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Seed bank longevity and age to reproductive maturity of *Calotropis procera* (Aiton) W.T. Aiton in the dry tropics of northern Queensland

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Abstract. Understanding the reproductive biology of *Calotropis procera* (Aiton) W.T. Aiton, an invasive weed of northern Australia, is critical for development of effective management strategies. Two experiments are reported on. In Experiment 1 seed longevity of *C. procera* seeds, exposed to different soil type (clay and river loam), pasture cover (present and absent) and burial depth (0, 2.5, 10 and 20 cm) treatments were examined. In Experiment 2 time to reach reproductive maturity was studied. The latter experiment included its sister species, *C. gigantea* (L.) W.T. Aiton, for comparison and two separate seed lots were tested in 2009 and 2012 to determine if exposure to different environmental conditions would influence persistence. Both seed lots demonstrated a rapid decline in viability over the first 3 months and declined to zero between 15 and 24 months after burial. In Experiment 1, longevity appeared to be most influenced by rainfall patterns and associated soil moisture, burial depth and soil type, but not the level of pasture cover. Experiment 2 showed that both *C. procera* and *C. gigantea* plants could flower once they had reached an average height of 85 cm. However, they differed significantly in terms of basal diameter at first flowering with *C. gigantea* significantly smaller (31 mm) than *C. procera* (45 mm). On average, *C. gigantea* flowered earlier (125 days vs 190 days) and set seed earlier (359 days vs 412 days) than *C. procera*. These results suggest that, under similar conditions to those that prevailed in the present studies, land managers could potentially achieve effective control of patches of *C. procera* in 2 years if they are able to kill all original plants and treat seedling regrowth frequently enough to prevent it reaching reproductive maturity. This suggested control strategy is based on the proviso that replenishment of the seed bank is not occurring from external sources (e.g. wind and water dispersal).

Additional keywords: calotrope, giant rubber bush, reproductive maturity, rubber bush, seed persistence, seed viability.

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Introduction

Calotropis procera (Aiton) W.T. Aiton is a native species of tropical Africa, Arabia and Asia (Everist 1974; Forster 1992). It has become naturalised in South Africa, Australia, South-western USA, Mexico, Pacific and Caribbean Islands, Venezuela, Brazil and Paraguay (Holm *et al*. 1979; Parsons and Cuthbertson 2001; Weber 2003). In Australia, it is most commonly known as calotrope or rubber bush, and is believed to have been introduced as a garden plant or from seed in packing of Afghan cameleers' equipment (Hall 1967; Smith 2011). It has become naturalised in several areas in north Queensland, the Northern Territory and the Kimberley region of Western Australia (Gardner and Bennetts 1956; Chippendale and Murray 1963; Everist 1974; Forster 1992; Department of Agriculture, Fisheries and Forestry 2013).

Most reproduction of *C. procera* is from seeds which have a silky pappus which not only facilitates wind-dispersal over several hundred metres (Francis 2002; Staples and Herbst 2005) but also flotation in water thus promoting dispersal along water bodies, including irrigation and drainage channels (Brandao 1995).

Three species of *Calotropis* have been reported in the literature – *C. procera*, *C. gigantea* (giant rubber bush) and *C. acia* Buch-Ham (Ali 1980; Rahman and Wilcock 1991). In India, three varieties of *C. procera* (Rajarkah, Suklarkah and Sveta mandarah) have been identified in the region of Dhanvantari Nigantu (Sharma *et al*. 2011). Although both *C. procera* and *C. gigantea* are commonly found in Australia (Forster 1992; Parsons and Cuthbertson 2001; Smith 2011; Discover Nature at JCU 2013), there have been no reports of different varieties being present.

In Australia, *C. procera* is considered an invasive weed that threatens the sustainability of pasture production, particularly in the dry tropics of north Queensland (Kleinschmidt and Johnson 1977; Forster 1992; Martin 1996; Vitelli *et al*. 2008; Campbell *et al*. 2013), in the Northern Territory (Miller 2003) and in Western Australia in the Kimberley region (Forster 1992; Smith 2011). It has the ability to form dense infestations, which are difficult and costly to control (Grace 2006; Vitelli *et al*. 2008). Adoption of pasture management practices that promote perennial grasses (Crothers and Newbound 1998; Milson 2000; Parsons and Cuthbertson 2001), in conjunction with chemical control is a recommended strategy for management of *C. procera* invading the tropical savannahs of northern Australia (Vitelli *et al*. 2008). Currently available information on the ecology and biology of *C. procera* does not allow an assessment of how frequently control activities would need to be undertaken and for what duration to achieve effective control.

