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Seed fall, seed predation, twigging and litter fall of *Cascabela thevetia* (L.) Lippold

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Abstract. *Cascabela thevetia* (L.) Lippold is a garden ornamental in northern Australia and two biotypes, the peach and the yellow, are recognised. In some areas it has naturalised and now has environmental and economic effects. As part of a broader research program into the ecology of *C. thevetia*, a field study was undertaken in northern Queensland to quantify seed fall and seed predation (by avian wildlife) of the peach biotype. The amount of twigging caused by birds while they fed on the seeds and the level of litter production were also recorded. Seed fall, seed predation, twigging and litter production occurred in all months of the year. Seed fall increased slowly over late spring and summer before peaking in mid- to late autumn (April–May) and then declining until October. Mean (± s.e.m.) estimated total annual seed fall was 19 140 ± 2880 and 17 030 ± 2930 seeds ha^{-1} in the first and second years respectively. Seed predation by birds was substantial, with 57% of all seeds predated. Birds also chewed an average of 600 twigs ha^{-1} $year^{-1}$. Litter production varied from 430 to 950 kg dry weight (DW) ha^{-1} $month^{-1}$. In total, 7900 ± 640 and 7390 ± 1420 kg (DW) litter was produced during the first and second years respectively. Although seed production of *C. thevetia* is less than a lot of other rangeland weeds, seed predation by birds further reduces the number of seeds entering the soil seed bank. The stem damage that occurred in conjunction with seed predation contributed to overall litter production and warrants further investigation in terms of its effect on plant growth.

Additional keywords: Captain Cook tree, litter production, predispersal predation, seed production, yellow oleander.

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Introduction

Cascabela thevetia (L.) Lippold (syn. *Thevetia peruviana* (Pers.) Schum. Apocynaceae) is native to tropical South America and the West Indies (Everist 1974; Lippold 1980). It has naturalised in Australia, Africa and numerous other countries and islands, where it commonly exists as two biotypes or varieties based on flower colour: peach and yellow (Ibiyemi *et al*. 2002; Schmelzer 2006; Alvarado-Cárdenas and Ochoterena 2007; Nyadoi 2010; Kishan *et al*. 2012; Bebawi and Crowley 2013*a*, 2013*b*; Bebawi *et al*. 2014, 2015; S. M. Csurhes, unpubl. obs.). In Queensland, it is commonly called either Captain Cook tree or yellow oleander (Department of Agriculture, Fisheries and Forestry 2013).

C. thevetia is capable of growing into a large tree (up to 10 m high) and has often been grown as an ornamental plant. It is most distinguished by its narrow, pointed leaves, bell-shaped and slightly fragrant flowers and its fruit. The indehiscent fruit is a drupe that has a fleshy exocarp, stony mesocarp and endocarps (mericarps) free from each other. As the fruit ripens, it changes from green to reddish-brown to leathery black (Schmelzer 2006; Kishan *et al*. 2012). Each fruit contains two to four flattened seeds with a small wing, with each seed surrounded by its own mericarp. The seeds produce bright yellow oil, which burns well and is also used in medicine (Cowen 1957; Schmelzer 2006). A study of *C. thevetia* growing in South Africa found that the seeds contained 57–63% oil, which, after purification, consisted primarily of oleic acid (60%), palmitic acid (16%), stearic acid (11%), linolenic acid (7%) and linoleic acid (5%; Lippold 1980). This seed oil is used to make a 'paint' with antifungal, antibacterial and antitermite properties (Kareru *et al*. 2010). The species perpetuates itself primarily by seed, but can reproduce vegetatively from broken stems, root cuttings and from intact exposed parts of its root system (Schmelzer 2006; Kishan *et al*. 2012; F. F. Bebawi, unpubl. obs.).

All parts of the plant, including the milky sap and especially the seeds, contain the extremely poisonous cardiac glycoside thevetin (Everist 1974; Covacevich *et al*. 1987; de Padua *et al*. 1999; Randall 2002; Kishan *et al*. 2012; McKenzie 2012), as well as cardiac glycosides of the cardenolide type, such as neriifolin and cerberin (Schmelzer 2006). This makes the plant toxic to most vertebrates. Many cases of intentional and accidental poisoning of humans are known to have occurred (Langford and Boor 1996; Fonseka *et al*. 2002; de Silva *et al*. 2003). An extract from this plant has also been reported to possess antifertility and/or spermicidal activity (Gupta *et al*. 2011).

