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The Biology, Ecology, Distribution and Management of Two Globally Invasive Weeds: *Calotropis procera* (Calotrope) and *Calotropis gigantea* (Giant Calotrope)

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ABSTRACT

Calotropis procera and *C. gigantea* are emerging as globally invasive plants that can significantly alter ecosystems in areas where they have escaped from attended cultivation. Without effective management, these species can form dense monospecific stands, resulting in severe economic, environmental and social impacts. Current control measures for these species are often limited in effectiveness, especially when applied as single-use approaches. To address this issue, this review synthesises key biological and ecological traits, current and potential invasion dynamics and management options available for *C. procera* and *C. gigantea*. Although more detailed investigation is required in some areas, it appears that an integrated approach is emerging as a possible option. Such an approach should consider (i) early detection and preventative strategies, including creating and maintaining competitive pastures and reducing soil disturbance, (ii) biological control, with the potential development and release of host-specific insects and plant pathogens, (iii) chemical control with diverse modes of action, (iv) physical control including manual removal of all plant propagules from the soil and (v) ecological burn programs to remove the aboveground biomass followed by chemical or physical interventions. It is anticipated that the implementation of these strategies is likely to significantly mitigate the impacts posed by established *C. procera* and *C. gigantea* stands, while also addressing and removing newly emerging individuals before they develop robust populations.

1 | Introduction

It is widely recognised that without appropriate and ongoing management interventions, invasive alien plants will continue to pose a serious and ongoing threat towards the economic, environmental and social maintenance of the land in which they have invaded (Kumar Rai and Singh 2020; Kumar et al. 2021). Exacerbating this issue is that the influence of global climate change stressors including (i) increased temperatures and atmospheric carbon dioxide levels, (ii) anthropomorphic land use change, (iii) more frequent stochastic weather events and (iv) variable precipitation rates, are likely to increase the abundance and persistence of these species (Amare 2016; Varanasi et al. 2016; Kaur et al. 2024). In addition, inappropriate or unsuccessful management interventions can further increase the challenges and long-term impacts of these species (Varanasi et al. 2016; Kaur et al. 2024). To address these issues, tailored weed management programs that account for species' biological and ecological traits, including their current and projected distribution, are essential for effective, economic and environmentally sustainable control (Ameena et al. 2025).

Calotropis procera (calotrope) and *C. gigantea* (giant calotrope), have been described as invasive alien plants that are now found within all continents except Antarctica (Parsons and Cuthbertson 2001; Wijeweera, Senaratne, and Dhileepan 2021; Wijeweera, Senaratne, Dhileepan, and de Silva 2021). If left unattended within the landscape, these plants have the capacity to form dense monospecific stands which can significantly alter the surrounding ecosystem which they have invaded (Bebawi et al. 2015; Kanchan and Atreya 2016; Menge, Stobo-Wilson, et al. 2016; Kaur et al. 2021; Wijeweera, Senaratne, and Dhileepan 2021; Wijeweera, Senaratne, Dhileepan, and de Silva 2021). Once established, *C. procera* and *C. gigantea* can strongly compete against and displace agricultural and native species, whilst also restricting the movement of livestock and reducing the carrying capacity of the land (Kanchan and Atreya 2016; Menge, Stobo-Wilson, et al. 2016). Of noticeable concern is that *C. procera* and *C. gigantea* also exhibit various levels of acute toxicity which can result in severe health concerns when ingested by animals or humans with both species being recognised as cardiotoxic and hepatotoxic (Vitelli et al. 2008; Iyadurai et al. 2020). *Calotropis procera* and *C. gigantea* are also allelopathic, with *C. procera* being reported to inhibit the germination and growth of various crops, including *Cucumis sativus* L (cucumber), *Hordeum vulgare* L (barley), *Lactuca sativa* L (lettuce), *Solanum lycopersicum* L (tomato), *Solanum melongena* L (eggplant) and *Triticum aestivum* L (wheat) (Hassan et al. 2015; Radwan et al. 2019; Hussain et al. 2020). *Calotropis gigantea* has also been observed to inhibit many of these species despite not being as widely reported as *C. procera* (Mangal et al. 2014; Malarkodi et al. 2019).

Calotropis procera and *C. gigantea* also have several beneficial uses which has probably contributed to their widespread introduction around the world. Such uses include (i) their ability to be made into various products such as biofuel, fodder, ropes, nets and fishing equipment (Barbosa et al. 2014; Kanchan and Atreya 2016; Batool et al. 2020), (ii) their aesthetical appearance (de Oliveira et al. 2009), (iii) their phytoremediation potential (D'Souzaa et al. 2010) and (iv) their pharmaceutical properties. The latter of which can assist in the treatment of various diseases, illnesses or injuries including asthma, bronchitis, cholera, epilepsy, leprosy, malaria, pneumonia, ringworm infection, smallpox infection, snake bites and toothaches (Kumar and Kumar 2015; Al Sulaibi et al. 2020; Kaur et al. 2021). In parallel with these beneficial uses, *C. procera* and *C. gigantea* have displayed various morpho-physiological adaptations and a wide tolerance of environmental conditions that have allowed them to readily invade new areas (Hassan et al. 2015; Kaur et al. 2021). Although there are a range of management options available, including chemical, cultural and physical actions, these often show limited long-term success when applied as single-use approaches (Vitelli et al. 2008; Dhileepan 2014; Bebawi et al. 2015; Campbell et al. 2015, 2020; Hassan et al. 2015; Al Sulaibi et al. 2020; Wijeweera et al. 2020). To address this concern, this review explores their key biological and ecological traits, including their current and future distribution patterns, to help guide and identify the most appropriate management interventions for their successful long-term control. This review also explores key gaps within the current research that can be utilised to help improve the future management of these two globally invasive alien plants.

2 | Methodology

This review was conducted between August 2025 and March 2026 and explored the available global English literature that directly relates to *C. procera* and *C. gigantea*. The literature search was conducted using Google Scholar by searching the term '*Calotropis procera*' and '*Calotropis gigantea*', plus one or more of the following terms: biology, climate change, control, distribution, ecology, impacts, invasive and management. Each paper that was identified during this process that had these key terms within their title, abstract or presented as a keyword, was scanned in detail to identify its suitability for this review.

3 | Taxonomy and Genetic Diversity

The *Calotropis* genus comprises three distinctive species, *C. procera*, *C. gigantea* and *C. acia* Buch-Ham (milkweed), which are all found within the Asclepiadaceae family (Rahman and Wilcock 1991). *Calotropis procera* and *C. gigantea* are more common than *C. acia*, which is described as a small herb often found in very low abundance across Bangladesh, India and Nepal (Rahman and Wilcock 1991). *Calotropis procera*, which is the more common of the three species, is known by a range of names including calotrope, Indian milkweed, milkweed, rooster tree, rubber bush and sodom apple (Forster 1992). The reported synonyms for *C. procera* include *Asclepias procera* Aiton, *C. busseana* K Schum, *C. heterophylla* Wall, *C. inflexa* Chiov, *C. procera* L Dryand and *C. syriaca* Woodson (Forster 1992; Boulos 2000). There are also reports of two subspecies of *C. procera*, which can be distinguished by their fruit size and ovule numbers, with *C. procera* subsp. *procera* distinguished by slightly larger fruits and having 183 ovules, whilst *C. procera* subsp. *hamiltonii* has smaller fruits and 285 ovules (Forster 1992; Ali and Ali 1989; Hassan et al. 2015). *Calotropis gigantea* is very similar to *C. procera*, and the two species can often be mistaken for each other (Rahman and Wilcock 1991). The common names for *C. gigantea* include akonda, crown flower, dhola akara, giant milkweed, madar and swallowwort (Chaudhary et al. 2017). Synonyms of *C. gigantea* include *Asclepias gigantea* L, *Madorius giganteus* L Kuntze, *Periploca cochinchinensis* Lour and *Steptocaulon cochinchinese* G Don (Kadiyala et al. 2013).

