Seed bank persistence and germination of chinee apple (*Ziziphus mauritiana* Lam.)

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Abstract. Chinee apple (*Ziziphus mauritiana* Lam.) is a thorny tree that is invading tropical woodlands of northern Australia. The present study reports three experiments related to the seed dynamics of chinee apple. Experiment 1 and 2 investigated persistence of seed lots under different soil types (clay and river loam), levels of pasture cover (present or absent) and burial depths (0, 2.5, 10 and 20 cm). Experiment 3 determined the germination response of chinee apple seeds to a range of alternating day/night temperatures (11/6°C up to 52/40°C). In the longevity experiments (Expts 1 and 2), burial depth, soil type and burial duration significantly affected viability. Burial depth had the greatest influence, with surface located seeds generally persisting for longer than those buried below ground. Even so, no viable seeds remained after 18 and 24 months in the first and second experiment, respectively. In Expt 3 seeds of chinee apple germinated under a wide range of alternating day/night temperatures ranging from 16/12°C to 47 /36°C. Optimal germination (77%) occurred at 33/27°C and no seeds germinated at either of the lowest (11/6°C) or highest (52/40°C) temperature regimes tested. These findings indicated that chinee apple has the potential to expand its current distribution to cooler areas of Australia. Control practices need to be undertaken for at least two years to exhaust the seed bank.

Additional keywords: burial depth, germination requirements, Indian jujube, seed longevity.

Received 29 September 2015, accepted 15 January 2016, published online 17 February 2016

Introduction

Ziziphus mauritiana Lam. (Rhamnaceae), commonly known as chinee apple or Indian jujube, is a native tree of Southern Asia and Tropical Africa (Huwale 1985; Grice 1996; Orwa *et al*. 2009; CABI 2014) but is also found in arid and semiarid tracts of the Americas and Australasia (World Agroforestry Centre 2002). It was introduced into northern Australia in 1863, where its current distribution appears to be associated with early settlements in northern parts of Queensland, the Northern Territory and Western Australia (Grice 1996; Grice *et al*. 2000; Land Protection 2006; Grice *et al*. 2008; Anon. 2014*a*).

Chinee apple is a long-lived (several decades) deciduous tree with single or multi-stems that are intricately branched and contain unequal stipular spines (Grice 2002, 2009; Anon. 2014*b*). Plants can grow up to 8 m high with a spreading canopy up to 10 m across (Grice *et al*. 2000; Orwa *et al*. 2009; Anon. 2014*a*, 2014*b*). It has a deep and lateral root system and can reproduce vegetatively from root suckers (Weber 2003). Plants flower from late summer to early winter and seed dispersal is seasonal and generally occurs in winter (June–August) and early spring (September) (Grice *et al*. 2008; Grice 2009; Anon. 2014*c*). Fruits of chinee apple are 3–5 cm long, fleshy, edible, rounded and

reddish–brown when ripe. The endocarp (kernel) normally contains two seeds (Orwa *et al*. 2009).

Large trees are prolific fruit producers, with individual plants producing more than 5000 fruits per year (Schirarend 1991; Grice 1996) and infestations up to 18 000 fruits per hectare per year (Grice 1996). Greatest fruit production tends to occur in seasons with higher rainfall (Schirarend 1991; Grice 1996). Under natural conditions in India, chinee apple usually fruits well every year from the age of three years (Singh 1989).

Fruits are dispersed by several species of birds, domestic and wild animals and humans (Noble 1975, 1991; Gardiner and Gardiner 1996; Grice 1996; Grice *et al*. 2008). Intact kernels are dispersed following ingestion by cattle, goats, donkeys, horses, camels, sheep, macropods, antelopes, feral pigs, wallabies, bustards (*Ardeotis australis*) and other birds in addition to deliberate historical plantings by humans for shade or for fruit (Grice 1996; Grice *et al*. 2008; Grice 2009).

The fruit consists of a leathery exocarp, a fleshy mesocarp and a woody irregularly furrowed endocarp known as the 'kernel', which in most cases encloses two rounded, dark-brown seeds. The kernel is known to inhibit germination in fresh seeds (Hocking 1993; Grice 1996; Maraghni *et al*. 2010; Anon. 2014*a*,

2014*b*; F. Bebawi, pers. obsv.). Pareek (2001) indicated that abrasion of the endocarp by natural processes over time may break this physical dormancy in seeds of *Ziziphus* species. Grice (1996) found that removal of the endocarp increased germination from 10% to 56%. Although germination capacity is generally high, it may vary from 31% to 95% (Luna 1996). It is not completely known how long seed banks of chinee apple will persist. Grice (1996) followed seed lots placed either on the soil surface or buried at 2 cm below ground for 12 months and found that less than 10% of retrieved seed was germinable after 12 months. However, several landholders have reported having to control seedlings for many years (>5) after killing all mature plants. There are two plausible explanations for this variation. First, when testing the longevity of chinee apple seed banks, Grice (1996) only measured germination and there may still have been viable seeds that were dormant (Hocking 1993; Grice 1996; Maraghni *et al*. 2010; Anon. 2014*a*, 2014*b*; F. Bebawi, pers. obsv.). Alternatively, the soil seed banks of the local landholders may have been replenished from neighbouring infestations through one or more of the dispersal vectors of chinee apple. This conjecture needs to be resolved in order to provide land managers with an accurate recommendation of how long control activities may be needed to exhaust soil seed reserves. The characteristics of the biology and ecology of chinee apple have allowed it to eventually predominate the vegetation in many areas where it has naturalised, particularly in savanna woodland environments (Weber 2003; Short *et al*. 2011; CABI 2014) and abandoned or fallow land (Morton 1987). In areas of northern Australia, where it has formed dense thickets, it is impacting on the cattle industry by reducing stocking rates, impeding mustering and restricting stock access to water (Grice 1996; ISSG 2003). At the same time, it is impacting on the biodiversity and conservation of woodland habitats by outcompeting native plants and altering species assemblages (Grice *et al*. 2000; Parsons and Cuthbertson 2001; Weber 2003); Grice and Martin 2005; Azam-Ali *et al*. 2006; Grice 2006).