Several bird species are known to feed on the fruit of *C. thevetia* without any ill effect, including the Asian koel (*Eudynamis scolopaceus*; Krishnan 1952; Kannan 1991), red-whiskered bulbul (*Pycnonotus jocosus*; Raj 1963), white-browed bulbul (*Pycnonotus luteolus*; Raj 1959), red-vented bulbul (*Pycnonotus cafer*; Raj 1963), brahminy myna (*Sturnia pagodarum*; Rajasingh and Rajasingh 1970), common myna (*Acridotheres tristis*; Krishnan 1952) and common grey hornbill (*Tockus birostris*; Neelakantan 1953). Australian birds, such as the sulphur-crested cockatoo (*Cacatua galerita*; Bebawi *et al*. 2015), little corella (*Cacatua sanguinea*; Bebawi *et al*. 2015), red-tailed black cockatoo (*Calyptorhynchus magnificus*; Bebawi *et al*. 2015) and rainbow lorikeet (*Trichoglossus haematodus*; Bebawi *et al*. 2015), have also been observed to feed on the sap flowing from cut terminals of stem branches, as well as on seeds on the tree after extracting them from mature pods with their sharp beaks (Fig. 1; Bebawi *et al*. 2015). In addition, Australian mammals, such as flying foxes (*Pteropus* spp.; Bebawi *et al*. 2015), livestock and insects, such as native ants, feed on the fruit pulp and assist in seed dispersal, suggesting that seeds can be dispersed by animals (i.e. zoochory; Bebawi *et al*. 2015). Hydrochory (dispersal by water flow, rain and/or floods) also plays a major role in the seed dispersal of *C. thevetia* because mature pods float in water (F. F. Bebawi, unpubl. obs.). In Ghana and Australia, the foliage of *C. thevetia* is sometimes grazed by livestock, especially cattle and goats (Adjei 2003; Bebawi *et al*. 2015).

C. thevetia is a high-impact, invasive, woody weed of riparian habitats, a threat to rangeland biodiversity in Australia (Grice and Martin 2005) and a declared weed (Category 3 Restricted Matter) under State Legislation in Queensland (*Biosecurity Act 2014* – Schedule 2, Part 2; www.legislation.qld.gov.au (accessed 20 July 2016)). Dense thickets along creek lines and floodplains may severely degrade productive land. *C. thevetia* may threaten the sustainability of some grazing enterprises through diminishing economic returns (Grice and Martin 2005) because it out-competes most pasture species found beneath its canopy.

The National Weeds Program requires information on the ecology of target weed species before control or eradication strategies are designed (Csurhes and Edwards 1998; GRDC 2007; Dyer 2008; Rural Industries Research and Development Corporation 2010). The aims of the present study were to assess seed fall, seed predation, twigging and amount of litter fall for the peach biotype of *C. thevetia* (Fig. 2). Twigging is used to describe when terminal young branches (often the last 20–40 cm) are chewed and cut-off by birds, causing them to drop to the ground beneath the canopy. This process was considered important in the present study because twigging is similar to garden management practices imposed by humans. For example, stem tips of young plants of *C. thevetia* are pinched out to encourage a bushy habit and, once established, plants are pruned to shape and size before the growing season to induce profuse flowering (Schmelzer 2006). Litter fall production was considered important in the present study because of its potential allelopathic effects (Schmelzer 2006). For example, extracts of dried leaf of *C. thevetia* inhibit seed germination and early growth of *Parthenium hysterophorus* L. (Pavithra *et al*. 2012). The present study formed one component of studies to understand the ecology of *C. thevetia* and to better manage it in the dry tropics of northern Australia.

Fig. 1. Sulphur-crested cockatoo (*Cacatua galerita*) feeding on a green, mature pod of *Cascabela thevetia*.