Recent research has developed high-quality chromosome and genome assemblies for *C. procera* and *C. gigantea* which detail high level genomic blueprints of these species (Muriira et al. 2015, 2018; Dash et al. 2019; Gadri et al. 2025). Both species are diploid and have a somatic chromosome number of $2n = 22$ (Dash et al. 2019; Gadri et al. 2025). Genetic studies have shown a moderate level of genetic diversity within *C. procera* and *C. gigantea*, with substantial genetic differences recorded between the two species (Muriira et al. 2018; Majeed et al. 2020). Furthermore, research has also identified distinct genetic groups within these species, with significant genetic-geographic correlations recorded for *C. procera* (Muriira

FIGURE 1 | Physical characteristics of *C. procera*, (A) mature plant, (B) flowers and leaves, (C) ovoid-shaped seed pods and (D) bell-shaped seed pods. Figures provided by Kunjithapatham Dhileepan.

et al. 2018; Majeed et al. 2020). Because this genetic diversity has been identified within both *Calotropis* species, it is likely that they have the capacity to readily adapt to new environments in which they invade by being able to withstand a range of climatic and environmental conditions (Muriira et al. 2018).

4 | Plant Characteristics

4.1 | Physical Description

Calotropis procera is an evergreen, soft-wooded, perennial that typically grows between 1 and 4 m tall, occasionally reaching 6 m (Figure 1) (Amritphale et al. 1984; Parsons and Cuthbertson 2001; Grace 2006; Hassan et al. 2015; Al-Rowaily et al. 2020). Juvenile stems are green to grey and pubescent, developing deeply fissured, cork-like bark upon maturity (Parsons and Cuthbertson 2001; Hassan et al. 2015). Leaves are large (5–20 cm long by 4–10 cm wide), ovate with pointed tips, arranged oppositely and borne on short petioles (0.3–0.4 cm) (Amritphale et al. 1984; Ranade and Acharya 2015; Batool et al. 2020). They exhibit a waxy adaxial surface, abaxially fine white hairs and six prominent veins (Amritphale et al. 1984; Ranade and Acharya 2015). The small (1.5–3 cm wide) bell-shaped flowers are white to pink with purple to brown tips and form umbellate cymes of three to 15 flowers (Amritphale et al. 1984; Boulos 2000; Al Sulaibi et al. 2020). Fruit capsules can vary in shape, being mostly ellipsoid (Figure 1C) to boat-shaped (Figure 1D), but can also be ovoid to spherical. These capsules are coated with a thick sponge pericarp enclosing 350–500 lightweight (0.6 cm by 0.4 cm, 5.9–7 mg) brown seeds bearing silky white pappus (Amritphale et al. 1984; Al Sulaibi et al. 2020). The root system consists of a deep taproot (> 4 m) and numerous lateral roots with a starchy, sponge-like cortex (Amritphale et al. 1984; Grace 2006).

Calotropis gigantea (Figure 2) is also an evergreen perennial with several similar characteristics to *C. procera* (Table 1). However, *C. gigantea* generally grows larger, typically reaching 1–6 m in height and occasionally up to 10 m (Kumar et al. 2021; Dwivedi et al. 2024). Its stems are similar to *C. procera*, but tend to be more cylindrical and erect (Dwivedi et al. 2024). The leaves are also larger (5–30 cm by 2.5–16 cm), elliptic-oblong or obovate in shape, arranged in an opposite phyllotaxy formation and attached to a short petiole (0.3–0.4 cm long) (Ranade and Acharya 2015; Kumar et al. 2021; Dwivedi et al. 2024). The flowers of *C. gigantea* are crown-shaped, white, purple, or lilac in colour, arranged in an umbellate cyme inflorescence and contain three to 15 flowers (Ranade and Acharya 2015; Dwivedi et al. 2024). Fruit capsules are large (6–12 cm long by 3–7 cm wide), ovoid to boat-shaped and contain up to 300 small, obovate, flattened seeds bearing silky white pappus (Kumar et al. 2021; Dwivedi et al. 2024). The root system of *C. gigantea* is also defined as a deep taproot system characterised by several secondary lateral roots (Dwivedi et al. 2024).

4.2 | Reproduction, Dispersal and Establishment

Calotropis procera and *C. gigantea* reproduce both by seed germination and by vegetative propagation through root or stem suckers, which can develop when plant parts become broken or detached from the parent plant (Morcelle et al. 2004; Bebawi et al. 2015; Hassan et al. 2015; Menge, Bellairs, and Lawes 2016).

FIGURE 2 | Physical characteristics of *C. gigantea*, (A) mature plant, (B) flowers and leaves and (C) mature seed pod. Photographs provided by Kunjithapatham Dhileepan.

Pollination and subsequent flowering can occur at any time of the year, although it is more frequent during spring when temperatures rise and insects become more active and contribute to the pollination of the species (Table 2) (Bebawi et al. 2015; Menge et al. 2017; Al Sulaibi et al. 2020; Batool et al. 2020). Flowering of *C. procera* and *C. gigantea* often begins in the second year of growth, or when the plants reach a height of 85 cm and can continuously flower for 2–6 months of the year (Parsons and Cuthbertson 2001; Sobrinho et al. 2013; Bebawi et al. 2015).

Calotropis procera and *C. gigantea* require specialist insect pollinators for successful pollination to occur (Ali and Ali 1989; Menge et al. 2017; Wijeweera, de Silva, et al. 2022; Wijeweera, Senaratne, et al. 2022). This is due to the flowers of *Calotropis* species having a unique, fused gynostemium structure in which their pollen grains are fused into waxy masses known as pollinia (Ali and Ali 1989; Menge et al. 2017). To assist in pollination, a translator mechanism is required. This involves specialist insects, where pollinia is pulled from the flowers and attached to the insect legs via adhesive discs. It is then transferred to another flower (Ali and Ali 1989; Menge et al. 2017). The most common pollinating insects recorded for *C. procera* include *Apis florea* Fabricius (red dwarf honeybee), *A. mellifera* L (western honeybee), *Xylocopa fenestrata* Fabricius (windowed carpenter bee), and *X. pubescens* Spinola (pubescent carpenter bee) (Ali and Ali 1989; Menge et al. 2017). For *C. gigantea*, the most common translators include *A. cerana* Fabricius (Asian honeybee), *Xylocopa caerulea* Fabricius (blue carpenter bee) and *X. fenestrata* Fabricius (windowed carpenter bee) (Wijeweera, de Silva, et al. 2022; Wijeweera, Senaratne, et al. 2022). Although these are some of the more common species, there is a diverse range of insects from the Hymenoptera, Diptera and Hemiptera orders that have also been observed to visit *C. procera* and *C. gigantea* flowers. Specifically, there are several insects from the Apidae, Calliphoridae, Colletidae, Dolichopodidae, Formicidae, Halictidae, Lygaeidae, Megachilidae, Muscidae, Scoliidae and Vespidae families (Menge et al. 2017; Charan et al. 2020; Wijeweera, de Silva, et al. 2022; Wijeweera, Senaratne, et al. 2022).