Current options for effective control of established plants of chinee apple are limited to the application of herbicides and mechanical techniques (Grice *et al*. 1999; Land Protection 2006). It is resilient to fire (Grice 1997; Weber 2003; Grice 2009; Anon. 2014*a*) and has not been the focus of any biological control programs in Australia.

While research undertaken to date has provided a reasonable understanding of the ecology and control of chinee apple (Grice 1996, 1997; 1998; Grice *et al*. 1999), there are still several gaps in knowledge relating to its management. In this study, we have undertaken two experiments (Expts 1 and 2) to confirm the seed persistence of chinee apple under a range of conditions, including different soil types, levels of pasture cover and burial depths. We also investigated the response of seed germination to fluctuating temperatures (Expt 3) to better understand its potential distribution.

Materials and methods

Experiments 1 and 2: Seed persistence

Site description

The experimental site (38 m × 36 m) was located at the Tropical Weeds Research Centre, Charters Towers, north

Queensland (20° 09′S, 146° 26′E; elevation 318 m). The site was secured with a rabbit and kangaroo exclusion fence. It had been previously cleared of shrubs and trees, but would have originally comprised an open-woodland. The ground cover vegetation included buffel grass [*Pennisetum ciliare* (L.) Link], 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 to February) (BOM 2012). The mean summer maximum daily temperature is 37.6 ± 0.4°C and in winter (June to August) is 28.2 ± 0.7°C. The mean lowest daily temperature in summer is 29.9 ± 0.5°C and in winter (June to August) is 22.3 ± 0.6°C. Rainfall and ambient temperature at the field site were measured using an on-site automatic weather station (Campbell Scientific, USA).

Fruit collection

Ripe fruits of chinee apple were collected in September 2008 for Expt 1 by physically removing them from mature trees growing wild in the vicinity of Ravenswood (20° 06′ S, 146° 67′ E; elevation 266 m above sea level), 62 km South–East of Charters Towers. These fruits were taken back to the Tropical Weeds Research Centre, where the kernels were manually removed and placed in jackets of aluminium mosquito gauze (1 m²) to dry for two weeks in a dry glasshouse. Six hundred and forty sub-samples of 25 kernels 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 allow seed retrieval while maximising soil/seed contact.

A second collection of ripe fruits was made in October 2010 for Expt 2 from the same location and these were similarly processed.

Experimental design

A multi-factor split plot design with four replications was implemented. There were two soil types (alluvial river loam and clay), two levels of pasture cover (pasture present or pasture excluded), three or four seed burial depths (depending on the experiment) and nine retrieval times. Kernels were buried at four depths (0, 2.5, 10 and 20 cm) in Expt 1, but only three depths (0, 2.5, and 10 cm) in Expt 2.

A full description of the design and implementation of treatments is provided in the methodology section of Bebawi *et al*. (2015), which describes the seed longevity of *Calotropis procera* (Aiton) W.T. Aiton.

Experiment 1 commenced in October 2008 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. Experiment 2 commenced in November 2010, with retrievals designated to occur 3, 6, 9, 12, 18, 24, 36, 48 and 72 months after burial or until no viable seeds were recorded for two consecutive retrievals.

Germination and viability testing

Kernels still containing seeds were removed from retrieved bags and transferred to the laboratory for seed extraction. Garden secateurs with a flat corrugated base and a sharp upper blade were used to crack open the kernels (i.e. the endocarp) to release seeds. These 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. Dishes containing seeds were then put into a growth cabinet set at 30/20°C day/night with alternating 12 h of light and dark. Seeds that germinated (identified by radicle emergence) were counted and removed daily for 14 days (Fig. 1). Seeds that did not germinate were checked for dormancy using the tetrazolium method (Moore 1985). Viable but dormant seeds were pink when cut longitudinally with a sharp scalpel.

Germinability was calculated as a percentage of the number of seeds that germinated out of the original 50 seeds buried in individual packets, given that two seeds were usually found within each kernel (endocarp) and there were 25 kernels per bag. Viability included those seeds that germinated in the Petri-dishes (i.e. germinable) plus those that did not germinate but were considered viable (i.e. dormant) after tetrazolium testing. Viability was also expressed as a percentage of the original 50 seeds buried in individual packets.

At the three 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 3 – seed germination at alternate day/night temperature regimes

This experiment commenced on 7 December 2012 to determine the germination temperature tolerance (germination temperature range) of fresh seeds of chinee apple. Fruits of chinee apple were collected from the same area described for Expts 1 and 2.

Lots of 50 chinee apple seeds that had been removed from the outer kernel were placed on moist extra-thick absorbent paper towels in covered plastic trays (11 cm × 17 cm × 7 cm) in the laboratory. Towels were kept moist during the course of the experiment by regularly spraying with distilled water. Tray lids were perforated at the four corners to allow air circulation. Four trays were placed on top of each other in each of 10 temperature compartments (Multi-Temperature Incubator Model: LMMT-10, Linder and May, Northgate, Queensland) delivering alternate regimes of light (light 12 h/dark 12 h) and temperature (12 h day/12 h night) for the duration of the experiment. The 10 temperature compartments delivered a temperature range of 11°C to 52°C during the day and 6°C to 40°C during the night in progressional order (see Table 1). The temperatures in each compartment are given in Table 1. The trays in each compartment were re-mixed randomly each day. Compartment temperatures were recorded on an hourly basis using type K steel encased thermocouples placed inside each of the 10 compartments. The thermocouples were hooked to a data logger (Data Electronics Pty Ltd, Brisbane, Qld) connected to a main power supply, with data downloaded monthly.