Materials and methods

Site description

The site was a riparian habitat along Will Creek (19°49′S, 146°33′E; elevation 250 m above sea level), near Mingela in north Queensland. The vegetation type was an open eucalypt woodland with a mixture of native and exotic vegetation present in the area (Table 1). The study was undertaken within a ~1000 m × 30 m (L × W) area along both sides of the creek bank. This area was dominated by a shrub layer densely infested with an almost pure stand of the peach biotype of *C. thevetia* (average 63 000 plants, of which 260 were adult). The ground cover beneath the canopy of the infestation was virtually devoid of pasture species, which is an indicator of the toxic effects of this species, as reported by Everist (1974).

Maximum average daily temperature at the study site was 28.5°C in December, compared with a minimum of 17.4°C in July (Fig. 3). Rainfall followed a more-or-less similar pattern to that exhibited by ambient temperature. The climate was monsoonal with a summer rainfall; more than 88% of annual precipitation fell from November to April over both years (Fig. 4). However, rainfall during the first year was 66% greater than that in the second year. Over both years, rainfall was 24% greater than the long-term average rainfall for the area (659 mm).

Study design

The study ran from 14 April 2008 until 31 March 2010 and comprised six permanent plots (5.3 m^2) randomly positioned under pure stands of adult *C. thevetia* plants along a 1-km stretch of the riparian area of either side of the creek bank of Will Creek. The plots were used to collect fruits (i.e. drupes) of *C. thevetia* and any leaves or twigs of *C. thevetia* that fell from the infestation canopy above.

All plots were cleared of any plant material at the beginning of each month. At the end of each month, all plant material lying on the ground in each plot, including drupes (intact and cracked), twigs and leaf litter, was removed using a rake. Plant

Fig. 2. Intact and cracked seed pods, twigs and leaf litter beneath the canopy of the peach biotype of *Cascabela thevetia* at Will Creek, Mingela (Qld, Australia).

Table 1. List of native and exotic vegetation within and in the vicinity of the study site at Will Creek, Mingela (Qld, Australia)

Native vegetation		Exotic vegetation	
Common name	Scientific name	Common name	Scientific name
Black speargrass	*Heteropogon contortus* (L.) P.Beauv. ex Roem. and Schult.	Albizia	*Albizia lebbeck* (L.) Benth.
Black tea tree	*Melaleuca bracteata* F.Muell.	Buffel grass	*Pennisetum ciliare* (L.) Link
Carbeen	*Corymbia tessellaris* (F.Muell.) K.D. Hill and L.A.S. Johnson	Calotrope	*Calotropis procera* (Aiton) W.T.Aiton
Narrow-leaved red ironbark	*Eucalyptus crebra* F.Muell.	Gambia pea	*Crotalaria goreensis* Guill. and Perr.
Pink bloodwood	*Corymbia intermedia* (R.T.Baker) K.D.Hill and L.A.S.Johnson	Indian couch	*Bothriochloa pertusa* (L.) A.Camus
Red bauhinia	*Lysiphyllum cunninghamii* (Benth.) de Wit	Lantana	*Lantana camara* L.
River sheoak	*Casuarina cunninghamiana* Miq. subsp. *cunninghamiana*	Parthenium	*Parthenium hysterophorus* L.
Screw palm	*Pandanus spiralis* R.Br.	Rattle pod	*Crotalaria pallida* var. *obovata* (G.Don) Polhill
Yellow wood	*Terminalia oblongata* F.Muell.	Rubber vine	*Cryptostegia grandiflora* R.Br.
		Snake vine	*Argyreia nervosa* (Burm.f.) Bojer

material was placed inside labelled brown paper bags. Samples were then taken back to the Tropical Weeds Research Centre in Charters Towers for processing. From these samples, monthly seed fall for each plot was calculated by counting all intact drupes plus those that had been split open by birds (i.e. cracked drupes). In the case of cracked drupes, two halves of a cracked drupe were counted as a single fruit. The cracked drupes were almost always devoid of seed and predation was therefore considered to have occurred. In the present study, seed fall and predation calculations were based on an average number of two seeds per drupe. The number of twigs was also recorded and leaf litter was oven dried for 48 h at 80°C and dry weights (DW) recorded.