Parsons and Cuthbertson (2001) tentatively suggested that *C. procera* flowers once plants are 2 years old. Long *et al*. (2008) predicted that seeds would persist for between 1 and 3 years, after *C. procera* was subjected to a laboratory-based, controlled-aging test along with 12 other emerging and common weeds of Queensland. To test these assumptions/predictions, two experiments were undertaken. Experiment 1 determined the effect of soil type, pasture cover and burial depth on seed longevity of fresh seeds of *C. procera* and was repeated to test the influence of different environmental conditions, particularly soil moisture. Experiment 2 determined the age to reproductive maturity (flowering and seed production) of both *C. procera* and its sister species, *C. gigantea* (L.) W.T. Aiton]. *Calotropis gigantea* was included for comparison with *C. procera*, to gain an insight into the relative invasiveness of these two species, which appear capable of growing in similar environments in the dry tropics of northern Australia (Dunlop 1987; Forster 1992; Parsons and Cuthbertson 2001; Smith 2011; Discover Nature at JCU 2013).

Materials and methods

Experiment 1: seed longevity

Site description

The experimental site (38 m × 36 m) was located in the grounds of the Tropical Weeds Research Centre, Charters Towers, north Queensland (20°09′S, 146°26′E; elevation 318 m). It was large enough for the longevity of up to 12 different seed lots of various weed species to be tested at any one time under the same treatment conditions.

The site was fenced to exclude livestock, rabbits and kangaroos. It had been previously cleared of woody vegetation and had a ground cover that comprised buffel grass [*Cenchrus ciliaris* L.], 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 76% of this occurring during the summer months (December–February) (BOM 2012). The mean maximum daily temperature ranges in summer between 32.6°C and 34.8°C and in winter (June–August) between 24.8°C and 26.6°C. Specific details on rainfall and ambient temperature at the field site during the study were measured using an on-site automatic weather station (Campbell Scientific, Logan, UT, USA).

Seed collection

An initial collection of ripe follicles of *C. procera* was undertaken in December 2008 from two locations: 43 km south-east (20°13′S, 146°38′E) and 15 km north-west of Charters Towers (19°59′S, 146°30′E). Follicles were placed in jackets of aluminium mosquito gauze (1 m^2) to dry for 2 weeks in a dry glasshouse before seeds were extracted and pooled. Six-hundred and forty subsamples of 50 seeds were then randomly selected and placed in bags of shade cloth (4 cm × 4 cm × 0.5 cm; 1.1 mm × 2.4 mm mesh size) to simplify seed retrieval while maximising soil/seed contact.

A second seed collection of ripe follicles was undertaken in October 2011 from an infestation of *C. procera* located in the Gulf of Carpentaria Region (18°13′S, 140°38′E), 820 km north-west of Charters Towers. The same procedure as that used for the initial seed collection was followed for selection and containment of seed lots.

Experimental design

A factorial combination of 2 soil types × 2 pasture levels × 9 retrieval times × 4 seed burial depths was implemented in four blocks in a multiple split-plot design as described in the following paragraphs.

The main plot treatments were established in March 2008 by digging eight trenches (1.0 m wide × 0.5 m deep × 36 m long) 2 m apart. The soil/landform into which the trenches were dug was heavy clay loam. The trenches were then grouped into four blocks, each comprising two neighbouring trenches. In each block, one trench was randomly filled with river loam and the other with clay soil that had been collected in the vicinity of Charters Towers. These soils are common soil types in the vicinity of Charters Towers on which *C. procera* can occur.

To establish the subplots, half of each trench (i.e. 18 m) was randomly allocated to be kept bare (i.e. pasture excluded) through physical removal of all vegetation whereas the other half was allowed to revegetate from the local seed bank and encroachment from the 2-m buffer strips. After 6 months (September 2008), the revegetated portions (i.e. pasture present) had a dense cover of pasture that was ~40–50 cm high.

The pasture present and pasture excluded portions of each trench were divided into 12 1-m-long by 1-m-wide sections with a 50-cm buffer in between, to enable longevity testing of up to 12 seed lots of various weed species at any one time. For both the first and second seed lots of *C. procera*, subplots were implemented by first randomly selecting one of the 1-m-long sections in both the pasture present and pasture excluded portions of each trench. Within this 1-m-long × 1-m-wide section of trench, nine 12–15-cm-diameter cylindrical holes were dug to a depth of 30 cm using a manually operated auger. They were positioned so that there were three rows each containing three holes, equal distances apart. Each hole was randomly allocated one of nine retrieval dates. These holes were then filled with a cylindrical PVC pipe (11 cm in diameter × 30 cm in height) containing seed bags that had been buried at the designated burial depths using the same soil within respective trenches. Seed lots randomly selected to be tested at time zero were not buried, but directly subjected to germination and viability testing.