The time taken to reach maturity and set seed is longer in *C. procera* (412 days) than *C. gigantea* (359 days) (Bebawi et al. 2015). Once pollinated, *C. procera* can produce up to 485 seeds per fruit, whereas *C. gigantea* produces fewer seeds and averages only 126 seeds per fruit, although these numbers can vary based on environmental conditions and the age of the plant (Bebawi et al. 2015; Menge et al. 2017). Interestingly, the number of seeds produced by *C. procera* has been observed to vary between global populations, with the average number of seeds per fruit ranging from 230 ± 19 in India (Sharma and Amritphale 2008), 285 in Pakistan (Ali and Ali 1989), 290 ± 57 to 371 ± 5 in Brazil (Fabricante et al. 2013; Leal et al. 2013), 389 in Sudan (Salem and Algalib 2011) and 433 ± 19 in Australia (Menge, Bellairs, and Lawes 2016). Such differences may be attributed to specific climatic or environmental conditions, or the influence of pre-dispersal seed predation which may result in lower seed output (Ali and Ali 1989; Sharma and Amritphale 2008; Menge, Bellairs, and Lawes 2016). It is also noted that the average time taken between flowering and seed production is longer in *C. procera* (190 days) compared to *C. gigantea* (125 days) (Bebawi et al. 2015). Such differences may be due to seed pod size, number of seeds produced, pollinator availability and the energy requirements of the plant (Bebawi et al. 2015). It is noted that whilst the seeds of *C. procera* and *C. gigantea* primarily fall close to the parent plant, they have the capacity to be transported several hundred metres by the process of anemochory. This process is assisted by the silky white pappi connected to the seeds (Al Sulaibi et al. 2020; Menge and Lawes 2023). These seeds can also be transported via human-mediated dispersal along with the processes of hydrochory and zoochory, with some seeds capable of surviving ingestion from various animals and readily germinating afterwards (Al Sulaibi et al. 2020).

Seed germination requirements of *C. procera* and *C. gigantea* are very similar and generally occur following a rain event between spring and summer (Grace 2006; Bebawi et al. 2015). Maximum germination rates for *C. procera* and *C. gigantea* occur between 23°C and 33°C and take on average 2.58 days to germinate (Labouriau and Valadares 1976; Bebawi et al. 2015; Menge, Bellairs, and Lawes 2016). Germination rates will begin to decline when temperatures reach above 35°C or below 20°C, although seeds can experience environment-imposed inhibition and readily germinate once temperatures return to ideal growing conditions (Brink et al. 2013; Bebawi et al. 2015; Menge, Bellairs, and Lawes 2016). The benefit of environment-imposed inhibition is that the seeds can quickly germinate as soon as conditions become favourable, whereas during physiological dormancy they often require a specific event to break their dormancy (Dalling et al. 2011; Yang et al. 2012). In this respect, although most *C. procera* and *C. gigantea* seeds experience environment-imposed inhibition, some studies have suggested that they may also experience a low-level dormancy (Labouriau and Valadares 1976; Amritphale et al. 1984). High levels of salinity and water stress have also been observed to significantly reduce the germination and growth of *C. procera* and *C. gigantea* (Boutraa 2010; Menge, Bellairs, and Lawes 2016). Water stress in *C. procera* seeds is dependent on temperature, with seeds capable of germinating under slight water stress if temperatures are below 30°C (Menge, Bellairs, and Lawes 2016). This is an adaptive ability that allows for greater germination and early establishment of *Calotropis* species, allowing them to quickly obtain valuable resources such as water compared to surrounding species (Menge, Bellairs, and Lawes 2016).

TABLE 1 | Comparison of the plant characteristics of *C. procera* and *C. gigantea*.[a]

Plant attribute	*Calotropis procera*	*Calotropis gigantea*
Average plant height	1–4 m, sometimes 6 m	1–6 m, sometimes 10 m
Growth habit	Upright and spreading	Cylindrical and erect
Stems	Deeply fissured bark on stems when mature	Fissured and cocky bark when mature
Leaf shape	Ovate, pointed tip	Elliptic-oblong or obovate
Leaf colour	Green to grey	Light green, heart shaped
Flower structure	Bell-shaped to ovoid	Crown-shaped
Flower colour	White to pink with purple-brown tips	White, purple or lilac
Fruit shape	Ellipsoid to boat-shaped or ovoid to spherical	Ovoid to boat-shaped
Number of seeds produced per fruit	250–500	Up to 300
Root system	Deep tap root (down to 4 m) with woody lateral roots	Deep tap root (down to 4 m) with woody lateral roots
Fragrance	Fragrant	No fragrance

[a]Boulos (2000), Ranade and Acharya (2015), Kumar et al. (2021), Al-Rowaily et al. (2020), Al Sulaibi et al. (2020) and Dwivedi et al. (2024).

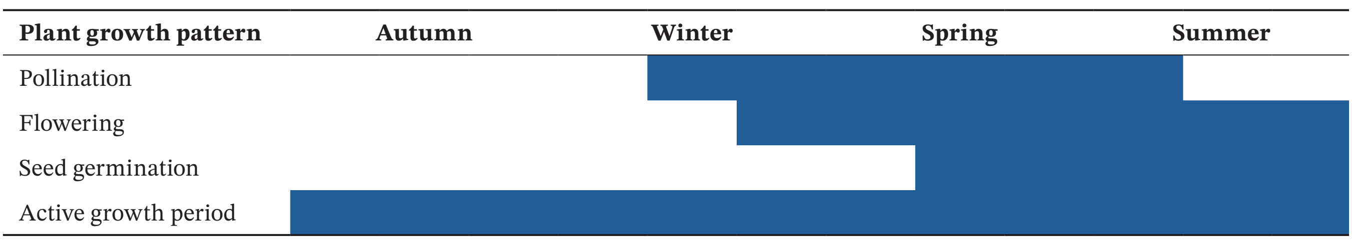
Burial depth plays a critical role in the emergence of *Calotropis* species. Minimal germination occurs on the soil surface (5.8%), while seeds buried at a depth of 3 cm show the highest emergence (88.5%), particularly for *C. procera* (Grace 2006; Leal et al. 2013; Bebawi et al. 2015; Menge, Bellairs, and Lawes 2016). Reduced surface germination is likely due to unfavourable temperature and moisture conditions, whereas burial provides protection from such environmental extremes (Bebawi et al. 2015; Menge, Bellairs, and Lawes 2016). The ability of *C. procera* and *C. gigantea* seeds to germinate from depth suggests they are non-photoblastic, indicating that light is not essential for germination (Leal et al. 2013). Seed longevity in both *C. procera* and *C. gigantea* appears short, with viability typically lasting 1–3 years under field conditions (Grace 2006; Bebawi et al. 2015).

5 | Distribution, Habitat Requirements and Invasion Risk

5.1 | Distribution

Calotropis procera and *C. gigantea* can be found growing across a diverse range of Köppen-Geiger climate types, these being dry, temperate and tropical climates (Parsons and Cuthbertson 2001; Campbell et al. 2013; Al Sulaibi et al. 2020; Rivas et al. 2020). *Calotropis procera* is known to

TABLE 2 | Average seasonal growth patterns of *C. procera* and *C. gigantea*.[a]



[a]Blue shading represents the average seasonal growth pattern for both *C. procera* and *C. gigantea* (Bebawi et al. 2015; Hassan et al. 2015; Menge, Stobo-Wilson, et al. 2016; Menge et al. 2017; Al Sulaibi et al. 2020; Batool et al. 2020).