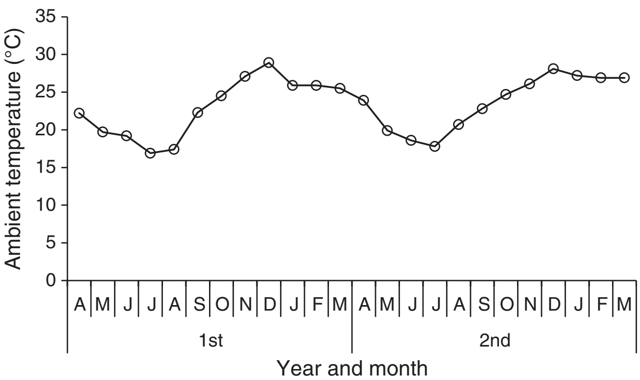

Fig. 3. Monthly ambient temperature recorded during the first (April 2008–March 2009) and second (April 2009–March 2010) years of the study at Will Creek, Mingela (Qld, Australia).

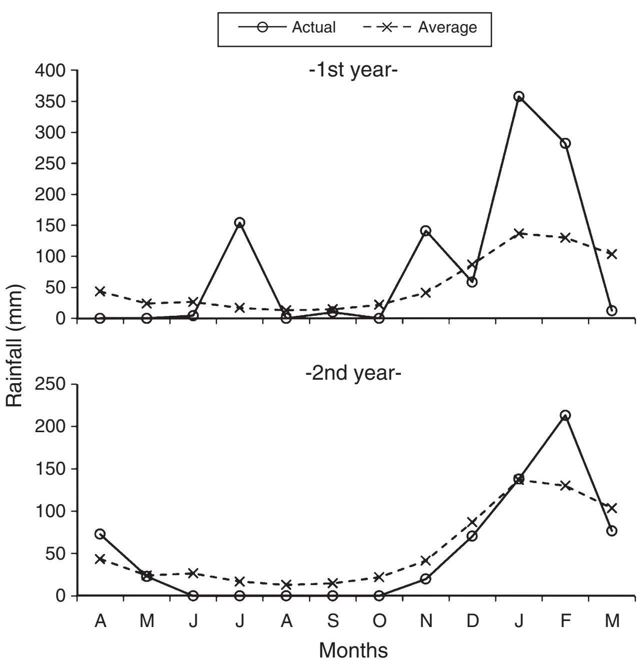

Fig. 4. Monthly rainfall recorded during the (*a*) first (April 2008–March 2009) and (*b*) second (April 2009–March 2010) years of the study at Will Creek, Mingela (Qld, Australia).

To translate seed fall into yield, three lots of 50 ripe drupes were randomly harvested in August from adult trees and measured. The 'x ± y' values mentioned hereafter represent the mean value ± standard error of the mean. Mean (± s.e.m.) drupe fresh weight, DW and moisture content were 14.8 ± 0.6 g, 4.0 ± 0.2 g and 72.9 ± 0.4% respectively. Mean (± s.e.m.) drupe length, width and height were 34.9 ± 0.5, 31.5 ± 0.5 and 29.9 ± 0.4 mm respectively. Seventy seeds were also freshly harvested from random drupes for determination of seed weight, which averaged 0.48 ± 0.01 g per seed.

Results

Seed fall

Seed fall, estimated from fruit fall, occurred in all months of the year, but increased slowly over the late spring and summer period before peaking in mid- to late autumn (April–May) and then declining until October (Fig. 5). A monthly maximum of 5500 ± 650 seeds ha^{-1} was recorded in April during the first year, compared with 3360 ± 420 seeds ha^{-1} in May of the second year. In both years, minimum monthly seed fall was recorded in October, averaging only 400 ± 155 seeds ha^{-1} over both years. Total annual seed fall was 12% greater in the first compared with second year (19 140 ± 2880 vs 17 030 ± 2930 seeds ha^{-1} respectively; Fig. 5).

The infestation produced 9.4 ± 0.2 and 8.4 ± 0.1 kg seed ha^{-1} in Years 1 and 2 respectively. Monthly yields ranged from a minimum of 0.2 ± 0.1 kg ha^{-1} to a maximum of 2.6 ± 0.3 kg ha^{-1}.