The PVC pipes were perforated at the base and also had four holes drilled on the sides to allow for drainage. Blotting paper was placed at the base and in the holes to prevent soil loss but allow free drainage. Pipes were systematically filled on site using ~6.5 kg of soil, with a bag of seeds placed at depths of 0, 2.5, 10 and 20 cm. The top of the PVC pipe was then covered with rabbit mesh wire to prevent loss of bags containing seeds placed on the soil surface (0 cm in depth). Sensors connected to two separate data loggers (DT85 model – Data Electronics Pty Ltd, Brisbane, Qld, Australia) were inserted at each burial depth in dummy PVC pipes that were buried at the head of each soil trench to monitor soil temperature (Type K steel encased thermocouples) and soil moisture (SM200) on an hourly basis.

The first seed lot of *C. procera* was buried in March 2009 with retrievals designated to occur 3, 6, 12, 18, 24, 36, 48, 60 and 72 months after burial or until no viable seeds were recorded for two consecutive retrievals. The second seed lot was buried in January 2012, with retrievals designated to occur 3, 6, 12, 15, 18, 24, 36, 48 and 60 months after burial. On each retrieval date, one PVC pipe from each replicate of the 16 soil type × pasture cover plots was randomly retrieved. The bags containing buried seeds were then removed from the PVC pipes and washed gently to remove attached soil particles.

Germination and viability testing

To determine ‘germinability’, remaining intact seeds were removed from the bags and 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 placed into a growth cabinet set at 30°C/20°C day/night with alternating 12 h of light and dark. Germinable seeds (identified by radicle emergence) were counted and removed daily for 14 days. Seeds that did not germinate were checked for dormancy using the tetrazolium method (Moore 1985). Seed viability (germinable + dormant) was expressed as a per cent of total seeds initially buried.

At the 3-month retrieval, the number of seeds that germinated in the packets was also recorded by counting emerged seedlings. However, this was not possible in later retrievals due to disintegration of emerged seedlings.

Experiment 2: days to flowering and seed production, plant height and basal diameter

The experiment was conducted at the Tropical Weeds Research Centre between September 2006 and December 2008. A completely randomised design with six replications was used to grow single plants of *C. procera* and *C. gigantea* in plastic pots (40 cm in diameter × 40 cm in depth) filled with garden soil potting mix. Pots were regularly watered to field capacity. Seeds of both *C. procera* and *C. gigantea* were collected in August 2006 and came from pods near the Gregory River (Fig. 1) in the Gulf of Carpentaria (18°57′S, 139°27′E). Three seeds of *C. procera* and *C. gigantea* were initially sown and seedlings were subsequently thinned 3 weeks after emergence to one plant per pot. Number of seeds per pod of *C. procera* and *C. gigantea* averaged 486 ± 10.1 ($n = 14$) and 127 ± 12.2 ($n = 14$), respectively.

Plant height (cm) and basal diameter (mm) at flowering and seed production (when first swollen follicle was observed) were recorded for each plant, along with days to flowering and seed production.

Data analyses

Genstat was used for all statistical analyses (Genstat 8.1, VSN International, Hemel Hempstead, Hertfordshire, UK) and Fisher’s least significant differences test was used to determine differences between treatments whenever analysis showed

Fig. 1. Distinct follicle size and shape and inflorescences colour and form of *C. procera* (back) and *C. gigantea* (front).

treatment effects to be statistically significant ($P < 0.05$). All statistical analysis concerning seed germination and viability was undertaken on arcsine-transformed data, which was later back-transformed for display.

In Experiment 1, viability data was analysed using a multiple split-plot ANOVA as dictated by the experimental design: 4 blocks × 2 soil types split for 2 pasture levels split for 9 retrieval times split for 4 burial depths. All other data was only analysed at a single time (i.e. germination at 3 months) or was an average over time (i.e. soil moisture content and temperature), and was thus subjected to an analysis of 4 blocks × 2 soil types split for 2 pasture levels split for 4 burial depths.

For Experiment 2, all measurements undertaken on *C. procera* and *C. gigantea* were subjected to one-way ANOVA using a completely randomised design.