Germinated seeds (Fig. 1) were counted and removed daily from trays for up to 12 days, but monitoring continued for an additional 7 days to confirm that germination had ceased. Germination was expressed as a percentage of the initial number of seeds (i.e. 50).

Data analysis

All statistical analyses were performed using GENSTAT (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 ($P < 0.05$). For datasets with a typical binomial distribution, analysis was undertaken on arcsine-transformed values, which were later back-transformed for display.

For the seed persistence experiments, viability data were analysed using a multiple split-plot analysis of variance as dictated by the experimental design: 4 blocks × 2 soil types split for two pasture levels split for nine retrieval times split for 3–4 burial depths. For the effect of temperature on germination experiment, one way analysis of variance was undertaken to distinguish differences between the 10 temperature regimes that were tested.

Fig. 1. Germinating seeds of chinee apple showing reddish-brown seed coat and radicle emergence.

Table 1. Alternating day and night temperatures (°C) for the 10 compartments of the multi temperature incubator for Expt 3

Compartment No.	Day (12 h light)	Night (12 h dark)
1	11	6
2	16	12
3	21	16
4	25	19
5	29	23
6	33	27
7	37	30
8	42	33
9	47	36
10	52	40

Results

Experiments 1 and 2 - seed persistence

Rainfall

Annual rainfall recorded at the site between 2008 and 2012 was consistently greater than the long-term mean for Charters Towers (658 mm), totaling 1365, 1105, 1323, 1037 and 832 mm per annum, respectively (Fig. 2).

Despite commencing at different times, both Expts 1 and 2 were exposed to similar amounts of rainfall over their two year duration (2095 and 2117 mm), but there were seasonal differences. During the wettest six months of the year in North Queensland (November–April), Expts 1 (1240 mm) and 2 (1190 mm) both received more than twice the long-term average of 541 mm over their first wet season following burial in spring. Experiment 1 was exposed to a particularly wet January and February (~1000 mm) while Expt 2 received consistently above average rainfall in all months of the wet season. For their second wet season, Expt 1 (658 mm) received less than experiment 2 (874 mm), but it was still more than the long-term mean. Dry season rainfall (May to October) was relatively close (within 40 mm) to the long-term mean of 117 mm for both experiments during their first dry period. However, the second dry seasons were above average, by 123 and 91 mm for Expts 1 and 2, respectively.

Seed viability

Experiment 1. At the time of burial, viability and germinability (after removal of the endocarp) of the chinee apple seed averaged $86.3 \pm 1.4\%$ (per cent of total seed number) and $75.8 \pm 2.4\%$ (per cent of viable seeds), respectively. Following burial, significant burial duration × soil type × burial depth interactions

($P < 0.001$) were recorded for seed viability. In contrast, the presence or absence of pasture cover did not have a significant effect ($P > 0.05$).

No viable seed remained in any treatments at the 18 month retrieval and even after only six months burial, viability was ≤2% (Fig. 3). Significant variation due to the effects of burial depth and soil type occurred during the first six months. This was mainly because of the greater persistence of surface located seeds (0 cm) in the river loam soil after three months, compared with all other treatments which exhibited relatively low viability (Fig. 3). Surface located seed lots (across both soil types) had the largest proportion of seeds germinate in the field (53%) during the first three months (Fig. 4). Field germination steadily declined thereafter with increasing burial depth.

Experiment 2. Seeds used in Expt 2 had lower viability ($64.1 \pm 1.9\%$) but higher germinability (100%) than those used in Expt 1 at the time of burial, yet similar treatment responses were recorded. Significant burial duration × soil type × burial depth interactions ($P < 0.001$) occurred (Fig. 5). As with Expt 1 the presence or absence of pasture cover did not have a significant effect ($P > 0.05$) on seed viability.

Irrespective of soil type, seed viability declined rapidly for seed lots buried 2.5 and 10 cm below ground and was totally exhausted at the 12 and 6-month retrievals, respectively. Even after three months, <1% viability was recorded for these treatments. In contrast, surface located seed lots exhibited a steadier rate of decline in viability and took until the 24 month retrieval to record nil viability (Fig. 5). Soil type had an influence on surface located seeds with loss of viability tending to occur at a faster rate on clay soil compared with river loam.

In contrast to Expt 1, the field germination during the first three months burial was low (<5%) at all burial depths (Fig. 4).
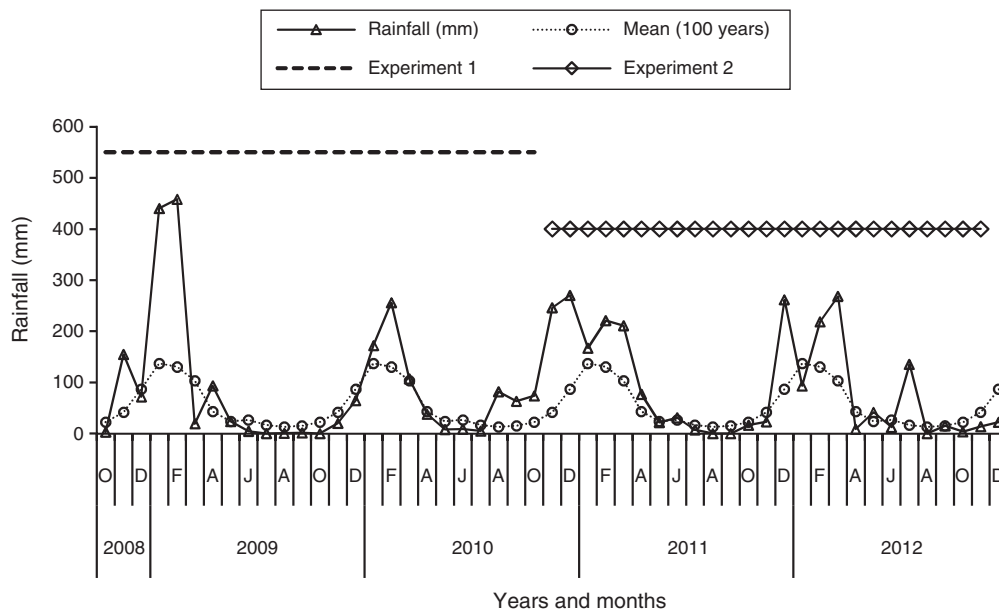