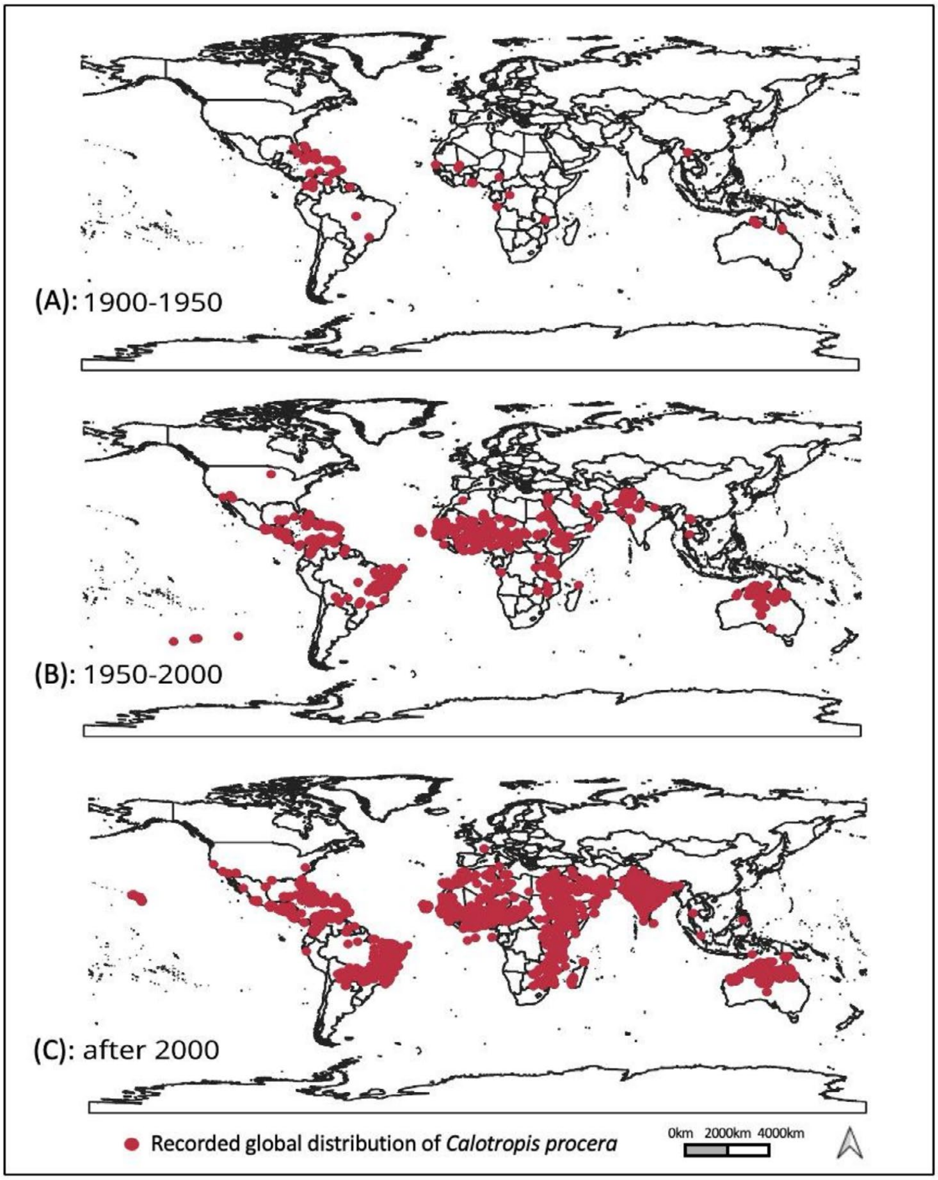


FIGURE 3 | Recorded distribution of *Calotropis procera* grouped by year (A) 1900–1950, (B) 1950–2000 and (C) after 2000. Data of the species global recorded occurrence was obtained from the Global Biodiversity Information Facility (2025a), with a total of 26 145 recorded occurrences from 413 published datasets. https://doi.org/10.15468/dl.4x2j3F.

be native to several countries across Africa (Algeria, Angola, Egypt, Ethiopia, Gambia, Ghana, Kenya, Libya, Madagascar, Morocco, Nigeria, Somalia, Sudan, Tanzania and Uganda), and Asia (Afghanistan, India, Iran, Israel, Jordan, Malaysia, Myanmar, Nepal, Oman, Pakistan, Saudi Arabia and Yemen) (Rahman and Wilcock 1991; Parsons and Cuthbertson 2001). On the other hand, *C. gigantea* is only reported as native within Asia (Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Iran, Laos, Malaysia, Myanmar, Nepal, Pakistan, Philippines, Sri Lanka, Thailand and Vietnam) (Dhileepan 2014; Wijeweera, Senaratne, and Dhileepan 2021; Wijeweera, Senaratne, Dhileepan, and de Silva 2021). However, outside of these areas, *C. procera* and *C. gigantea* have now been found to occupy a large area across Africa, Asia, North America, Oceania and South America, with their distribution expanding significantly over the last century (Figures 3 and 4). Of particular interest, *C. procera* can now be found growing as a cultivated plant or invasive species within Africa (Seychelles and South Africa), Oceania (Australia), Asia (Thailand and Vietnam), North America (Mexico and the United States of America) and South America (Argentina, Bolivia, Brazil, Colombia, Venezuela, Peru and Paraguay) (Rahman and Wilcock 1991; Parsons and Cuthbertson 2001; Ellison and Barreto 2004; Dhileepan 2014). Likewise, *C. gigantea* has also been recognised as a cultivated plant or invasive species within Africa (Algeria, Angola, Burkina Faso, Gabon, Ghana, Kenya, Mauritius, Mozambique, Seychelles, Sudan, Tanzania and Zaire), Asia (Afghanistan), Oceania (Australia, Fiji and Papua New Guinea), Northern America (Hawaii and Mexico) and South America (Brazil, Guyana, Suriname and Venezuela) (Kumar et al. 2013; Kadiyala et al. 2013; Witt et al. 2018).

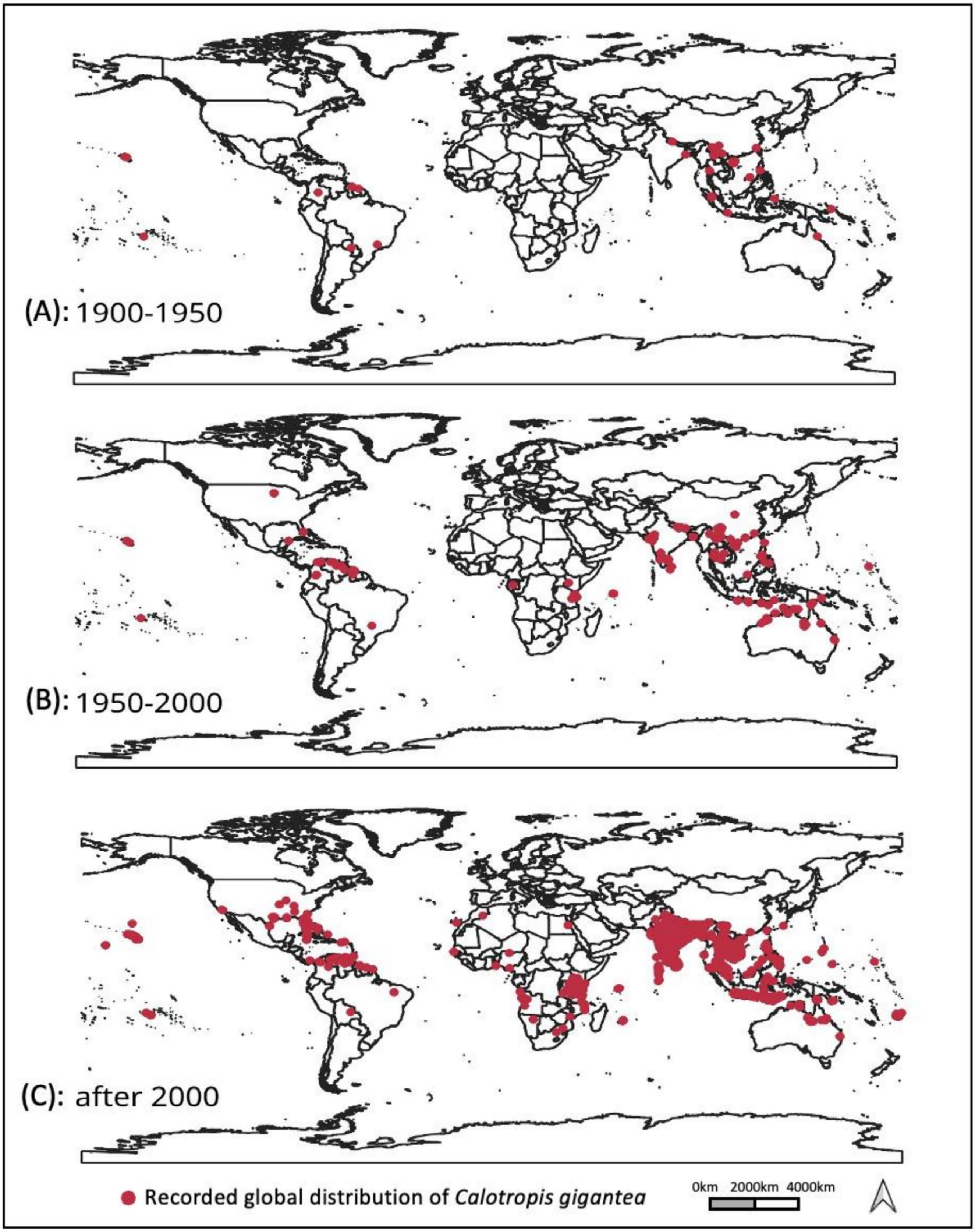


FIGURE 4 | Recorded distribution of *Calotropis gigantea* grouped by year (A) 1900–1950, (B) 1950–2000 and (C) after 2000. Data of the species global recorded occurrence was obtained from the Global Biodiversity Information Facility (2025b), with a total of 7369 recorded occurrences from 145 published datasets. https://doi.org/10.15468/dl.cu8seB.