Results

Experiment 1 – seed longevity

Rainfall and soil moisture

Annual rainfall, recorded at the site between 2009 and 2012, was consistently greater than the long-term mean for Charters Towers (658 mm), averaging 1105, 1323, 1037, 832 mm per annum, respectively. For the first 5 months of 2013 before the second seed lot finished being tested in May 2013, 452 mm of rainfall was recorded (Fig. 2).

Despite high annual rainfall, the first and second seed lots were exposed to different seasonal patterns of rainfall, particularly in the first 12 months, which was a critical period in the longevity of soil seed banks of *C. procera*. After burial in March 2009, the first seed lot received 118 mm of rainfall for the remainder of the autumn period. This was followed by a very dry winter and spring period where only 21 mm of rainfall were recorded, before the onset of a wet summer where 493 mm fell. In contrast, the second seed lot buried in January 2012 received 218 mm of rainfall in February followed by 319 mm during autumn. Even the winter period received high rainfall with 189 mm being recorded. However, the following spring was dry (32 mm) and summer rainfall was below average, with 294 mm recorded (Fig. 2).

The prevailing rainfall resulted in no significant difference ($P > 0.05$) in average daily proportion of soil moisture content conditions between the first and second seed lots (average of 0.1%), when calculated for the full duration of burial. However, during the first 3 months when rainfall patterns differed markedly and major reductions in seed viability occurred, average proportion of daily soil moisture content was significantly higher ($P < 0.01$) for the second seed lot than the first one, averaging 0.14 and 0.08, respectively.

Soil type, pasture cover and soil depth did not have a significant effect ($P > 0.05$) on average daily soil moisture content for the first and second seed lots, when calculated for the full duration of burial. If calculated for the first 3 months of burial when major changes in viability occurred, there was no significant difference ($P > 0.05$) during testing of the second seed lot, but a significant soil type × pasture cover interaction ($P < 0.05$) occurred during testing of the first seed lot. The clay soil had consistently higher soil moisture content than the river loam and the pasture-excluded plots had higher soil moisture contents than those where pasture was present, with differences greatest in the clay soil treatment (Fig. 3).

Temperature conditions

The second seed lot was exposed to slightly higher (26.8°C) average daily soil temperatures than the first seed lot (26.3°C) when averaged across all soil types, levels of pasture cover and burial depths ($P < 0.05$). During burial of both seed lots, soil type did not have a significant effect ($P > 0.05$) on average daily soil temperatures, but both the level of pasture cover and burial depth did ($P < 0.05$). Temperatures were higher in the absence of pasture

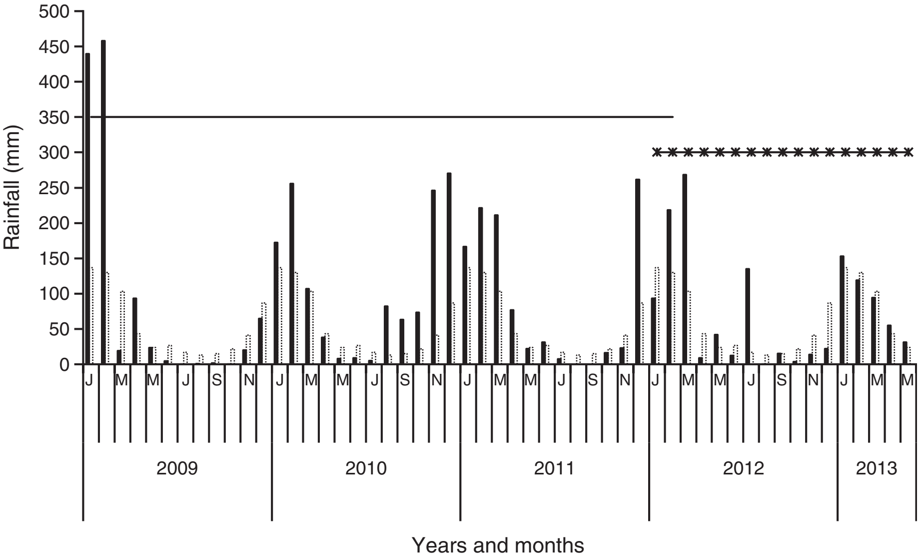

Fig. 2. Monthly rainfall (■ mm) at the research site between March 2009 and May 2013, and the average monthly rainfall (□ mm) for Charters Towers associated with burial duration for seed lot 1(_____) and seed lot 2 (****).

cover (Fig. 4) and there was a positive correlation between average daily soil temperature and burial depth ($r = 0.98$) (Fig. 4).