Seed predation

Commonly observed seed-eating birds at the study site were the sulphur-crested cockatoo, little corella, red-tailed black cockatoo and rainbow lorikeet. Seed predation was recorded throughout the year, with a highly positive correlation with seed fall ($r = 0.96$; Fig. 6). During peak seed fall periods (April–July), the predation percentage was high, with an average of 69% and 63% during the first and second years, respectively. Across the 2 years, maximum seed predation averaged 2580 ± 485 seeds ha^{-1} during April, compared with a minimum of 180 ± 56 seeds ha^{-1} in December. Total annual

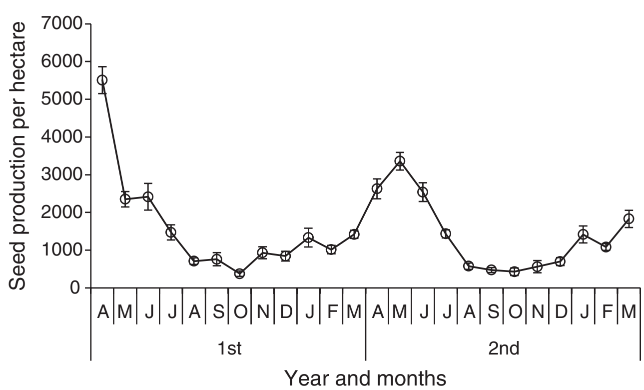

Fig. 5. Mean (± s.e.m.) monthly seed fall for the peach biotype of *Cascabela thevetia* recorded during the first (April 2008–March 2009) and second (April 2009–March 2010) years at Will Creek, Mingela (Qld, Australia).

seed predation averaged 12 140 ± 2570 and 8310 ± 1825 seeds ha^{-1} during the first and second years respectively. This equated to 57% of all seeds produced within the infestation over both years.

Twigging

Twigging occurred across all months except October over both years (Fig. 7). Maximum monthly twigging during the first and second years (290 ± 80 and 110 ± 17 twigs ha^{-1} respectively) occurred in April. The total number of twigs chewed was 800 ± 90 and 400 ± 50 twigs ha^{-1} year^{-1} during the first and second years respectively. There were highly positive correlations between twigging and seed production ($r = 0.97$), as well as between twigging and seed predation ($r = 0.97$).

Litter production

Litter production was variable but occurred in all months of the 2-year study period (Fig. 8). Mean maximum litter production in April in year 1 and in February in year 2 averaged 1050 ± 100 and 1380 ± 1050 kg (DW) ha^{-1}. In contrast, mean minimum litter production in November in year 1 and in May in year 2 averaged 410 ± 70 and 270 ± 25 kg (DW) ha^{-1}. Total annual litter production averaged 7900 ± 640 and 7390 ± 1420 kg (DW) ha^{-1} during the first and second years respectively.

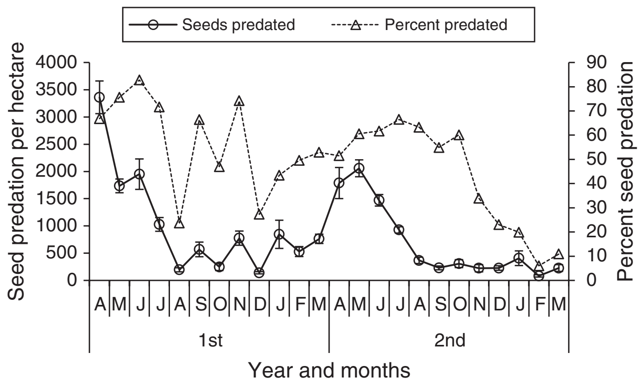

Fig. 6. Mean (± s.e.m.) monthly seed predation and percentage seed predated of the peach biotype of *Cascabela thevetia* recorded during the first (April 2008–March 2009) and second (April 2009–March 2010) years at Will Creek, Mingela (Qld, Australia).

Discussion

The invasive woody weed *C. thevetia* produced fruit all year round in a riparian habitat, although it exhibited a cyclical pattern with distinct low and high periods of production. Seed predation by avian wildlife was found to destroy many of the seeds produced (mean 57%), but a proportion was still regularly available to replenish soil seed reserves. In addition to predating on seeds, the birds also chewed, cut and often removed the terminal parts of young branches, thus contributing to the supply of litter onto the ground surface.