Fig. 2. Monthly rainfall (△) at the research site between October 2008 and November 2012, and the average monthly rainfall (○) for Charters Towers during Expt 1(–) and Expt 2 (◇).
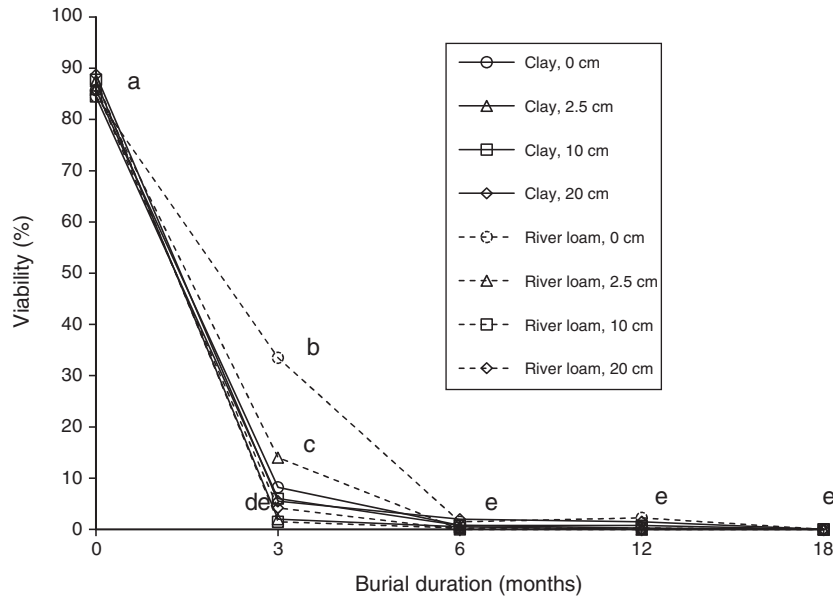
Fig. 3. The effect of burial depth, soil type and burial duration on mean seed viability of chinee apple in Expt 1. Values followed by the same letter are not significant at $P < 0.05$.
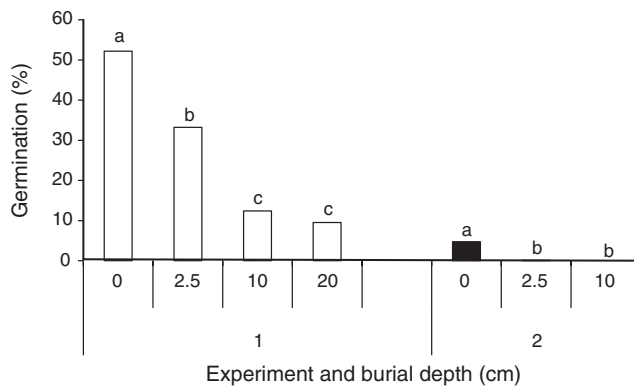

Fig. 4. The proportion (%) of chinee apple seed that germinated in the field (at different depths) during the first 3 months of Expt 1 (□) and Expt 2 (■). In Expt 2 no seed was buried at 20 cm depth. Within the same group, columns associated with the same letter are not significantly different at $P < 0.05$.

Experiment 3 – seed germination at alternate temperature regimes

Significant differences ($P < 0.001$) in seed germination occurred between the temperature regimes that were tested (Fig. 6). Nil germination occurred at the coolest alternating temperature regime of 11°C /6°C or at the hottest temperature regime of 52°C/40°C. Maximum germination of 77% occurred at an alternating day/night temperature regime of 33°C/27°C. Minimum germination (16%) occurred at alternate day/night temperatures of 16/12°C. Increasing day temperatures from 16°C to 33°C promoted increased germination whereas day temperatures greater than 33°C reduced germination.

Discussion

This study confirmed that viable seed reserves of chinee apple in the soil are relatively short-lived (<2 years), irrespective of soil type, burial depth and the level of pasture cover. Viability tended to decline most rapidly if seeds were buried below ground compared with those on the soil surface. Chinee apple germinated across a wide range of alternating day/night temperatures, ranging from 16/12°C to 47/36°C, with maximum germination of 77% at 33/27°C day/night temperatures.

Seed persistence

Chinee apple seeds have the potential to remain viable for greater than 2 years if stored under favourable conditions (i.e. cool/dry) (Luna 1996). However, the findings of the current study and those of Grice (1996) suggest that environmental conditions in rangeland environments reduce the persistence of chinee apple seed banks. While Grice (1996) only followed changes in germinability of soil seed banks over time, the trends reported are consistent with the current study where viability was recorded. With no viable seeds remaining in seed lots after 24 months, chinee apple would be considered to have a short-term persistent seed bank, according to the classification system developed by Thompson *et al.* (1997).

