Impact of biocontrol on the seed regenerative capacity of *Lantana camara* L. (*sensu lato*) (Verbenaceae)

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The combined impact of biocontrol agents on the seed regenerative capacity, i.e. seed production, seed-rain, soil seedbank, seed germination and seedling density, of *Lantana camara* L. (*sensu lato*) (Verbenaceae), was measured in an inland area of South Africa. The study was conducted on 10 plots (20 × 50 m each) along part of the Sabie River catchment. The most prevalent biocontrol agents at the site were *Aceria lantanae* (Cook) (Acari: Trombidiiformes: Eriophyidae), *Hypena laceratalis* Walker (Lepidoptera: Noctuidae), *Octotoma scabripennis* Guérin-Méneville (Coleoptera: Chrysomelidae), *Ophiomyia camarae* Spencer (Diptera: Agromyzidae) and *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae). Using the insecticidal exclusion method, comparisons of seed regenerative capacity were made between exclusion (insecticide treated) and biocontrol (untreated) plants over a three-year period. *Lantana camara* seed production per plant was slightly lower in biocontrol (5831 ± 844 seeds) compared to exclusion plants (6718 ± 1571 seeds), seed-rain density was significantly lower in biocontrol (1080 ± 122 seeds m⁻²) compared to exclusion plants (1419 ± 154 seeds m⁻²). Seed germination was lower in biocontrol (98 ± 41 seeds m⁻²) compared to exclusion plants (116 ± 38 seeds m⁻²). Seedling density was higher in biocontrol (36 ± 14 seedlings m⁻²) compared to exclusion plants (32 ± 11 seedlings m⁻²). Adult plants appeared to suppress their own seedlings. This study showed that the impact of the current suite of biocontrol agents on the recruitment potential of *L. camara* is minimal, emphasising the need for additional agents, better adapted to the cooler high altitude inland environmental conditions.

1. Introduction

Biological invasions, particularly those of alien plants, pose an imminent threat to the conservation of biodiversity and the functioning of ecosystems worldwide (Le Maitre et al., 2002; Mooney, 2005). In the face of this challenge, the use of biocontrol, often in conjunction with conventional control methods, i.e. chemical and mechanical control, is advocated for selected priority invasive alien plants (IAPs) (Moran et al., 2005; Zimmermann et al., 2004). A biocontrol programme is incomplete if it does not
empirically measure the effectiveness of an agent or a suite of agents on a target weed (Kluge, 2000; Osunkoya et al., 2010). Biocontrol of IAPs tends to employ multiple biocontrol agents, a method referred to as the ‘cumulative stress model’, which relies on the ability of biocontrol agents to interact in concurrence and thus increase the control of a target weed (Rayamajhi et al., 2010; Turner et al., 2010). Competition among multiple agents released has been cited as one of the factors responsible for the failure or limited success in biocontrol (McEvoy, 2002), at least this is not the case with biocontrol of Lantana camara L. (sensu lato) (Verbenaceae) (Simelane et al., 2021).

Lantana camara, commonly referred to as lantana, ranks among the most damaging IAPs worldwide (Bhagwat et al., 2012; Urban et al., 2011). Aided by frugivorous birds on one hand, and various pollinators such as bees on the other (Johansen & Mayer, 1990), lantana has the propensity to invade natural ecosystems, transforming native vegetation into impenetrable thickets, impeding crop production, animal production, forestry and water resource availability (Day et al., 2003). The estimated land mass covered by lantana in South Africa is 560,000 ha (Kotze et al., 2010). The proliferation and spread of IAPs such as lantana can be attributed to many factors, including their predisposition to produce large amounts of seeds each year, ranging between 6000 and 12,000 per plant (Muvengwi & Ndagurwa, 2015; Osunkoya et al., 2012; Priyanka & Joshi, 2013).

