level of germination declined at the lower and higher temperature ranges. Similarly, Mott (1978) compared the germination of five native grasses from tropical regions of the Northern Territory in Australia and found that all species had a germination range between ~9°C and 42°C. An early study on buffel grass found that it could germinate at temperatures between 10°C and 40°C (Andersen 1953). The much lower overall rates of germination and viability of seeds recorded in the constant temperature experiment compared with the alternating temperature trial was possibly due to differences in the temperature regimes.

By comparing the pattern of seed viability and seed germination at the various temperatures it was apparent that at the cooler temperatures, viability was not affected and that seeds remained in a state of dormancy. In fact, the highest level of seed viability was recorded at the lowest constant temperature regime (13°C) and at the two lowest alternating temperatures (11/7°C and 16/12°C), with viability declining at higher temperatures. At the higher temperature range (e.g. constant temperatures of 39°C–43°C and alternating temperatures of 47/39°C) both dormancy and loss of seed viability was occurring, and when alternating and constant temperatures rose above 47/39°C and 43°C all seeds were rendered unviable. Surface soil temperatures can exceed 50°C during the dry season in tropical and sub-tropical areas of Australia (Mott 1978; Mott *et al*. 1981; McKeon *et al*. 1985), which would cause surface located seeds of gamba grass to lose viability. Nevertheless, gamba grass's ability to maintain seed viability and go into a state of dormancy under unfavourable temperature conditions, highlights its ability to survive temperatures which occur in its invasive range. Seeds of other species such as *Coreopsis lanceolata* L. (Asteraceae) have exhibited similar behaviour when exposed to low temperatures (Banovetz and Scheiner 1994). This seed trait enables seeds to remain temporarily inactive and consequently protected until more favourable conditions occur (Baskin and Baskin 2001; Kos and Poschlod 2007).

Seed longevity

Seed longevity and persistence in soil seed banks can compensate for the effects of unfavourable environmental conditions on seedling germination over the long term (Gutterman 1994; Holmgren *et al*. 2006) and increase odds that viable seeds are available when conditions are optimal for recruitment. Seed banks are important for population persistence in ecosystems where opportunities for seedling establishment and disturbance are unpredictable (Baskin and Baskin 2001; Fenner and Thompson 2005).

Thompson *et al*. (1997) developed a key, which classifies seed longevity into three categories [transient (viable $\leq$1 year), short-term persistent (viable 1–5 year) and long-term persistent (viable $\geq$5 year)]. The findings from the present suggest that gamba grass has a short-term persistent seed bank. Despite falling into this category, gamba grass's seed bank persistence was markedly influenced by burial depth with seeds remaining viable for longer at burial depths >2.5 cm. However, across all burial depths, soil types and pasture cover, less than 1% of seed survived in the seed bank after 2 years with nil survival after two and a half years.

These results are in agreement with those reported earlier by Setterfield *et al*. (2004) and Flores *et al*. (2005) who assessed seed longevity of gamba grass over 12-month periods and found that survival rates were ~2.3% and less than 1%, respectively. Such similar responses indicate consistency across the broad provenances from where seeds were sourced. With gamba grass setting seed generally during the autumn–winter period (Rossiter *et al*. 2004; Western Australia Government 2017) soil seed bank decline would be greatest during the first wet season, if control activities prevented replenishment of soil seed reserves. Only a small percentage of seed may then be available to germinate over the subsequent wet season. This is consistent with the findings of several studies that monitored changes in gamba grass seed banks over time (Barrow 1995; Setterfield *et al*. 2004). At two savanna sites in the Northern Territory, Setterfield *et al*. (2004) found that seed banks of gamba grass that averaged 2100 seeds m^{-2} in June, declined to an average of 20 seeds m^{-2} by December. Similarly, Barrow (1995) reported that in disturbed monsoon vine thickets in the Northern Territory the seed bank declined to zero during the first wet season, but on a well drained rocky slope, the seed bank persisted over two wet seasons. This suggests that persistence of gamba grass seed banks varies with habitat, although Flores *et al*. (2005) buried seeds in both savanna and floodplain habitats in the Northern Territory and found similar patterns of decline over time.