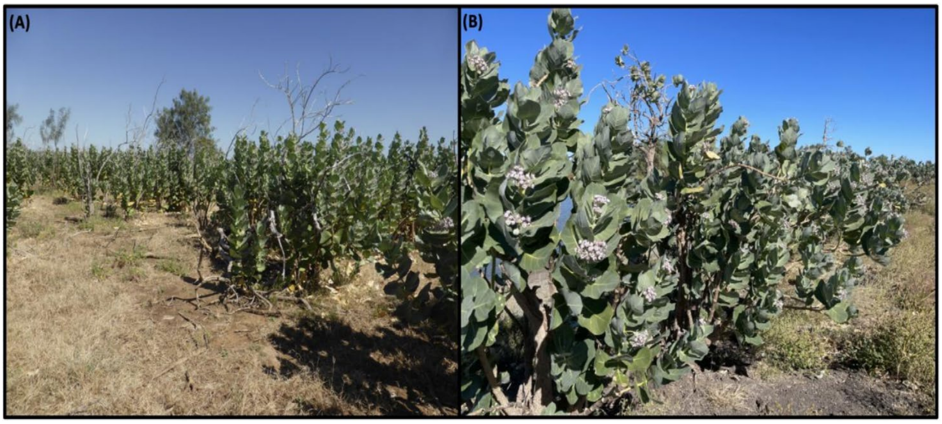


FIGURE 5 | Dense infestation of *C. procera* within Queensland, Australia, (A) landscape view and (B) close up of the infestation. Photographs provided by Kunjithapatham Dhileepan.

The distribution and spread of *C. procera* and *C. gigantea* from their native to non-native areas around the world has been mostly attributed to their deliberate human movement for both their medicinal and ornamental uses (Parsons and Cuthbertson 2001; Campbell et al. 2013; Al Sulaibi et al. 2020; Rivas et al. 2020). For example, *C. procera* was introduced into Australia for its ornamental use but also came as a seed contaminant within the padding of camel saddles imported from India in the early 1900s (Parsons and Cuthbertson 2001; Campbell et al. 2013; Dhileepan 2014). Since its introduction, it is estimated that *C. procera* has now spread over 3.7 million hectares across the arid and semi-arid regions of Northern Territory, Queensland and Western Australia (Figure 5) (Campbell et al. 2013, 2015). It has also been introduced for ornamental and forage purposes across South America during the nineteenth century, where it soon became an aggressive invader across Brazil before quickly becoming established in several surrounding countries, particularly Bolivia, Columbia, Venezuela, Peru and Paraguay (Frosi et al. 2013; Al Sulaibi et al. 2020; Rivas et al. 2020). The distribution of *C. gigantea* is not as vast as *C. procera*, although it too was introduced into many countries for its ornamental and medicinal purposes or as a seed contaminant (Friedel 2020).

5.2 | Habitat Requirements

Calotropis procera and *C. gigantea* are commonly found in areas with an average daily temperature between 20°C and 30°C, and with an annual precipitation range between 150 and 1000 mm (Alwadi and Abulfatih 1996; Sharma et al. 2012; Kumar et al. 2013). Both of these species can also survive across a range of soil types, including alkaline to saline soils, although they are more commonly found within free-draining sandy or very coarse textured (gravel-like) soils with good nutrient availability (Alwadi and Abulfatih 1996; Sharma et al. 2012; Divya and Singh 2021). Stunted or slower growth has been reported in areas with frost-like conditions, heavy clay soils, low nutrient levels and within regions with poor drainage (Alwadi and Abulfatih 1996; Sharma et al. 2012). Growth is also slower in regions with shallow soils or soils over unfractured rock (Sharma et al. 2012). There is very little or no morphological difference between *C. procera* plants that grow at low altitudes (0–300 m) and high altitudes (1700–2000 m), suggesting that the species has the adaptive ability to survive across a diverse set of regions (Alwadi and Abulfatih 1996). On a local scale, *C. procera* and *C. gigantea* are described as widespread pioneer species that can survive a range of habitats and are commonly found growing within disturbed areas, grasslands, coastal dunes, roadsides, riverine flats and disturbed or overgrazed agricultural regions (Parsons and Cuthbertson 2001; Divya and Singh 2021).

5.3 | Invasion Risk

Over the next decade, it is anticipated that the distribution of *C. procera* and *C. gigantea* will continue to expand into new areas or areas where it is currently only found in low abundance (Campbell et al. 2013; Bebawi et al. 2015; Menge, Stobo-Wilson, et al. 2016; Wijeweera, Senaratne, and Dhileepan 2021; Wijeweera, Senaratne, Dhileepan, and de Silva 2021; Gonçalves-Oliveira et al. 2022). Based on ecological and climatic modelling, it has been suggested that the influence of anthropogenic activities, such as climate change, in addition to land use change and increased human-mediated disturbance, will likely be a key driver for their increase and unintentional spread (Bebawi et al. 2015; Menge, Stobo-Wilson, et al. 2016; Wijeweera, Senaratne, and Dhileepan 2021; Wijeweera, Senaratne, Dhileepan, and de Silva 2021). Of particular concern is that the influence of climate change may also increase the length of the fruiting season of these species, which will further aid in their abundance and distribution across the landscape (Menge, Stobo-Wilson, et al. 2016). Based on temperature and rainfall projections in Australia, it is anticipated that *C. procera* may expand its range between 22.2% and 715.8% across the Northern Territory, Queensland and Western Australia (Campbell et al. 2015). Similarly, it is also anticipated to increase in abundance within dry biomes across South America (Gonçalves-Oliveira et al. 2022). Adding to the expansion of *C. procera* and *C. gigantea*, both species have been reported to have high plasticity, which allows them to continue to adapt and readily establish across a diverse range of environments (Menge and Lawes 2023; Iqbal et al. 2024). Of particular interest, these species have a range of structural and functional features which could enhance their ability to invade new areas. These include (i) deep root system, (ii) lignification of vascular tissues, (iii) thickening of the epidermis, (iv) enhanced biomass and chlorophyll production, (v) total antioxidant activity, (vi) enlargement of its storage parenchymatous tissues and (vii) wind-mediated seed dispersal mechanisms (Menge and Lawes 2023; Iqbal et al. 2024). Such traits will likely contribute to their future expansion under predicted climatic and ecological models (Campbell et al. 2015; Menge and Lawes 2023; Iqbal et al. 2024).

6 | Management Options

6.1 | Early Detection and Prevention

Calotropis procera and *C. gigantea* become challenging and costly to control if appropriate management interventions are not applied at the early stages of invasion (Vitelli et al. 2008; Bebawi et al. 2015; Al Sulaibi et al. 2020; Rivas et al. 2020; Divya and Singh 2021). To minimise these impacts, it is important to implement various preventative and early detection strategies to quickly identify and control these species before they have the opportunity to establish robust populations (Bebawi et al. 2015; Campbell et al. 2015). Various measures may include (i) limiting soil disturbance and grazing pressure in areas with known infestations, (ii) maintaining good on-farm biosecurity and hygiene, (iii) quickly controlling any plants as soon as they are identified and (iv) regularly monitoring areas around known infestations to identify any spread of the species across the landscape (Vitelli et al. 2008; Bebawi et al. 2015; Sheffield and Dugdale 2020). It is also suggested that the introduction of local or community-based education or science programs should be developed in regions where *Calotropis* species currently invade or have the potential to invade. Such programs, assisted by national phytosanitary regulations, would assist in mitigating the spread and improve the early detection and control of these species.