Seed viability

First seed lot. Initial seed viability and germinability was high, averaging 85.0 ± 2.4% (per cent of total seed number) and 100% (per cent of viable seeds), respectively. Following burial, significant burial depth × burial duration ($P < 0.001$) and soil type × burial duration ($P < 0.01$) interactions were recorded for seed viability. In contrast, the level of pasture cover did not have a significant influence ($P > 0.05$) on seed viability over time.

Viability declined most rapidly in the first 3 months, particularly in seed lots that were buried. After 6 months, <1% of buried seeds remained viable, compared with 28% of surface-located seeds (Fig. 5). This rapid decline in viability coincided with high germination of seeds in the field in the first 3 months after burial. On average, 92% of seeds germinated within 3 months if buried, significantly more ($P < 0.05$) than surface-located seeds, which averaged only 38% (Fig. 6). No viable seeds were retrieved from buried seed lots after 18 months, whereas surface-located seed lots had no viable seed after 24 months.

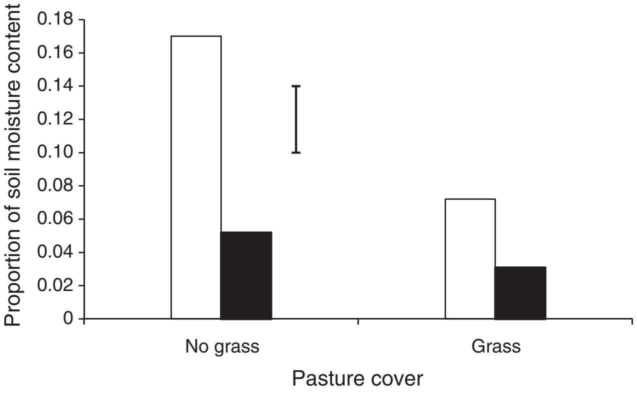

Fig. 3. Average proportion of daily soil moisture content recorded during the first 3 months of burial of the first seed lot, as affected by soil type (clay ☐ and river loam ■) and level of pasture cover. Vertical bar indicates the least significant difference at $P = 0.05$.

With regards soil type, a more rapid rate of decline in viability occurred in the clay soil compared with the river loam soil (Fig. 7). No viable seeds were retrieved from the clay soil after 18 months, whereas nil viability was recorded in the river loam soil at the 24-month retrieval.

Second seed lot. Initial seed viability and germinability was extremely high, averaging 99.5 ± 0.1% (per cent of total seed number) and 100% (per cent of viable seeds), respectively. Following burial, viability was significantly affected by burial duration ($P < 0.05$), but not by soil type, pasture cover or burial depth ($P = 0.93$). The rate of decline in viability was faster than that of the first seed lot tested.

After 3 months, no viable seed was recorded across all burial depths, soil types and pasture cover treatments. However, subsequent 6- and 12-month assessments recorded 0.1% viability. No viable seeds were retrieved from any seed lots 15, 18 or 24 months after burial. As for the first seed lot, the rapid decline in viability was associated with a high percentage of seeds germinating in the field, particularly those buried below ground. Surface-located seeds averaged 82% germination after 3 months compared with 99% for those buried between 2.5 and 20 cm (Fig. 6).

Experiment 2 – days to flowering and seed production, plant height and basal diameter

Plant height and basal diameter at flowering

Plant height at flowering did not differ significantly between *C. procera* and *C. gigantea* ($P > 0.05$), averaging 85 ± 2 cm. In contrast, *C. procera* had a significantly larger ($P < 0.05$) basal diameter at flowering than *C. gigantea*, averaging 45 mm and 31 mm, respectively.

Days to flowering and seed production,

Significant differences ($P < 0.05$) in days to flowering occurred between *C. procera* and *C. gigantea* (Fig. 8). Plants of