Seed fall

Although there is a paucity of information on seed fall of *C. thevetia*, the range reported in the present study (17 030–19 140 seeds ha^{-1} year^{-1}) is comparable with chinee apple (*Ziziphus mauritiana* Lam.), another woody weed and relatively similar-sized tree to *C. thevetia* that grows in the rangelands of northern Australia. Like *C. thevetia*, chinee apple produces a fleshy fruit containing only a few seeds. In a 2-year study, Grice (1996) found that a population of chinee apple (689 plants ha^{-1}) produced approximately 2800 and 18 000 seeds ha^{-1} in successive years.

The annual pattern of seed fall by *C. thevetia* is consistent with findings reported by Schmelzer (2006) and those of a pot trial (Bebawi *et al*. 2014). Regular replenishment of the soil seed bank appears necessary for *C. thevetia* because the soil seed bank is short lived and in the order of years (F. F. Bebawi, unpubl. data). Rubber vine (*Cryptostegia grandiflora* ex R.Br.) and bellyache bush (Tomley 1998; Bebawi *et al*. 2005) are another two invasive rangeland weeds with the capacity to produce seeds all year round under favourable environmental conditions. In contrast, rangeland weeds such as mesquite (*Prosopis* spp.; Van Klinken and Campbell 2009) and lantana

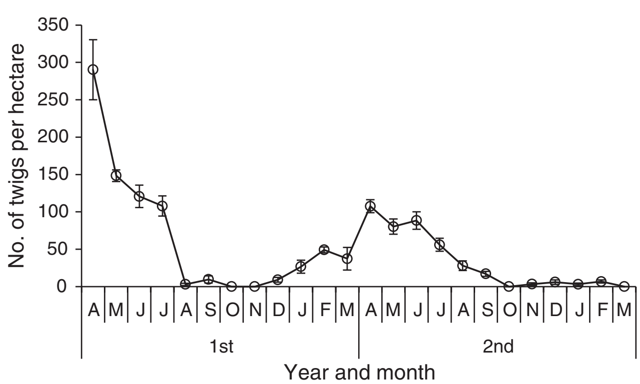

Fig. 7. Mean (± s.e.m.) monthly twig density on the ground beneath the peach biotype of *Cascabela thevetia* recorded during the first (April 2008–March 2009) and second (April 2009–March 2010) years at Will Creek, Mingela (Qld, Australia).

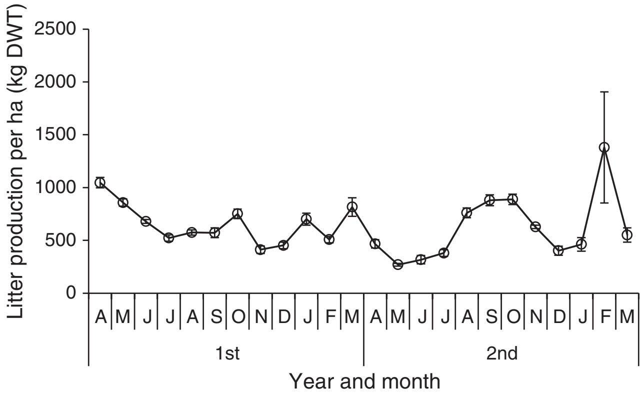

Fig. 8. Mean (± s.e.m.) monthly litter production of the peach biotype of *Cascabela thevetia* recorded during the first (April 2008–March 2009) and second (April 2009–March 2010) years at Will Creek, Mingela (Qld, Australia). DW, dry weight.

(*Lantana camara* L.; Gosper and Vivian-Smith 2006) tend to have distinct periods when seed production occurs.

Although seed fall of *C. thevetia* varied between years, this phenomenon is common among tree species. For example, Dale and Hawkins (1983) found that a heavy seed crop of *Eucalyptus maculata* Hook. in southern Queensland was preceded by at least 2 years of comparatively poor seed yield. Specht (1986) indicated that such variations can be caused by the amount of photosynthate available for floral bud initiation and development, whereas Boland *et al*. (1980) attributed such variations to the degree of pollination, damage by birds and insects and environmental conditions during fruit ripening and development. In the present study, the relatively greater rainfall during the first than second year may have contributed to the variation in seed fall of *C. thevetia* between years. Grice (1996) reported greater seed production of chinee apple when there was higher rainfall.