To assist in the area of weed detection, there is a range of emerging technology that could be used to help identify *C. procera* and *C. gigantea* across the landscape (Roberts and Florentine 2024). Such examples include the use of (i) field robotics, such as autonomous vehicles (Sujaritha et al. 2017), (ii) proximal sensing (Rançon et al. 2023), (iii) remote sensing (Sheffield and Dugdale 2020) and (iv) unmanned aerial vehicles such as drones (Esposito et al. 2021). Although *C. procera* has only been a minor subject of such research, with little work yet to be done on *C. gigantea* (Alharthi et al. 2020; Borana and Yadav 2020). Such spatial technology has the potential to enhance the capability of land managers to quickly identify these weeds across the landscape (Roberts and Florentine 2024). This is particularly important in regions that may not be easily accessible and if left unchecked, could result in robust *C. procera* or *C. gigantea* populations developing (Kumar Rai and Singh 2020; Rilov et al. 2023). Such technology has already been implemented to support the management of various woody weeds, including *Ailanthus altissima* Miller Swingle (Tree of Heaven) (Naharki et al. 2024), *Chromolaena odorata* L King & Robinson (Siam weed) (Gautam et al. 2025), *Elaeagnus commutate* Bernh ex Rydb (silverberry), *Populus tremuloides* Michaux (Quaking aspen) and *Symphoricarpos occidentalis* Hooker (western snowberry) (Pu et al. 2025).

6.2 | Chemical Control

A range of herbicides with diverse modes of action have been investigated and used to control *C. procera* and *C. gigantea* (Table 3). Herbicide application techniques include (i) aerial application, (ii) basal bark application, (iii) cut stump application, (iv) foliar application and (v) soil-based application (Vitelli et al. 2008; Campbell et al. 2015; Biosecurity Queensland 2024). Foliar application with different modes of action has been investigated by Vitelli et al. (2008), and it was identified that imazapyr (ALS inhibitor) and metsulfuron-methyl (ALS inhibitor) provided the highest mortality of *C. procera*. 2,4-D amine (auxin mimic), a combination of imazapyr and glyphosate (EPSP inhibitor), or picloram-based (auxin mimic) herbicides have also shown satisfactory mortality rates in *C. procera*, particularly when applied to plants less than 1.5 m in height (Parsons and Cuthbertson 2001; Campbell et al. 2015). Indeed, smaller plants (less than 1.5 m in height) will generally obtain greater mortality compared to larger plants when treated using any foliar-based application method (Campbell et al. 2015). For larger plants, a combination of imazapyr and glyphosate, or metsulfuron-methyl will achieve greater mortality; however, these results may vary depending on surrounding environmental conditions or the current health of the plant (Vitelli et al. 2008; Campbell et al. 2015). To obtain greater efficacy when applying these herbicides, it has been suggested that the use of a paraffinic oil surfactant will help to increase uptake by the plant (Biosecurity Queensland 2024).

For larger plants (≤ 2 m) or dense infestations, aerial or ground application of hexazinone (PS II Serine 264 inhibitor) or tebuthiuron (PS II Serine 264 inhibitor) can control *C. procera* with varying success (Campbell et al. 2015; Biosecurity Queensland 2024). However, off-target damage and environmental regulations must be considered to minimise unintended impacts (Campbell et al. 2015; Biosecurity Queensland 2024). It is also important to note here that such chemical application may not be suitable for all environments; thus, careful consideration is needed to ensure the application is appropriate to limit any unwanted impacts to the surrounding environment. In some cases, more specific or targeted chemical control is required to reduce these risks or to treat small or isolated patches of *C. procera* and *C. gigantea*. This can be achieved through the use of basal bark and cut stump treatments (Vitelli et al. 2008; Campbell et al. 2015). When applying these application techniques, 2,4-D butyl ester (auxin mimic), fluroxypyr (auxin mimic), triclopyr (auxin mimic) and a combination of triclopyr and picloram-based herbicides have shown to obtain high levels of mortality ($>80\%$) for *C. procera* (Vitelli et al. 2008). Herbicides containing the active ingredients fluroxypyr, glyphosate, picloram and triclopyr have also shown a high level of success in controlling *C. procera* when applied as either a basal bark or cut stump application (Campbell et al. 2015; Biosecurity Queensland 2024). For cut stump treatments, stems should be cut as low as practical (<20 cm) without contaminating the stump surface with soil or debris, and herbicide applied immediately to maximise uptake (Vitelli et al. 2008). *Calotropis procera* plants that are cut closer to the ground (less than 5 cm) will obtain higher mortality rates and less re-sprouting compared to those cut higher (>20 cm) above the ground level (Vitelli et al. 2008). The use of 2,4-D butyl ester, fluroxypyr, triclopyr and a combination of triclopyr and

TABLE 3 | Summary of the herbicides and their modes of action used to control *C. procera* and *C. gigantea*.

Herbicide group and chemical family	Herbicide (active constituent)	Mode of action	References
Group 2: Sulfonylureas	Metsulfuron-methyl	ALS inhibitors: Inhibition of acetolactate synthase, and acetohydroxyacid synthase (AHAS)	(Vitelli et al. 2008; Crop Life Australia 2025)
Group 2: Imidazolinones (IMIs)	Imazapyr	ALS inhibitors: Inhibition of acetolactate synthase, and acetohydroxyacid synthase (AHAS)	(Parsons and Cuthbertson 2001; Vitelli et al. 2008; Campbell et al. 2015; Crop Life Australia 2025)
Group 4: Phenoxy-carboxylates (Phenoxys)	2,4-D amine	Auxin mimics: Disruptors of plant cell growth	(Vitelli et al. 2008; Campbell et al. 2015; Crop Life Australia 2025)
Group 4: Pyridine carboxylates (Pyridines)	Clopyralid	Auxin mimics: Disruptors of plant cell growth	(Parsons and Cuthbertson 2001; Vitelli et al. 2008; Crop Life Australia 2025)
Group 4: Benzoates	Dicamba	Auxin mimics: Disruptors of plant cell growth	(Vitelli et al. 2008; Crop Life Australia 2025)
Group 4: Pyridyloxy-carboxylates	Fluroxypyr	Auxin mimics: Disruptors of plant cell growth	(Vitelli et al. 2008; Biosecurity Queensland 2024; Crop Life Australia 2025)
Group 4: Pyridine carboxylates (Pyridines)	Picloram	Auxin mimics: Disruptors of plant cell growth	(Parsons and Cuthbertson 2001; Vitelli et al. 2008; Campbell et al. 2015; Biosecurity Queensland 2024; Crop Life Australia 2025)
Group 4: Pyridyloxy-carboxylates	Triclopyr	Auxin mimics: Disruptors of plant cell growth	(Vitelli et al. 2008; Biosecurity Queensland 2024; Crop Life Australia 2025)
Group 5: Triazinones	Hexazinone	Photosynthesis inhibition: Inhibits photosynthesis via blocking electron transport at photosystem II (PSII) on D1 Serine 264 binders and other non-histidine binders	(Biosecurity Queensland 2024; Crop Life Australia 2025)
Group 5: Ureas	Tebuthiuron	Photosynthesis inhibition: Inhibits photosynthesis via blocking electron transport at photosystem II (PSII) on D1 Serine 264 binders and other non-histidine binders	(Vitelli et al. 2008; Crop Life Australia 2025)
Group 9: Glycines	Glyphosate	EPSP inhibition: Inhibition of 5-enolpyruvyl shikimate-3 phosphate synthase	(Parsons and Cuthbertson 2001; Campbell et al. 2015; Biosecurity Queensland 2024; Crop Life Australia 2025)

picloram have shown over 80% mortality rates when using this method (Vitelli et al. 2008). Direct stem injection with glyphosate has also shown success in controlling *C. procera* in sensitive areas; although such method can be costly and time-consuming and may not be practical for large or dense infestations (Kavana et al. 2024).