Several workers including Chesson (2000), Facelli *et al.* (2005), Arroyo *et al.* (2006), Ozinga *et al.* (2007) and Mondoni *et al.* (2014) have reported an inverse relationship between seed persistence and adult longevity. For example, Arroyo *et al.* (2006) found that annual herbs of *Chaetanthera* (Asteraceae) from Chile have a greater capacity to form persistent seed banks than perennials of the same genus. Persistent seed banks are ecologically important (Fenner 1985) because they permit species to explore environmental variability in time (Venable and Lawlor 1980; Venable and Brown 1988). This helps protect
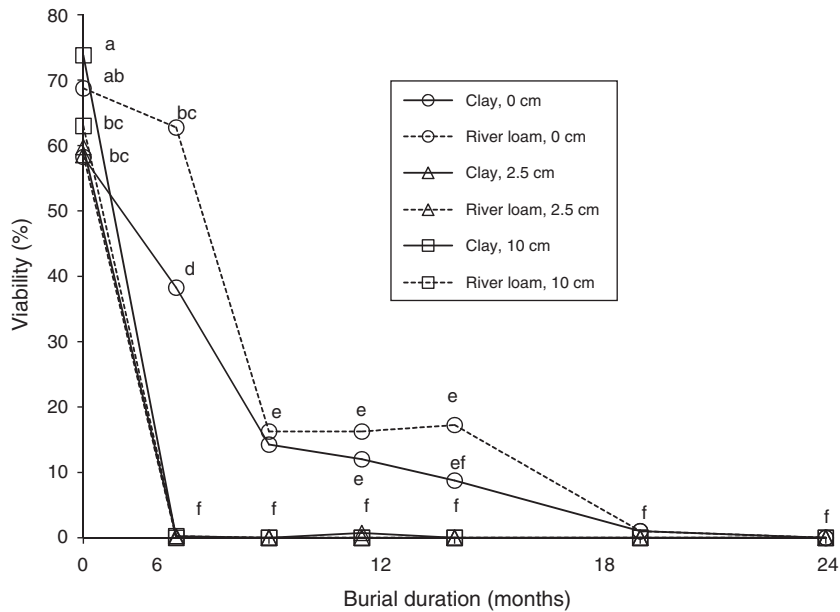
Fig. 5. The effect of burial depth, soil type and burial duration on mean seed viability of chinee apple in Expt 2. Values followed by the same letter are not significant at $P < 0.05$.
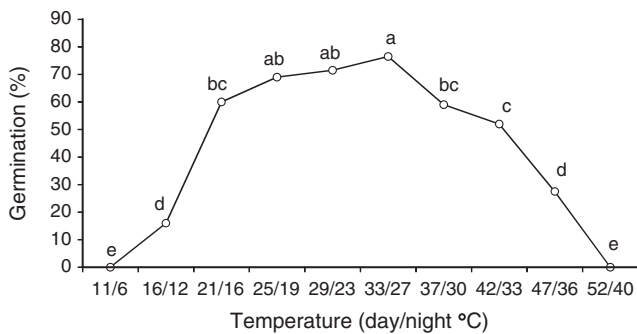

Fig. 6. Germination response of chinee apple seed under different alternating day/night temperature regimes. Values followed by the same letter are not significant at $P < 0.05$.

populations from local extinction when aboveground vegetation is removed, and hence is important for restoration and conservation purposes (Bakker *et al*. 1996; Kalisez *et al*. 1997). Chinee apple appears to conform with the above relationship and is not dependent on a long-lived seed bank to persist in an area, with plants capable of surviving for several decades (Grice 2002, 2009). Combined with their ability to consistently produce large quantities of fruit on an annual basis (Schirarend 1991; Grice 1996), regular replenishment of soil seed reserves occurs in the absence of any control activities, providing the opportunity for infestations to increase in density under favourable environmental conditions (Grice 1996).

Species with short-lived seed banks often have highly germinable seeds (i.e. no dormancy mechanisms), with the seed bank depleted quickly due to large scale germination during favourable rainfall events. Some rangeland weeds that display such characteristics include calotrope (*Calotropis procera* (Aiton) W.T. Aiton) (Bebawi *et al*. 2015) and rubber vine

(*Cryptostegia grandiflora* R. Br.) (Grice 1996; Bebawi *et al*. 2003). In this study, chinee apple had highly germinable seed, but testing was undertaken after the seeds were removed from the hard endocarp, which appears capable of causing physical dormancy. Grice (1996) found that germinability of fresh seed within an intact endocarp was low (<10%) and increased substantially if the endocarp was removed. Grice (1996) also suggested that weathering of the outer layer would need to occur before the seed could germinate in the field, and that it would most likely occur faster for surface located seeds compared with buried seeds. This may explain why at the three month after burial retrieval in Expt 1 more chinee apple seedlings (i.e. field germination) were recorded in packets that were located on the surface, compared with those buried below ground. A similar trend occurred in Expt 2, but overall field germination was much lower than that recorded in Expt 1. Often the opposite occurs for rangeland weeds (Grice 1996; Bebawi *et al*. 2003, 2012; 2015) with germination lower for seeds located on the soil surface and consequently they persist for longer. This is usually attributed to the surface drying out quicker after rainfall events, providing less favourable conditions for germination to occur (Grice 1996; Bebawi *et al*. 2003, 2012; 2015). Obviously, the above average rainfall experienced during Expt 1 provided suitable moisture conditions for germination of the surface seeds to occur: Chinee apple is fairly slow to germinate (8 days), requiring favourable moisture conditions for an extended period to complete the process (Grice 1996). Despite Expt 2 also receiving above average rainfall, the pattern of rainfall must have been less favourable for field germination, with <5% recorded. It is feasible therefore that in drier years (e.g. droughts) chinee apple seeds may persist for longer, particularly if a large percentage remains on the soil surface after fruits fall from the trees.

The location of chinee apple seeds in the soil profile has not been quantified to date, but given that they are contained within

a relatively large endocarp, many would be expected to remain on the soil surface (Grice 1996). However, if the fruits are consumed by animals such as cattle they will be deposited in dung which may provide a moister environment, not dissimilar to being buried.

Despite greater field germination, surface located seed lots still retained viable seeds for longer than those buried below ground. Grice (1996) reported similar findings, with 31% germinability of surface located seeds recorded after 6 months, compared with only 7% for buried seeds. The reason why the persistence of buried seed was shorter than for surface located seed is not clear. The presence of pathogens and/or predators and failed germination are two factors known to reduce seed viability (Simpson *et al.* 1989) and Grice (1996) suggested that the endocarp of chinee apple can become heavily infected with fungal growth.