Under ideal environmental conditions, i.e. adequate soil moisture, temperature and light, lantana seeds (1–2 mm long) can germinate all year round (Duggin & Gentle, 1998; Parsons & Cuthbertson, 2001). Its germination rate is, however, reportedly low and variable (4–45%) (Osunkoya et al., 2013; Sharma et al., 2005). Although the germination rate of lantana seeds is low, because of seed dormancy and relatively low seed viability, its seed mortality is equally low attributing the weed its invasiveness (Duggin & Gentle, 1998; Osunkoya et al., 2012). Seedbank ecology is an important life-history stage which guarantees the continued survival of IAPs (Vivian-Smith & Panetta, 2009), yet little is known about lantana seed regenerative capacity (Muvengwi & Ndagurwa, 2015; Osunkoya et al., 2012; Vivian-Smith et al., 2006; Vivian-Smith & Panetta, 2009), and even less about the impact of biocontrol agents on this aspect. Invasion success of invaders, such as lantana, hinges on the plant’s ability to regenerate following perturbations such as fire, flood or logging (Osunkoya et al., 2013); and thus management interventions require biocontrol agents capable of attacking the plant’s early developmental stages, i.e. germination to seedling, seedling to juvenile transitions and fruit production (DeWalt, 2006; Osunkoya et al., 2010).

One of the pioneering lantana biocontrol studies showed the damaging impact of three lantana leaf-feeding agents (Cilliers, 1987). More recently, the suite of biocontrol agents, with a special focus on the flower-galling mite, Aceria lantanae (Cook) (Acari: Trombidiiformes: Eriophyidae), was found to be effective at reducing the reproductive output of lantana (Mukwevho et al., 2017). However, both aforementioned studies were conducted in the humid, warmer and frost-free coastal regions of KwaZulu-Natal Province in South Africa, which have been confirmed to be conducive to lantana biocontrol agents by virtue of their climatic conditions compared to the drier, colder, high altitude inland regions (Katembo et al., 2020; Urban et al., 2011; Zalucki et al., 2007). In addition, the combined impact of the suite of biocontrol agents on the vegetative growth of lantana was found to be minimal in an inland, higher altitude area, in Mpu- malanga Province, South Africa (Katembo et al., 2020).
The suite of established lantana biocontrol agents in South Africa comprises a guild of leaf-suckers, leaf-chewers, leaf-miners, flower/fruit-feeders, a root-feeder (Katembo et al., 2020; Urban et al., 2011; Winston et al., 2014) and fungal pathogens. It is worth mentioning that in addition to the leaf-spot pathogen, *Passalora* (formerly, *Mycovellosiella* *lantanae* (Chupp) U. Braun & Crous var. *lantanae*) and the rust fungus, *Puccinia lantanae* Farl. (Pucciniales: Pucciniaceae) has been approved and is yet to be released in South Africa (Simelane et al., 2021; Thomas et al., 2021; Wood & Den Breeyen, 2021). Although flower- and seed-feeders should naturally have a direct impact on the plant’s reproductive output, the pressure exerted by agents feeding on other plant parts, coupled with plant pathogens, will certainly have an indirect suppressing effect on seed production as well (Mukwevho et al., 2017). This study is a follow-up to Katembo et al. (2020), who measured the combined impact of lantana biocontrol agents, including associated indigenous insect species, on the vegetative growth of lantana in an inland area of the country. The present study aims to measure the same impact on the seed regenerative capacity of the plant. The term seed regenerative capacity hereafter describes some aspects of seedling recruitment (i.e. seed germination and seedling survival), seed production, seed-rain and soil seedbank.