Despite there being a range of research conducted on the chemical control of *C. procera* (Vitelli et al. 2008; Campbell et al. 2015), further research is still needed to explore the influence of various herbicides on *C. gigantea*. Also, although combinations of herbicides have been tested to control *C. procera*, not all combinations may be suitable for all treatment areas (Ou et al. 2018; Kavana et al. 2024). Future research should be tailored around identifying a range of application techniques and herbicides that provide over 80% control of *C. procera* and *C. gigantea* for registration purposes. Application techniques appropriate for both species include foliar (aerial and ground), cut-stump, basal stem,

stem injection and the application of herbicide to the soil at the base of the targeted plants.

6.3 | Cultural Control

Soil disturbance created by inappropriate stocking rates or pasture management can create ideal growing conditions for *C. procera* and *C. gigantea* (Grace 2006; Bebawi et al. 2015). With *Calotropis* plants reaching reproductive maturity in less than 2 years, it is important for management to act promptly to prevent seed development and subsequent germination of new seedlings in these areas (Bebawi et al. 2015). One method to prevent the establishment of *C. procera* and *C. gigantea* is creating and maintaining competitive pastures with limited soil disturbance (Vitelli et al. 2008; Bebawi et al. 2015). Research by Bastin et al. (2003) found that a combination of light stocking rates and good pasture management can reduce the emergence of *Calotropis* species. In particular, it was shown that several perennial species, such as *Cenchrus ciliaris* L (buffel grass), *Dichanthium* species (bluegrass) and *Heteropogon contortus* L Roem and Schult (bunch spear grass), in addition to light stocking rates, all created competitive conditions that can reduce *Calotropis* establishment (Bastin et al. 2003). While good pasture management is critical, it is always important to choose climatically suitable species that can withstand localised environmental conditions, and to be cautious of not introducing non-native species that may result in further environmental impacts (Parsons and Cuthbertson 2001). It has been noted that even with good pasture management, there is still the likelihood of *Calotropis* species emerging. As a consequence, an integrated approach that uses a range of management interventions such as chemical control or physical removal would be necessary to quickly remove the plants before they have the ability to establish across the landscape (Vitelli et al. 2008).

The use of fire has also been suggested as a potential weed management technique for *C. procera* and *C. gigantea*. Although this technique has the potential to limit the establishment of plants, the use of fire in isolation is unlikely to cause complete mortality of the plants as they can readily resprout from their root system (Parsons and Cuthbertson 2001; Grace 2006; Campbell et al. 2015). On the other hand, prescribed fire regimes at regular intervals or at different intensities could be used to remove or weaken the aboveground biomass of the species (Campbell et al. 2015). For this technique to provide a level of success, it should be integrated alongside other options including chemical, competitive pasture management, mechanical control or physical removal. However, such an integrated combination warrants further investigation to determine its effectiveness and may not be suitable to all environments in which the plants are found (Campbell et al. 2015).

6.4 | Physical and Mechanical Control

Physical and mechanical control of *C. procera* and *C. gigantea* can have varying results, although if integrated alongside other control methods, it can provide high success rates (Parsons and Cuthbertson 2001; Campbell et al. 2015, 2020; Hassan et al. 2015). To ensure appropriate control is achieved, the physical removal of any *Calotropis* species must include its roots and plant fragments from the soil (Parsons and Cuthbertson 2001; Hassan et al. 2015; Campbell et al. 2020). If part of the plant remains within the soil, it has the capacity to quickly reshoot using its stored energy reserves (Parsons and Cuthbertson 2001; Grace 2006; Campbell et al. 2015). Campbell et al. (2020) found that medium-sized *C. procera* plants that were cut at ground level using a pruning saw or mattock, were able to successfully regrow and even produce more stems than uncut plants after 4 months. On the other hand, plants that were cut to a depth of 10 or 20 cm below the surface soil manifested high mortality rate (Campbell et al. 2020). This suggests that the use of ploughs or other mechanical cutting devices to a minimum depth of 20 cm would be required to achieve a level of mortality of the species (Campbell et al. 2020). This technique would only be suitable to certain environments such as agricultural fields to avoid unwanted environmental impacts such as large soil disturbance events. It is also suggested that post-mechanical control such as creating competitive pastures, chemical control and physical control should be integrated to limit any potential re-emergence from the existing soil seed bank (Vitelli et al. 2008; Campbell et al. 2020). While this study was focused on *C. procera*, such methods may be appropriate for *C. gigantea* due to its similar biological and ecological characteristics, although further investigation to determine the actual depth of mechanical control needed for *C. gigantea* mortality is required.

6.5 | Biological Control

Several prospective biological control agents have been identified around the world for the control of *C. procera* and *C. gigantea* (Tables 4a and 4b) (Wilkinson et al. 2005; Sudan et al. 2013; Dhileepan 2014; Kiran et al. 2020; Wijeweera et al. 2020). Opportunistic surveys and literature search studies have identified over 65 insect species and five mite species feeding on *C. procera* and *C. gigantea* (Dhileepan 2014). While some of these species have the potential to be used as a biological control agent, it was evident that most of the leaf-feeding and stem-boring insects have a wide host range, thus, they are not suitable as a biological control agent for *C. procera* and *C. gigantea* (Dhileepan 2014).

Of the insect biological agents identified, *Dacus persicus* Hendel (Aak fruit fly), *D. longistylus* Wiedemann (sodom apple fruit fly) and *Paramecops farinosus* Schoenherr (Aak weevil) (Figure 6), which all feed on the fruit and seeds of *C. procera* and *C. gigantea*, have been identified as prospective biological control agents (Dhileepan 2014; Ali and Shabbir 2017; Ali et al. 2020, 2021; Wijeweera et al. 2020; Wijeweera, Senaratne, and Dhileepan 2021; Wijeweera, Senaratne, Dhileepan, and de Silva 2021; Wijeweera, de Silva, et al. 2022; Wijeweera, Senaratne, et al. 2022). *Paramecops farinosus* feeds externally on the leaves, flowers and flower buds of *C. procera* and *C. gigantea*, with their larvae also feeding on developing seeds and fruit capsules (Sudan et al. 2013; Wijeweera et al. 2020; Ali et al. 2021). Although these feeding habits cause significant damage to the plants, the low dispersal ability of *P. farinosus* can limit its successful long-term establishment across a wide geographic area (Wijeweera et al. 2020; Ali et al. 2021). The larvae of *D. persicus*

TABLE 4a | Summary of prospective insect biological control agents for *C. procera* and *C. gigantea*.