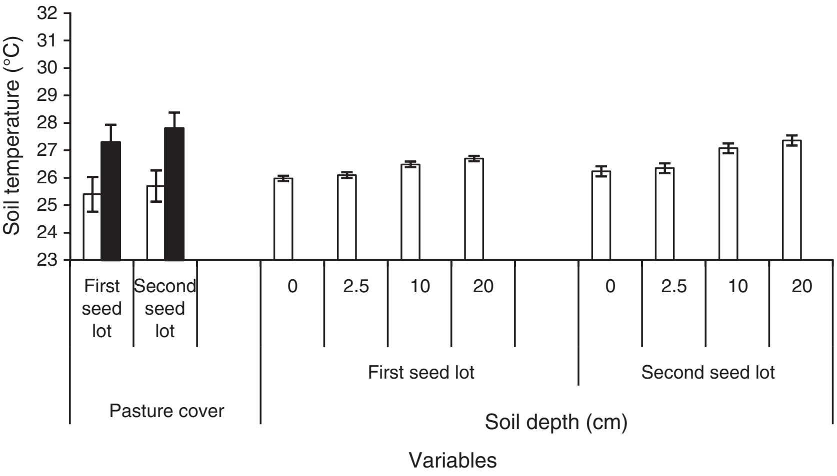

Fig. 4. Average daily soil temperature (°C) recorded during burial of the first and second seed lots, as affected by pasture cover (☐ present and ■ absent) and soil depth. Vertical bars indicate the least significant difference at $P = 0.05$.

C. gigantea took between 116 and 146 days to flower (average, 125 days) after germination, whereas *C. procera* took between 125 and 250 days (average, 190 days). Similarly, days to seed production differed significantly ($P < 0.05$), with *C. gigantea* producing seed between 352 and 365 days after germination (average, 359 days), compared with 399–425 days for *C. procera* (average, 412 days).

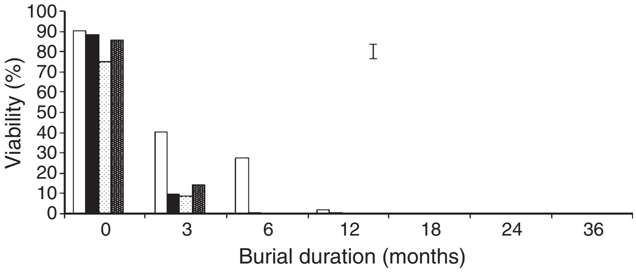

Fig. 5. Viability (%) at the time of testing of the first seed lot of *C. procera* as affected by burial depth (□ 0 cm, ■ 2.5 cm, ⬚ 10 cm and ▩ 20 cm) and burial duration. Vertical bars indicate the least significant difference at $P = 0.05$.

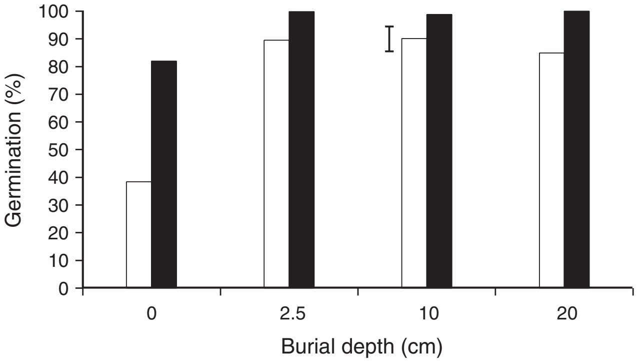

Fig. 6. The proportion (%) of the first (□) and second (■) seeds lot of *C. procera* that germinated in the field at different depths, 3 months after burial. Vertical bar indicates the least significant difference at $P = 0.05$.

Discussion

Under the prevailing environmental conditions experienced during the study, seed longevity of *C. procera* was relatively short (15–24 months) and young plants demonstrated the potential to flower and produce seeds within 6 and 14 months, respectively.

Seed longevity

Based on a dichotomous key, developed by Thompson *et al.* (1997) and which classifies seed longevity into three categories [transient (viable ≤1 year), short-term persistent (viable 1–5 year) and long-term persistent (viable ≥5 year)], our results suggest that *C. procera* has a short-term persistent seed bank depending on prevailing conditions. This is consistent with the earlier prediction of Long *et al.* (2008), who suggested that seeds would persist for between 1 and 3 years.

Germination and viability testing revealed that the seeds of *C. procera* had high viability and germinability, and should, therefore, readily germinate under favourable field conditions. Francis (2002) reported a similar finding with 89% germination recorded 64 days after sowing seeds in a potting mix. Similarly, Leal *et al.* (2013) recorded greater than 95% germination in fresh seeds after 35 days from two populations in north-eastern Brazil.