Seed predation

Seeds play an essential role in the maintenance and spread of invasive weeds, yet they are vulnerable to pre- and post-dispersal predators, some of which may affect the dynamics of weed populations, particularly the weed seed bank (Kremer and Spencer 1989; Landis *et al*. 2005; Schonbeck 2013). Nathan and Muller-Landau (2000) indicated that the distribution and abundance of plants may hinge upon the fate of their seeds. The present study showed that, on average, 57% of seeds produced annually by the peach biotype of *C. thevetia* in the study area were predated by Australian native birds, particularly cockatoos and lorikeets. Similarly, Grice (1996) indicated that red-tailed black cockatoos and sulphur-crested cockatoos appear to be effective seed predators of chinee apple, which can be found growing in association with *C. thevetia* in some areas.

The level of predation recorded for *C. thevetia* appears to be in the moderate range when compared with levels of seed predation elsewhere. For example, in the northern territories of Hong Kong, 73–86% of seeds were removed for four shrubland species and 33–83% of seeds were removed for six grassland species after 60 days (Hang Hau 1997). Similarly, in a tropical dry forest scrub in Mexico, 64% of seeds were removed (Gryj and Dominguez 1996). Researchers have also documented predation on seeds of several agricultural weeds, such as velvetleaf (*Abutilon theophrasti* Medik.) and giant foxtail (*Setaria faberi* R.A.W. Herrm.), often at rates high enough to reduce the current season's input to the seed bank by 80–90% or more (Cardina *et al*. 1996; Davis and Renner 2007).

In the British flora, the large seeds of species that lack seed banks tend to be short lived in the soil (Roberts 1986) and have lax requirements for germination (Thompson 1987). Seed predators often tend to prefer large seeds (Thompson 1987; Hulme 1994, 1996). These attributes of *C. thevetia* have been reported by Bebawi *et al*. (2014, 2015). The absence of seed banks among many tropical trees of north Queensland has been attributed to predation (Hopkins and Graham 1983).

An interesting observation in the present study relates to the 43% of intact seeds that were deposited on the ground beneath the canopy. Predation by avian wildlife and 'hydrochory' may promote distribution of mature green, intact pods on a restricted time scale downstream during floods. Plants use various strategies, including asynchronous fruit ripening, for dispersing seeds. A thorough understanding of how seed dispersal occurs for *C. thevetia* is essential if we want to understand and control the spread of this plant in space and time, especially with evidence of flooding events occurring periodically at Will Creek. Others (Buckley *et al*. 2006; D'Avila *et al*. 2010; Heleno *et al*. 2011) have stressed the importance of information on frugivores and the role of different dispersers at all stages of weed management.

Twigging

The optimal time for maximum seed fall, seed predation and twigging in April coincides with the onset of the breeding season of the sulphur-crested cockatoo and the red-tailed black cockatoo (May–September in northern Queensland; Pizzey and Knight 2007). This may help explain the greater incidence of predation and twigging observed between April and July of each year in the present study.

The process of twigging could have both short- and long-term ecological effects. The short-term effect relates to the annual reduction of seed production potential through loss of fruiting pods that would have developed on the terminal parts of these twigs. One long-term affect arises from the mechanical action involved in the process of twigging; this action leads to increased shooting where dormant axillary buds re-shoot, leading to increased reproductive points on the twigged stem (Smit and Rethman 1998). More reproductive points means potentially more food supply for the local avian fauna. A second long-term effect of twigging is that it simulates artificial pruning, resulting in increased shooting, leading to thickening of the tree canopy; however, this again depends on the intensity and frequency of twigging. For an evergreen plant this may increase the shade factor beneath the canopy, with potentially adverse consequences on ground vegetation that requires light for photosynthesis (Joubert and Zimmermann 2002). Grice (1996) also reported twigging by red-tailed black cockatoos on chinee apple. However, Grice (1996) indicated that canopy feeding by red-tailed black cockatoos often damaged the canopies of large trees.

Litter production

Although litter production of the peach biotype of *C. thevetia* occurred across all months of the year, the *C. thevetia* trees in the present study stayed evergreen through continuous leaf production. In contrast, litter fall of other invasive weeds, such as chinee apple and rubber vine, is strongly seasonal and generally occurs in the dry season between May and September (Grice 1997). Annual litter fall from three contrasting rainforest sites in north-eastern Queensland was found to be strongly seasonal, with the heaviest falls occurring in the latter part of the dry season and the early part of the wet season (Spain 1984).