While the findings from the current study back up previous suggestions in the literature that chinee apple has a relatively short lived seed bank (Grice 1996), how this relates to the anecdotal evidence from several landholders, who believe chinee apple has a long-lived seed bank, needs to be considered. It is highly plausible that replenishment of soil seed reserves could be occurring at some locations through dispersal from neighbouring infestations. Whether the methodology used in the studies (i.e. seeds buried in mesh bags) facilitated more rapid loss of viability than would otherwise occur in the field is unlikely, but cannot be discounted. Van Mourik *et al.* (2005) suggested that in some instances seeds clumped together in mesh bags (in high densities) could suffer greater attack from pathogens than would occur under natural conditions where the seeds may be more spread out. A field based study where rundown of natural seed banks is followed by taking and processing soil samples and/or observing seedling emergence on a regular basis (at least monthly) would help resolve this uncertainty, provided replenishment of the seed banks can be prevented.

Seed germination at alternating day/night temperature regimes

The alternating day/night temperature regime of 33°C/27°C that produced optimal germination (77%) of chinee apple in the present study was a little lower than that reported previously for other *Ziziphus* species. For example, Maraghni *et al.* (2010) found that optimal germination (100%) of *Z. lotus* (L.) Lam. occurred at an average temperature of 35°C. Despite this variation, the range of favourable germination temperature regimes for chinee apple (16°C/12°C−47°C/36°C) was fairly similar to those for *Z. Lotus* (15−45°C) (Maraghni *et al.* 2010).

Chinee apple's seed germination tolerance to the very cold (16°C/12°C) or very warm temperatures (47°C/36°C) tested in this study is indicative of its wide survival potential in terms of genetic plasticity of the species. It is also a biological indication that a substantial proportion of its seed population is genetically programmed to go into a state of 'enforced dormancy', in this case due to unsuitable temperatures as described by Harper (1977). This seed trait may enable seeds of chinee apple to remain temporarily inactive in very cold environments, such as in the southern latitudes of Australia. However, this inactivity may be broken if an environmental germination trigger arises from global warming or a shift in favourable ecological zones southwards.

In general, the present study showed that seeds of chinee apple were able to germinate over a wide range of temperatures. This indicates that chinee apple seeds could germinate any time of the year in a sub-tropical environment. However, greater germination under the intermediate and warmer temperature regimes tested suggests that increased germination would be expected during the summer months, provided water and light were not limiting.

Management implications

The findings from this study have implications for the management of chinee apple at a local level in the case of seed longevity and more broadly in terms of its potential germination range.

Seed bank longevity and the age to reproductive maturity are two important ecological attributes that influence whether weed eradication/control programs will be successful or not (Campbell and Grice 2000; Dodd *et al.* 2015). The likelihood of success increases if soil seed banks are short lived and if new seedlings that arise following control activities take a long time to reproduce (Dodd *et al.* 2015). Chinee apple appears to fit both categories, with the current study indicating that seed banks could be fully depleted within two years and Grice (2009) suggesting that plants may take around nine years to reach reproductive maturity. Therefore, follow-up control should not be as onerous as for some other rangeland weeds growing in northern Australia that possess more persistent seed banks and/or reach reproductive maturity earlier. Some examples include, the herbaceous weed parthenium (*Parthenium hysterophorus* L.) and the woody weed prickly acacia (*Acacia nilotica* (Benth.) Brenan) (Navie *et al.* 1996; Mackey 1997). However, if landholders are concerned about the quantity of chinee apple seedlings that may emerge after control of initial infestations, they could also consider burning infested areas either before or after treatment. Grice and Brown (1996) found that where there was sufficient fuel, burning destroyed a large proportion (>90%) of surface located seeds, which as mentioned previously is where most seed is likely to remain given the size of the endocarp that contains it. Surface-located seed also retains viability for longer than buried seed and therefore would be the major source of new seedlings if not destroyed.

Despite the apparent ecological weaknesses of chinee apple it does have other attributes that can make control/eradication from an area difficult: (*i*) large original plants will survive and reshoot if not effectively controlled (Grice 2002, 2009); (*ii*) the many dispersal mechanisms of chinee apple can result in replenishment of soil seed reserves from external sources, such as neighbouring infestations (Grice 2002, 2009); and (*iii*) while young plants are usually slow growing, if the stem is damaged (as in many mechanical clearing operations and fires), they will grow more rapidly afterwards and potentially reproduce in a quicker timeframe (Grice *et al.* 1999).

Control programs will therefore be most effective and cheaper if they are undertaken in the early stages of invasion, achieve high mortality of original plants, and involve groups of neighbouring

properties to minimise the risk of re-invasion. Once all original plants are controlled, a regular monitoring regime of ~1–2 years will provide several opportunities to find and treat new plants before they have the opportunity to reproduce.

In relation to the findings from the germination study, the ability of chinee apple to germinate across a broad temperature gradient not only shows that it could germinate at any time of the year under favourable rainfall conditions in Northern Australia, but also highlights its potential to germinate in more southerly parts of Australia. This is consistent with earlier predictive modelling (Thorp and Lynch 2000; Grice 2009), which suggested that much of eastern Queensland was favourable for chinee apple. Given its many dispersal mechanisms and the risk associated with movement of livestock from northern areas into southern districts, land managers in southern areas should be vigilant for chinee apple as part of routine management practices, particularly if they identify any pathways that link livestock from infested properties to their own property.

Acknowledgements

References

Anon. (2014a). Fact Sheet – Chinee apple *Ziziphus mauritiana*, Weeds of Australia, Biosecurity Queensland Edition. (Queensland Government: Brisbane, Qld.)

Anon. (2014b). Chinese apple – *Ziziphus mauritiana* (Heartbeat of the Nation – Myanmar Times). Available at: www.oilseedcrops.org (accessed 25 February 2014).