Calotropis procera seeds readily germinated after rainfall with an associated rapid decline in the proportion of viable seeds remaining over time. This was most evident in the second seed lot tested where <1% viability was recorded after 3 months. These seeds received much more rainfall in the first 3 months after burial than the first seed lot, and consequently would have had more favourable conditions for germination to occur. This differential response between the two seed lots highlights the influence of

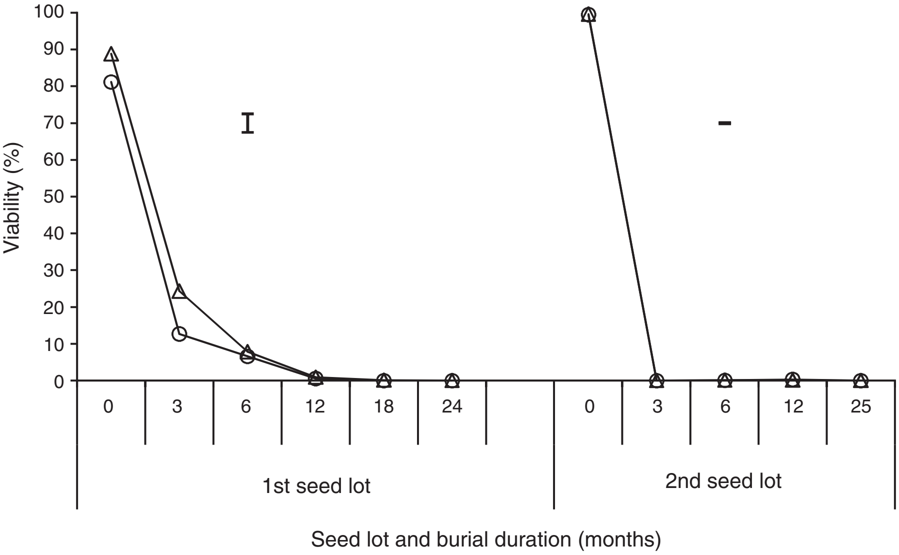

Fig. 7. Viability of the first and second seed lots of *C. procera* as affected by soil type (○ clay and △ river loam) and burial duration. Vertical bars indicate the least significant difference at $P = 0.05$.

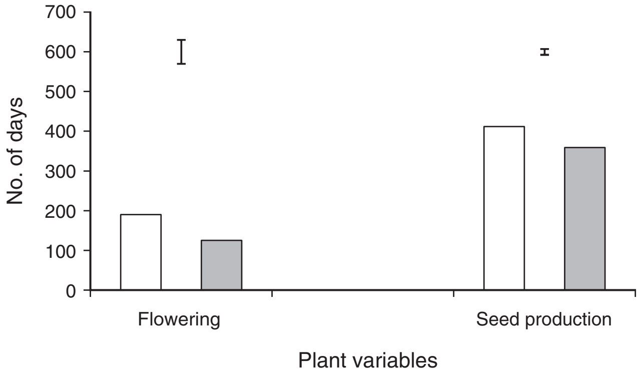

Fig. 8. Average days from the emergence of the first seedling to flowering and seed production of *C. procera* (□) and *C. gigantea* (▨). Vertical bars indicate the least significant difference at $P = 0.05$.

prevailing environmental conditions on seed longevity, as reported previously (Chambers and MacMahon 1994; Baskin and Baskin 2001). Given that both seed lots were tested during above-average rainfall conditions, it is feasible that seed banks of *C. procera* could persist for longer during droughts due to fewer opportunities to germinate and this warrants investigation. Studies on *Lantana camara* L. (lantana) and *Jatropha gossypiifolia* L. (bellyache bush) have highlighted major differences in the persistence of soil seed banks due to soil moisture availability. Vivian-Smith and Panetta (2009) predicted that the longevity of soil seed banks of *L. camara* could be reduced by 8 years under high soil moisture content conditions when compared with sites that received natural seasonal rainfall. Similarly, a rainfall-exclusion experiment found that the longevity of seed banks of *J. gossypiifolia* could be extended from ~3 to 4 years under natural rainfall conditions to greater than 10 years in the absence of rainfall (Bebawi *et al*. 2012).

The more rapid decline in viability of the first seed lot when buried in clay soils compared with loams is also most likely due to differences in soil moisture content. The clay soil had higher average daily soil moisture content than the river loam during the first 3 months (autumn) of the experiment, before going into a dry winter. This would have provided more favourable conditions for germination of *C. procera* seed that was in a highly germinable state at the time. A similar occurrence was reported for *J. gossypiifolia*, whose seed bank was depleted quicker due to greater seedling emergence under the higher soil moisture conditions in a clay soil compared with a red duplex soil (Bebawi *et al*. 2012). A more rapid decline in viability of seeds, located below ground compared with those on the surface, has also been reported for other weeds (Panetta 2001; Bebawi *et al*. 2012) and often attributed to greater soil moisture availability, although there are several factors that could have an influence such as seed-soil contact, such as aeration, light availability, temperature and dormancy (Bekker *et al*. 1998; Benvenuti *et al*. 2001; Harrison *et al*. 2007; Vivian-Smith and Panetta 2009). In our study, differences in average daily soil moisture between surface-located seeds and those buried below ground were not detected during testing of either seed lots, but this may have been associated with placement of the sensors, which had to be partially buried to keep them in place.