Target species	Species	Mode of action	Suitability	References
C. procera	*Crossotus* species (fringed flounder)	Stem borer. Host range unknown.	Potential, further investigation recommended.	(Al Dhafer et al. 2012)
	Epischnia ragonotella Rothschild (snout moth)	Feeds on the leaves of the plant. Host range unknown.	Potential, further investigation recommended.	(Al Dhafer et al. 2012)
	Niphona grisea Breuning (flat-longhorn beetle)	Stem borer. Host range unknown.	Potential, further investigation recommended.	(Al Dhafer et al. 2012)
	Ptyelus nebulosus Fab (raintree spittlebug)	Feeds on the leaves of the plant. Host range unknown.	Potential, further investigation recommended.	(Jana et al. 2012)
	Tegolophus calotropi Chakrabarti & Mondal (mite)	Feeds on the leaves of the plant. Host range unknown.	Potential, further investigation recommended.	(Chakrabarti and Mondal 1979)
	Thalerastria mesozona Hampson (owlet moth)	Feeds on the leaves of the plant. Host range unknown.	Potential, further investigation recommended.	(Al Dhafer et al. 2012)
C. procera and *C. gigantea*	*Paramecops farinosus* (Aak weevil)	Feeds on the leaves and the fruits of the plant.	Yes, further investigation recommended.	(Dhileepan 2014; Ali and Shabbir 2017; Wijeweera et al. 2020; Ali et al. 2021; Wijeweera, de Silva, et al. 2022; Wijeweera, Senaratne, et al. 2022)
	Dacus longistylus (Sodom apple fruit fly)	Feeds on the fruits and seeds of the plant.	Yes, further investigation recommended.	(Dhileepan 2014; Fernandes et al. 2020)
	Dacus persicus (Aak fruit fly)	Feeds on the fruits and seeds of the plant.	Yes, further investigation recommended.	(Dhileepan 2014; Ali and Shabbir 2017; Ali et al. 2020; Fernandes et al. 2020; Wijeweera, Senaratne, and Dhileepan 2021; Wijeweera, Senaratne, Dhileepan, and de Silva 2021)

also feed on the fruit capsules of *C. procera* and *C. gigantea*, although the thickness of the fruits' pericarp can sometimes limit its successful penetration (Sharma and Amritphale 2008; Ali et al. 2020; Wijeweera, Senaratne, and Dhileepan 2021; Wijeweera, Senaratne, Dhileepan, and de Silva 2021). The life cycle of *D. persicus* spans 48 days with five to seven generations developed each year, and there have been observations of up to 100% mortality to immature seeds and 62% mortality in the reduction of fruit biomass due to this agent (Dhileepan 2014). *Dacus longistylus* has also been observed to feed on the fruit of *C. procera* and *C. gigantea* and has been confirmed to show high host-specificity (Dhileepan 2014). Although *D. persicus*, *D. longistylus* and *P. farinosus* have shown to be prospective biological control agents for *C. procera* and *C. gigantea*, further research is still required to determine their suitability and longevity within a range of climatic and environmental conditions. The value of such added information will ensure that future releases will be able to sustain viable populations and have a sustainable and cost-appropriate impact on the future management of *C. procera* and *C. gigantea*.

Fungi-based biological agents have also shown potential in the control of *C. procera* and *C. gigantea* (Barreto et al. 1999; Kiran et al. 2020). *Passalora calotropidis* Ellis and Everh U Braun *(leaf spot fungal disease) has been* identified as a prospective agent due to its ability to reduce the chlorophyll and protein content within *C. procera* and *C. gigantea*, ultimately causing damage to the plant (Figure 7) (Wilkinson et al. 2005; Kiran et al. 2020). While *P. calotropidis* has the capacity to reduce the growth of *C. procera* and *C. gigantea*, its impact can sometimes be highly variable (Wilkinson et al. 2005; Kiran et al. 2020). *Puccinia oblique* Berk and Curt (rust fungus) and *Uredo calotropidis* Cummins (rust fungus) have also been identified as prospective biological agents for *C. procera* and *C. gigantea* in Brazil (Barreto et al. 1999). As neither of these species is found within the native regions of *C. procera* and *C. gigantea*, further investigation into their host specificity and ability to suppress the growth of the targeted plant is required before they can be seriously considered.

Insect and fungi-based biological agents have shown to provide high success when utilised within an integrated weed

TABLE 4b | Summary of prospective fungi biological control agents for *C. procera* and *C. gigantea*.

Target species	Species	Mode of action	Suitability	References
C. procera	*Mycosphaerella* Species (fungi)	Causes leaf necrosis and fruit deformities.	Potential, further investigation recommended.	(Barreto et al. 1999)
C. procera and *C. gigantea*	*Passalora calotropidis* (leaf spot fungal disease)	Develops lesions on the leaves and causes leaf spot disease, and defoliation.	Potential, further investigation recommended.	(Wilkinson et al. 2005; Kiran et al. 2020)
	Uredo calotropidis (rust fungus)	Causes rust disease in the plant.	Potential, further investigation recommended.	(Barreto et al. 1999)

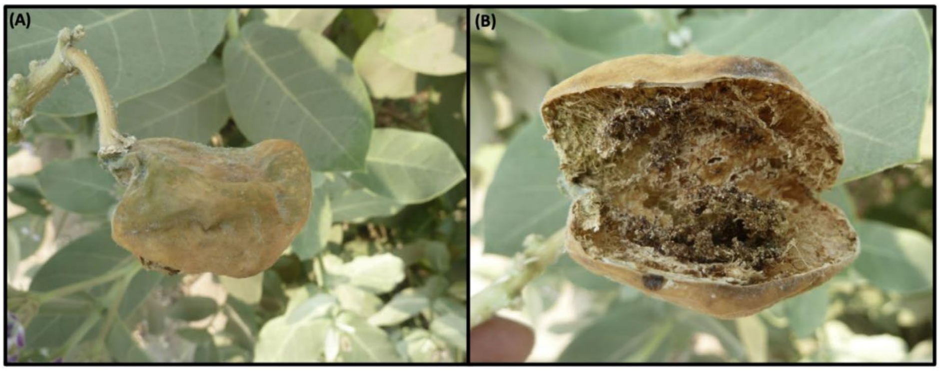


FIGURE 6 | The impact of the biological control agent *P. farinosus* on *C. gigantea* within India, (A) outside of the fruit capsule and (B) inside of the fruit capsule. Photographs provided by Kunjithapatham Dhileepan.

FIGURE 7 | The impact of the fungi-based biological agent *P. calotropidis* on *C. gigantea* leaves (A) early stage of leaf mortality, (B) mid stage of leaf mortality and (C) final stage of leaf mortality. Photographs provided by Kunjithapatham Dhileepan.

management program for various woody weed species (Galea 2021; Roberts et al. 2022). To ensure optimal release of such agents, application methods need to be carefully considered and released at appropriate times and locations (Roberts et al. 2022). One method that has shown direct success is the use of stem-injected capsules. For example, *Parkinsonia aculeata* L (Jerusalem thorn) has been effectively controlled using capsules containing the fungal agents *Lasiodiplodia pseudotheobromae* Alves and Crous (strain NT039), *Macrophomina phaseolina* Tassi Goid (strain NT094) and *Neoscytalidium* *novaehollandiae* Pavlic T.I. Burgess and M.J. Wingf (strain QLD003) (Galea 2021). Similarly, *Ailanthus altissima* Mill. Swingle (tree-of-heaven) has been successfully treated with *Verticillium nonalfalfae* H.W. Platt, Bostock, R.M. Davis and K.V. Subbarao, the causal agent of verticillium wilt (Shively et al. 2024). As such, further investigation into identifying suitable insect and fungi-based biological agents and the most appropriate application method would clearly assist in the control of *C. procera* and *C. gigantea*.

7 | Conclusion

Calotropis procera and *C. gigantea* will continue to impose substantial economic, environmental and social impacts in agricultural and other areas unless effectively managed. Evidence from this review highlights integrated management as the most suitable approach, targeting multiple aspects of plant biology and ecology, while also addressing newly emerging plants. Key strategies include (i) preventative measures, such as competitive pastures and minimising soil disturbance, (ii) chemical control with diverse modes of action, (iii) ecological burns to remove aboveground biomass followed by chemical or physical control and (iv) complete physical removal of the plant material from the soil. On the other hand, future research should prioritise (i) early detection methods using unmanned aerial vehicles such as drones, remote sensing or proximal sensing with algorithm-based analyses, (ii) assessing genetic diversity to trace invasion history and inform biological control, (iii) bioclimatic modelling to identify at-risk areas and potential sources of biological agents, (iv) native-range surveys to identify candidate biological control agents and (v) evaluating herbivory to guide selection of specialist insects. Together, these strategies and research priorities provide an encouraging pathway to mitigate the impacts of *C. procera* and *C. gigantea* within invaded landscapes.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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