2. Materials and methods

2.1. Study area

This study was conducted in Mpumalanga, one of the landlocked provinces of South Africa, between summer 2013 and summer 2016. The study sites lie along part of the Sabie River catchment, within 30 m of the river, at altitudes ranging between 763 and 1153 m a.s.l., with a temperate to subtropical climate (Katembo et al., 2020), characterised by hot, rainy summers and mild, dry winters (Beater et al., 2008). Ten plots (20 × 50 m each) previously established to monitor the clearing of alien invasive weeds (Beater et al., 2008; Witkowski & Garner, 2008) by the *Natural Resource Management Programme* (NRMP) of the South African Department of Forestry, Fisheries and the Environment, were selected for use in this study. To reduce variabilities due to different lantana biotypes (Day et al., 2003; Urban et al., 2011), field trials were conducted solely on the light-to-dark pink-flowered type, which is the most common weedy lantana biotype countrywide (Simelane & Phenye, 2005). Biocontrol agents found in the study area during the experimental period included the flower-galling, *A. lantanae*, the leaf-chewer, *Hypena laceratalis* Walker (Lepidoptera: Noctuidae), two leaf-miners, *Octotoma scabripennis* Guérin-Méneville (Coleoptera: Chrysomelidae) and *Ophiomyia camarae* Spencer (Diptera: Agromyzidae), and the leaf-sucker, *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae). Unless stated otherwise, biocontrol agents in this study refer to both released agents and lantana-associated arthropods without discrimination.

2.2. Experimental design

Ten 50 × 20 m experimental plots, scattered over an area of ~269 km², were set up with each enclosing two 4 × 4 m quadrats, > 5 m apart. Four lantana plants of comparable sizes (average height of 2.64 m and plant canopy cover of 11.09 m²) and level of
biocontrol agent infestation were identified and tagged per plot, with two centrally located per quadrat. The above-ground vegetation in all 20 quadrats was cleared. The tagged lantana plants were initially cut down to 10 cm above-ground level and allowed to resprout, while the rest of the vegetation within these quadrats was manually cleared to the ground trimonthly throughout the study period. The impact of the ambient suite of biocontrol agents present at the study sites on the recruitment potential of lantana was monitored on 40 pre-existing, coppicing plants (Katembo et al., 2020).

For comparison, the 40 plants were divided into two groups, each consisting of 20 exclusion (biocontrol agent-free) and 20 biocontrol plants. In each plot, exclusion plants were at least 5 m away from biocontrol plants to avoid unintended contaminations through insecticide leaching. A broad-spectrum, systemic, carbamate insecticide, carbofuran (10% active ingredient) was used to prevent biocontrol agents from attacking ‘exclusion plants’; whereas ‘biocontrol plants’ were kept insecticide free to allow agent colonisation. Carbofuran is registered for use in many countries including South Africa (Katembo et al., 2019; Quinn et al., 2011).

Three months after plants were cleared (spring 2012), carbofuran granules were soil applied at a dosage of 70 g m$^{-2}$ around each exclusion plant, followed by an application of 1 L of water per plant for ease of chemical uptake through the root system. To avoid bias, an equal amount of water was applied to the soil around biocontrol plants. Taking into account the increase in plant biomass over time, carbofuran application dosage was increased from 70 to 140 g m$^{-2}$ to retain the efficacy of the chemical (Katembo et al., 2020). Carbofuran application and data collection were undertaken quarterly throughout the study period, from summer 2013 to summer 2016.

### 2.2.1. Seed production

Seed production was measured only once in the summer of 2016 through destructive sampling at the end of the experiment. Lantana infructescences were counted on 20 biocontrol and 20 exclusion plants. The number of seeds was counted from five representative mature infructescences randomly selected per plant (in total, 100 biocontrol and 100 exclusion infructescences). Total seed production plant$^{-1}$ was calculated as follows:

\[
\text{Number of seeds plant}^{-1} = (\text{Number of infructescences plant}^{-1}) \\times (\text{Number of seeds infructescence}^{-1})
\]

### 2.2.2. Seed-rain density trial

Four 2 L plastic bottles, with a combined bottom surface area of 0.035 m$^2$ (diameter and height of bottle were 105 and 330 mm, respectively), were used as seed-rain traps per plant. They were secured 50 mm above ground using 8 mm steel pegs (fence droppers), and placed underneath a plant’s canopy at the four cardinal directions (500 mm radius around the plant’s stem) in summer 2013. The bottle’s neck was fitted with <1 mm stainless wire mesh to allow rain water to escape while keeping the seeds trapped. Traps were inspected quarterly, and mesh was replaced when needed. Seed traps were retrieved in the summer of 2014, 2015 and 2016 from 20 biocontrol and 20 exclusion plants, from which annual seed accumulation was estimated per plant. Summer was chosen because seed production was highest at this time of the year. There were no signs of
seed loss as seed traps never got filled up to the brim. Some seeds might have suffered damage by seed predators, but no further investigations were done beyond recording seed-rain density.