The absence of any correlation between seed fall and litter production suggests that both plant functions work independently in terms of allocation of nutrient resources. Leaves are produced regardless of the greater energy demand to produce seed. *C. thevetia* can allocate energy to seed production while at the same time replacing leaf loss to sustain growth. This may explain, in part, its success as an invasive species. The litter fall and nutrient dynamics of other plants located in the northern hemisphere, such as that of a *Lithocarpus* or *Castanopsis* montane moist evergreen broad-leaved forest in south-west China, also showed yearly variations in litter production that were attributed to tree masting (Liu *et al*. 2003). The seasonality of litter fall of this particular rainforest in the Chinese study was bimodal, with the primarily litter fall in the late dry season (April–May) and lesser litter fall in early winter (October–November). In the southern hemisphere, some native Australian dry sclerophyll woodland communities also exhibit variations in annual litter fall that may range from 900 to 2700 kg ha^{-1} (Burrows and Burrows 1992). Specht (1981) and Attiwill *et al*. (1978) attributed the seasonal nature of litter fall of some Australian woodland communities to temperature changes, with more litter fall associated with increasing temperatures. This may explain the greater litter fall (although not significant) of *C. thevetia* in the second compared with first year (7900 vs 7390 kg ha^{-1} respectively), although differences in moisture availability may also have been a contributing factor. Observations of *C. thevetia* plants growing in drier environments than the riparian habitat of the present study suggest that these plants can become wilted and not produce new leaf material during dry times. Under such conditions, litter production would also be expected to be higher.

In the present study, the total amount of litter produced per hectare every year by *C. thevetia* (7390–7900 kg) was between that reported for *Flindersia brayleyana* F.Muell. (6440 kg), an endemic Australian plant species found near the eastern and western margins of the Atherton Tableland in north-eastern Australia, and those of tropical rainforest and adjacent forest plantations of *Araucaria cunninghamii* Ait. Ex D.Don. (9830 kg; Brasell and Sinclair 1983). Litter fall production for the peach biotype of *C. thevetia* was also within range for three other contrasting rainforest sites in north-eastern Queensland, which averaged 8807 kg ha^{-1} $year^{-1}$ (Spain 1984), and also within the range reported within the Pacific region, particularly in Papua New Guinea (7550 and 8760 kg ha^{-1} $year^{-1}$; Edwards 1977; Enright 1979). However, litter fall of *C. thevetia* was nearly sixfold greater than that reported by Burrows and Burrows (1992) for the native Australian eucalypt *Eucalyptus crebra* in the 1983–84 season (1200 kg ha^{-1}).

Ecology and management implications

Based on the findings of the present study, *C. thevetia* seeds appear to provide an additional food source for some bird species (e.g. cockatoos and lorikeets) in areas where the plant has naturalised. Despite this predation, some of the seeds are still able to fall to the ground and enter the soil seed bank. Ecologically, this is important for *C. thevetia* given that it has a relatively short-lived seed bank (expires after 2 years).

The large density of younger plants present within the infestation used for the present study suggests that the current level of predation was not preventing seedling recruitment and population expansion from occurring. Consequently, land managers proposing to control infestations of *C. thevetia* will still need to plan for follow-up control of seedling regrowth.

The present study also highlighted the potential physiological strength of *C. thevetia*. Growing in a riparian habitat, it was able to produce litter all year round without any adverse effects on its capability to sustain seed production throughout the year. Avian wildlife also contributed to the supply of litter through the process we describe as twigging. Although, as mentioned previously, we think this could be associated with the birds trying to access the milky sap inside the stems, they could be doing it for other reasons also, such as for beak maintenance (i.e. keeping the beak sharp and worn down) or perhaps to entertain themselves between feeding on the seeds. Whether this pruning effect contributes to canopy thickening and increased fruit production of *C. thevetia* was not quantified in the present study but warrants investigation.

Because litter fall is a major source of fuel for fire (Walker 1981), the high litter yields of *C. thevetia* could provide adequate fuel for a ground fire to occur in most years. The implications of such fires on *C. thevetia* and the surrounding vegetation and whether they may produce toxic fumes should also be determined.

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