The high germination of *C. procera* under the prevailing temperatures of the present study was consistent with those reported in a Brazilian study (Labouriau and Valadares 1976), where germination was highest between 23°C and 33°C. It is plausible that longevity could be extended in areas that receive periods of extreme temperatures (too hot or cold) that may prevent germination. For example, Labouriau and Valadares (1976) recorded little germination once temperatures reached 34°C or above. Besides these potential inhibitory effects, surface seeds exposed to very high temperatures in summer could possibly lose viability. Ooi *et al*. (2009) indicated that soil temperatures, which increase as a result of global warming, may approach thresholds for seed death in ecosystems where high temperatures are already apparent. They found that, among other plant species, the initial viability of the physically dormant seeds of *Tephrosia sphaerospora* F. Muell. (Fabaceae) declined rapidly from almost 100% to 58% after 70 days exposure to high predicted soil temperatures (70/25°C).

The ability of *C. procera* to germinate in the field at depth suggests that light is not necessary and is consistent with findings from Leal *et al*. (2013) who reported high germination under a range of light intensities ranging from 0% to 100%. However, the general location of seeds of *C. procera* in the soil profile has not been clarified in this study, nor has the ability of seedlings to emerge from depth.

It is important to note that, although the seed lots used in this study exhibited high germinability, the literature does report limited instances of low-level dormancy in *C. procera*. Between 2% and 35% of *C. procera* seeds collected from an Indian population (Amritphale *et al*. 1984) and up to 6% from a Brazil population were reported to be dormant (Labouriau and Valadares 1976). The presence of dormancy may prolong the longevity of seed banks of *C. procera* beyond those reported in the present study.

Flowering and seed production

The average time taken for *C. procera* to produce seeds in the present study was slightly less (412 days) than the 2 years suggested by Parsons and Cuthbertson (2001). Plants did, however, have access to abundant soil moisture and differential responses could occur under drier field conditions or due to different levels of competition from desirable native and/or pasture species. The large lag time observed between flowering and seed production also warrants further consideration to determine whether this is a normal occurrence or not. It was much longer for *C. procera* than for *C. gigantea* (190 days vs 125 days) and was the main reason for the large difference between these two species in the time taken for plants to reach the seed production stage. Both species rely on insect pollination for reproduction (Wanntorp 1974; Ramakrishna and Arekal 1979; Morse 1981; Eisikowitch 1986; Ali and Ali 1989; Grace 2006) and perhaps differences in availability of pollinators could influence when flowers are fertilised and pod production occurs. Additionally, differences in pod size and number of seeds produced per pod may also explain differences between these two species in time taken to reach reproductive maturity, as more time will be required by *C. procera* compared with *C. gigantea* to produce the higher energy requirements (given similar photosynthetic area). It is also likely that the prolific production of seeds by *C. procera* (485.7 ± 10.1) compared with *C. gigantea* (126.5 ± 12.2) may be contributing to the pre-dominance of the former in the Australian rangelands.

Management implications

The short longevity of seeds of *C. procera* highlights the vulnerability of this species in terms of its soil seed bank, which makes it highly amenable for control and possible eradication from an area. It is notable that the apparently successful eradication program targeting a very large incursion of kochia [*Bassia scoparia* (L.) A.J.Scott] in Western Australia has involved a species whose seeds are short-lived (Dodd and Randall 2002).

Based on the findings of the present study, land managers controlling *C. procera* can expect a high density of seedling regrowth in the first 12 months under average or above-average rainfall conditions. If this seedling regrowth is treated along with any original plants that may have been missed or not controlled effectively, little germination should occur as the resident soil seed bank should be very low thereafter. In terms of the frequency of control activities, annual surveillance and treatment of plants should be sufficient in most years to prevent new plants from producing seeds and replenishing soil seed banks. However, as both *Calotropis* species investigated in this study produced seed as early as September (spring), it would be advisable to commence control operations at the onset of spring.

Given its dispersal mainly by wind and water, there is a risk that seed dispersal from neighbouring areas or external sources could occur resulting in ongoing recruitment. This will be particularly pertinent for land managers with large infestations that cannot all be controlled at the same time.

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