The relatively greater seed persistence observed in buried seed of gamba grass has also been reported for other members of the grass family. Walker *et al*. (2006) found that burial increased seed longevity of barnyard grass [*Echinochloa colona* (L.) Link]. They reported that after 24 months, seeds buried at 10 cm below the soil surface retained 19% viability compared with 2% at 0–2-cm depth. The reason for the greater viability of gamba grass seed under pasture cover in the clay soil compared with no pasture cover is most likely associated with differences in environmental conditions created by the imposed treatments (e.g. temperature and/or soil moisture), but warrants further investigation.

Comparison of gamba grass seed bank longevity with some other invasive perennial grasses in Australia, suggests it is at the shorter end of the spectrum. For example, the seed longevity of olive hymenachne was reported to be >8 years (Stephen Setter, pers. comm. 2017) and viability of giant rat's tail grass was exhausted after 10 years (Wayne Vogler, pers. comm. 2017). Buffel grass seed longevity ranged between 2 and 30 years (Friedel *et al*. 2007) and seeds of Chilean needle grass [*Nassella neesiana* (Trin. and Rupr) Barkworth] survived in the soil in excess of 3 years (Gardener *et al*. 2003). Mission grass (*Pennisetum polystachion* L. Schult) is one species that appears to display similar persistence to gamba grass, with Setterfield *et al*. (2004) reporting a decline in viability from 82% to 0.1% after 12 months' burial.

Ecology and management implications

Although the current distribution of gamba grass is still relatively restricted (Adams and Setterfield 2016), its ability to germinate under a wide range of temperatures supports distribution modelling by Csurhes and Hannan-Jones (2008) that indicates it could continue to spread within the tropics of northern Australia and also move further south into sub-tropical areas. With seeds remaining viable but exhibiting dormancy under the lowest constant (13°C) and alternating temperature regimes (11/7°C) imposed in the present study, gamba grass also demonstrates an ability to delay germination until the onset of favourable environmental conditions. Consequently, in sub-tropical areas germination may be restricted to warmer months of the year, whereas in the tropics it could germinate all year round if there is adequate soil moisture. There are already some herbarium records of gamba grass in the sub-tropical Rockhampton area in central Queensland (AVH 2017). Predictive modelling of climate change scenarios suggest that areas such as this could become even more suitable (Csurhes 2005; Csurhes and Hannan-Jones 2008), particularly if anticipated increases in temperatures eventuate (Nicholls and Collins 2006).

The findings from the seed longevity trial have important implications for strategic management of gamba grass infestations that are the target of control or eradication programs. The success of weed control programs is greatly enhanced if soil seed banks are relatively short lived (Campbell and Grice 2000; Panetta 2004; Panetta *et al*. 2011; Dodd *et al*. 2015), which appears to be the case for gamba grass.

The present study along with previous reports indicates that seed banks should be exhausted within a two-year timeframe in the absence of replenishment from internal and/or external sources. Under the tropical conditions experienced in the present and past studies only a small portion of seed remained viable (≤2.3%) after 12 months although with slight differences between habitats (Barrow 1995; Setterfield *et al*. 2004; Flores *et al*. 2005). However, even at such low rates there is still potential for reestablishment given the high seed production of gamba grass that can result in large soil seed banks. Under non-grazed situations, gamba grass can produce from 15 000 up to 244 000 seeds per plant per annum (Flores *et al*. 2005) resulting in seed banks of between 42 and 3200 seeds m^{-2} depending on the habitat and prevailing climatic conditions (Barrow 1995; Setterfield *et al*. 2004).

Preventing replenishment of the seed bank may also prove difficult due to the dispersal mechanisms of gamba grass together with an ability to reproduce seed twice a year in some situations (DSEWPC 2011). There is also a limited range of effective control options and, given the difficult terrain in which some infestations occur, achieving complete control of all original plants may prove problematic, resulting in continual replenishment of soil seed banks.

With the potential for gamba grass to greatly expand its distribution (Adams and Setterfield 2016), implementation of prevention and early intervention strategies should be a high priority for land managers to stop new infestations from establishing before they have an opportunity to cause deleterious impacts on the environment and human health. If new outbreaks are found, initial treatment of plants followed by on-going monitoring and control of seedling regrowth for at least two years should allow these outbreaks to be successfully controlled. In some invaded areas it appears that the seed banks of native grass species can persist for longer than gamba grass, which may provide an opportunity for regeneration of native species to occur following implementation of control programs on gamba grass (Setterfield *et al*. 2004).

Conflict of Interest

The authors declare no conflicts of interest.

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