2.2.3. Soil seedbank trial
In summer 2016, a total of 20 soil samples, 10 from underneath biocontrol and 10 exclusion plant canopies, were collected just before the final destructive sampling at the end of the experiment. A steel square frame (300 × 300 mm) was used to collect the soil at a depth of 0–50 mm (Muvengwi & Ndagurwa, 2015), after carefully scraping off the top layer of leaf litter. Soil samples were placed in brown paper bags and taken to a glasshouse at the University of the Witwatersrand in Johannesburg, South Africa. Each bag was emptied and spread out into a germination tray (450 × 200, 50 mm deep). Irrigation within the glasshouse was done twice a day for 15 min. Germination trays were exposed to full sunlight conditions. Minimum and maximum temperatures were 21 and 26°C, respectively, with an average relative humidity of 58%.

Germinable soil seedbank was measured using the emergence method through counting the number of seedlings per germination tray, and this was converted into seeds m⁻². The germination trial ran for 60 days. Observations were made daily, and germination was confirmed when a plumule was visible above the soil. Emerged seedlings were immediately removed after being recorded. Observations of the germination trays continued for a further 60 days (120 days of observation in total) after the last seedling emerged to ensure all germinable seeds had been exhausted from the soil within the trays. It is worth noting that this method does not take into consideration seed dormancy experienced under field conditions, and as a result, seedbank may have been underestimated.

2.2.4. Matrix of correlations between seedling density, plant canopy cover, plant height and leaf damage
Seedling density was measured by counting (count-and-pull) all rooted seedlings per quadrat (4 × 4 m) quarterly from 2013 to 2015, and comparisons were made between quadrats enclosing biocontrol and exclusion plants. Plant canopy cover of the two plants/quadrat was obtained by measuring two diameters (D) perpendicular to each other, and using their mean to determine the canopy cover with the following formula: Canopy cover = π (D/2)² (Mueller-Dombois & Ellenberg, 1974). Plant height was measured as the vertical distance from the ground to the highest living part of the plant (Anderson & Ingram, 1993).

Leaf damage (%) was calculated from the number of leaves counted on the distal 500 mm of three tagged stems per plant (Katembo et al., 2020). A matrix of correlations for the abovementioned parameters was drawn using values of the percentage change (reduction or increase) between biocontrol and exclusion plants per season during nine season-sampling occasions.

2.3. Statistical analysis
The impact of biocontrol agents on the seed regenerative capacity of lantana was measured by drawing comparisons between biocontrol and exclusion plants. Plant
height, canopy cover, leaf damage, seedling and seed-rain density were compared between biocontrol and exclusion plants using one-way ANOVAs with repeated measures, followed by LSD post-hoc tests. Independent t-tests were used to compare the cumulative seed-rain density and seed production between biocontrol and exclusion plants. A correlation matrix was used to determine bivariate relationships to be explored. The relationship between plant canopy cover and seedling density was determined using regression analyses. Data were arcsine-transformed for the assumption of normality before running regression analyses. All analyses used a significant criterion of .05, and analyses were performed using Statistica, version 12.

3. Results

3.1. Seed production

In 2016, no significant differences were found in the number of seeds produced between biocontrol (5831 ± 844 seeds per plant) and exclusion (6718 ± 1571 seeds per plant) plants (t18 = 0.49; P = .62). It was, however, slightly lower (by 13%) in biocontrol compared to exclusion plants.