Anon. (2014c). Jujube *Ziziphus jujube* Mill. – Jujube Fruit Facts. Available at: www.crfg.org (accessed 20 March 2015).

Arroyo, M. T. K., Chacon, P., and Cavieres, L. A. (2006). Relationship between seed bank expression, adult longevity and aridity in species of *Chaetanthera* (Asteraceae) in Central Chile. *Annals of Botany* **98**, 591–600. doi:10.1093/aob/mcl134

Azam-Ali, S., Bonkoungou, E., Bowe, C., deKock, C., Godara, A., and Williams, J. T. (2006). Ber and other jujubes, *Ziziphus* species. *In*: 'Fruits for the Future'. Revised edn. (International Centre for Underutilised Crops: Southampton, UK.)

Bakker, J. P., Poschlod, P., Strykstra, R. J., Bekker, R. M., and Thompson, K. (1996). Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* **45**, 461–490. doi:10.1111/j.1438-8677.1996.tb00806.x

Bebawi, F. F., Campbell, S. D., and Lindsay, A. M. (2003). Effects of burial and age on viability of rubber vine (*Cryptostegia grandiflora*) seeds. *Plant Protection Quarterly* **18**, 147–151.

Bebawi, F. F., Campbell, S. D., and Mayer, R. J. (2012). Persistence of bellyache bush (*Jatropha gossypifolia* L.) soil seed banks. *The Rangeland Journal* **34**, 429–438. doi:10.1071/RJ12051

Bebawi, F. F., Campbell, S. D., and Mayer, R. J. (2015). Seed bank longevity and age to reproductive maturity of *Calotropis procera* (Aiton) W.T. Aiton in the dry tropics of northern Queensland. *The Rangeland Journal* **37**, 239–247. doi:10.1071/RJ14130

BOM (2012). Mean annual rainfall and maximum daily temperature ranges. Available at: www.bom.gov.au (accessed 22 October 2012).

CABI (2014). *Ziziphus mauritiana* – Datasheet for CABI Invasive Species Compendium. Available at: www.cabi.org (accessed 14 March 2014).

Campbell, S. D., and Grice, A. C. (2000). Weed biology: a foundation for weed management. *Tropical Grasslands* **34**, 271–279.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**, 343–366. doi:10.1146/annurev.ecolsys.31.1.343

Dodd, A. J., Ainsworth, N., Burgman, M. A., and McCarthy, M. A. (2015). Plant extirpation at the site scale: implications for eradication programmes. *Diversity & Distributions* **21**, 151–162. doi:10.1111/ddi.12262

Facelli, J. M., Chesson, P., and Barnes, N. (2005). Differences in seed biology of annual plants in arid lands: A key ingredient of the storage effect. *Ecology* **86**, 2998–3006. doi:10.1890/05-0304

Fenner, M. (1985). 'Seed Ecology.' (Chapman and Hall: London, UK.)

Gardiner, C. P., and Gardiner, S. P. (1996). The dissemination of chinee apple (*Ziziphus mauritiana*): a woody weed of the tropical subhumid savanna and urban fringe of north Queensland. *Tropical Grasslands* **30**, 174.

Grice, A. C. (1996). Seed production, dispersal and germination in *Cryptostegia grandiflora* and *Ziziphus mauritiana*, two invasive shrubs in tropical woodlands of northern Australia. *Australian Journal of Ecology* **21**, 324–331. doi:10.1111/j.1442-9993.1996.tb00615.x

Grice, A. C. (1997). Post-fire regrowth and survival of the invasive tropical shrubs *Cryptostegia grandiflora* and *Ziziphus mauritiana*. *Australian Journal of Ecology* **22**, 49–55. doi:10.1111/j.1442-9993.1997.tb00640.x

Grice, A. C. (1998). Ecology in the management of invasive rangeland shrubs: a case study of Indian jujube (*Ziziphus mauritiana*). *Weed Science* **46**, 467–474.

Grice, A. C. (2002). The biology of Australian weeds. 39. *Ziziphus mauritiana* Lam. *Plant Protection Quarterly* **17**, 2–16.

Grice, A. C. (2006). The impacts of invasive plant species on the biodiversity of Australian rangelands. *The Rangeland Journal* **28**, 27–35. doi:10.1071/RJ06014

Grice, A. C. (2009). *Ziziphus mauritiana* Lam. *In*: 'The Biology of Australian Weeds, Vol. 3'. (Ed. F. D. Panetta.) pp. 295–310. (R.G. and F.J. Richardson: Melbourne, Vic.)

Grice, A. C., and Brown, J. R. (1996). Fire and the population ecology of invasive shrubs in the tropical woodlands. *In*: 'Frontiers of Population Ecology'. (Eds R. B. Floyd, A. W. Sheppard and P. J. De Barro.) pp. 589–597. (CSIRO: Canberra, ACT.)

Grice, T. and Martin, T. (2005). 'The Management of Weeds and their Impact on Biodiversity in the Rangelands.' (The CRC for Australian Weed Management: Townsville, Qld.)

Grice, A. C., Walker, L., and Whiteman, L. (1999). An invasive rangeland shrub responds rapidly to top removal. *In*: 'People and Rangelands: Building the Future. Proceedings of the VI International Rangeland Congress'. Townsville, Queensland, 19–23 July 1999, Vols 1 and 2. (Eds D. Eldridge and D. Freudenberger.) pp. 591–593. (International Rangeland Congress Inc.: Aitkenvale, Qld.)

Grice, A. C., Radford, I. J., and Abbott, B. N. (2000). Regional landscape-scale patterns of shrub invasion in tropical savannas. *Rangeland Invasions* **2**, 187–205. doi:10.1023/A:1010021515356

Grice, A. C., Campbell, S., Breaden, R., Bebawi, F., and Vogler, W. (2008). 'Habitat Management Guide – Rangelands: Ecological Principles for the Strategic Management of Weeds in Rangeland Habitats.' (CRC for Australian Weed Management: Adelaide, S. Aust.)

Harper, J. L. (1977). 'Population Biology of Plants.' (Academic Press: London, UK.)

Hocking, D. (1993). 'Trees for Drylands.' (Oxford & IBH Publishing: New Delhi, India.)

Huwale, T. D. (1985). Pollen studies in *Ziziphus mauritiana* cultivars. *Annals of Aridzone Journal* **1**, 47–50.

ISSG (2003). 'Global Invasive Species Database.' (Invasive Species Specialist Group, IUCN, University of Auckland: Auckland, New Zealand.)

Kalisez, S., Horth, L., and McPeek, M. A. (1997). Fragmentation and the role of seed banks in promoting persistence of *Collinsia verna* in isolated populations. *In*: 'Conservation in Highly Fragmented Landscapes'. (Ed. M. Schwartz.) pp. 268–312. (Chapman and Hall: New York, USA.)

Land Protection (2006). '*Ziziphus mauritiana*, Indian Jujube, Chinee Apple.' Facts Pest Series, p.26. (Department of Natural Resources and Water: Brisbane, Qld.)

Luna, R. K. (1996). 'Plantation Trees.' (International Book Distributors: Dehra Dun, India.)

Mackey, A. P. (1997). The biology of Australian weeds 29. *Acacia nilotica* ssp. *indica* (Benth.) Brenan. *Plant Protection Quarterly* **12**, 7–17.

Maraghni, M., Gorai, M., and Neffati, M. (2010). Seed germination at different temperatures and water stress levels, and seedling emergence from different depths of *Ziziphus lotus*. *South African Journal of Botany* **76**, 453–459. doi:10.1016/j.sajb.2010.02.092

Mondoni, A., Orsenigo, S., Dona, M., Balestrazzi, A., Probert, R. J., Hay, F. R., Petraglia, A., and Abeli, T. (2014). Environmentally induced transgenerational changes in seed longevity: maternal and genetic influences. *Annals of Botany* **113**, 1257–1263.

Moore, R. P. (1985). 'Handbook of Tetrazolium Testing.' (International Seed Testing Association: Zurich.)

Morton, J. (1987). Indian jujube. *In*: 'Fruits of Warm Climates'. pp. 272–275. (Center for New Crops and Plant Products: Purdue University, Miami, FL, USA.)

Navie, S. C., McFadyen, R. E., Panetta, F. D., and Adkins, S. W. (1996). The biology of Australian weeds 27. *Parthenium hysterophorus* L. *Plant Protection Quarterly* **11**, 76–88.

Noble, J. C. (1975). The effects of emus (*Dromaius novaehollandiae* Latham) on the distribution of the nitre bush *Nitraria billardieri* DC. *Journal of Ecology* **63**, 979–984. doi:10.2307/2258615

Noble, J. C. (1991). On ratites and their interactions with plants. *Revista Chilena de Historia Natural* **64**, 85–118.

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., and Anthony, S. (2009). Agroforestree Database: a tree reference and selection guide. Version 4.0. Available at: www.worldagroforestry.org/sites/treedbs/treedatabases.asp (accessed 4 January 2016).

Ozinga, W. A., Hennekens, S. M., Schaminée, J. H. J., Smits, N. A. C., Bekker, R. M., Römermann, C., Klimeš, L., Bakker, J. P., and van Groenendael, J. M. (2007). Local above-ground persistence of vascular plants: life-history trade-offs and environmental constraints. *Journal of Vegetation Science* **18**, 489–497. doi:10.1111/j.1654-1103.2007.tb02563.x

Pareek, O. P. (2001). 'The Ber.' (Indian Council of Agricultural Research, New Delhi.)

Parsons, W. T., and Cuthbertson, E. G. (2001). 'Noxious Weeds of Australia.' 2nd edn. (CSIRO Publishing: Melbourne, Vic.)

Schirarend, C. W. (1991). 'The systemic wood anatomy of Rhamnaceae JUSS (Rhamnales). Tribe zizipheae'. *Humboldt University Iowa Bulletin* **12**, 359–388.

Short, P. S., Albrecht, D. E., Cowie, I. D., Lewis, D. L., and Stuckey, B. M. (2011). 'Checklist of the Vascular Plants of the Northern Territory.' (Northern Territory Herbarium, Department of Natural Resources, Environment, the Arts and Sport: Darwin, NT.)

Simpson, R. L., Leck, M. A., and Parker, V. T. (1989). Seed banks: general concepts and methodological issues. *In*: 'Ecology of Soil Seed Banks'. (Eds M. A. Leck, V. T. Parker and R. L. Simpson.) pp. 3–21. (Academic Press: San Diego, CA, USA.)

Singh, S. P. (1989). 'Wasteland Development.' (Agricole Publishing Academy: New Delhi, India.)

Thompson, K., Bakker, J. P., and Bekker, R. M. (1997). 'Soil Seed Banks of NW Europe: Methodology, Density and Longevity.' (Cambridge University Press: Cambridge, UK.)

Thorp, J. R., and Lynch, R. (2000). 'The Determination of Weeds of National Significance.' (National Weeds Strategy Executive Committee: Launceston, New Zealand.)

Van Mourik, T. A., Stomph, T. J., and Murdoch, A. J. (2005). Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks. *Journal of Applied Ecology* **42**, 299–305. doi:10.1111/j.1365-2664.2005.01016.x

Venable, D. L., and Brown, J. S. (1988). The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. *American Naturalist* **131**, 360–384. doi:10.1086/284795

Venable, D. L., and Lawlor, L. (1980). Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* **46**, 272–282. doi:10.1007/BF00540137

Weber, E. (2003). 'Invasive Plant Species of the World. A Reference Guide to Environmental Weeds.' (CABI Publishing: Wallingford, UK.)

World Agroforestry Centre (2002). Agroforestree database. ICRAF, Nairobi, Kenya.