3.2. Seed-rain density

Lantana seed-rain density (m$^{-2}$) was not significantly different between biocontrol and exclusion plants ($F_{1, 144} = 2.67; P = .10$) or the interaction between treatment and time (years) ($F_{2, 144} = 0.48; P = .61$) (Figure 1); however, overall (cumulative) density was significantly higher in exclusion compared to biocontrol plants ($t_{38} = 1.72; P = .04$). There were significant increases in seed-rain accumulation over the three-year period as the plants grew larger ($F_{2, 144} = 17.19; P < .001$). Cumulatively, a total of 1418 ± 154 seeds m$^{-2}$ were produced by the exclusion plants versus 1080 ± 122 seeds m$^{-2}$ by biocontrol plants, which is a 32% reduction in seed production.

3.3. Soil seedbank germination

There were no significant differences in the cumulative number of germinated seeds in soils collected around biocontrol and exclusion plants during the course of the trial period ($F_{1, 18} = 0.36; P = .55$) (Figure 2). At the end of the germination period, the trend observed suggested a slight percentage reduction (18%) in the number of germinable soil seedbank seed density in biocontrol (98 ± 41) compared to exclusion (116 ± 38) germination trays.

There were no significant differences in the daily germination rate ($t_{18} = 0.32; P = .75$) (1.69 ± 0.70 seeds m$^{-2}$), (1.99 ± 0.65 seeds m$^{-2}$); and days to germinate ($t_{18} = 0.04; P = .96$) (39.40 ± 4.38 days), (39.10 ± 4.38 days) between biocontrol and exclusion germination trays, respectively.

3.4. Seedling density, plant canopy cover, plant height and leaf damage

Over the nine observation periods (2013–2015), plant cover grew from about 1 m$^2$ to a peak of 15 m$^2$ and then declined to about 12 m$^2$ most probably as a result of the 2015/16
There were no significant differences in either the cumulative number of seedlings ($F_{1, 18} = 0.07; P = .79$), plant canopy cover ($F_{1, 18} = 0.19; P = .66$) or plant height ($F_{1, 36} = 0.009; P = .92$) between biocontrol and exclusion treatments. Leaf damage, however, was greater in biocontrol compared to exclusion plants ($F_{1, 36} = 0.43; P < .001$). With the exception of significant seasonal changes, there were no interactions between treatment and season (Table 1), suggesting that treatment effect remained the same irrespective of the time of survey (i.e. season).

A matrix of correlations revealed seedling density and plant cover as a significant bivariate to be explored (Table 2). There was a positive linear relationship between the percentage increase in plant canopy cover and the percentage reduction in seedling density. This relationship was calculated using differences (increase or reduction) between biocontrol and exclusion mean values expressed as percentages (Figure 3).

**4. Discussion**

The combined impact of biocontrol agents on the recruitment potential of lantana in an inland area of South Africa had not yet been previously measured. Through an exclusion experiment, it was found that the established cohort of lantana biocontrol agents reduced plant seed-rain by 32%. However, this impact was relatively small on other seed output parameters, with lower reductions in seed production per plant (13%), the number of
germinable soil seedbank seeds (18%) and seedling density (13%). In the case of seed production and the soil seedbank, the impact of biocontrol is likely to be underestimated because these parameters were measured at one census period only. Nevertheless, the trend shows that there have been minimal reductions in the overall seed regenerative capacity of inland lantana, compared to results reported from the country’s coastal

Figure 2. Cumulative numbers of germinable soil seedbank seed m$^{-2}$ compared between biocontrol and exclusion plants in 2014 (mean ± SE). The two parallel oblique lines on the x-axis indicate a graph break as no seeds germinated during the first 41 days. No significant differences were noted between treatments ($P > .05$). Germination stopped after 58 days of the 120-day observation period.

Table 1. Summary of the effects of insecticidal exclusion (treatment) and season on the impact of biocontrol on lantana seedling density, plant canopy cover, plant height and leaf damage along the Sabie River in Mpumalanga Province, South Africa ($P < .05$).

| Parameters                  | Factor variables | d.f. | F-value | P-value |
|-----------------------------|------------------|------|---------|---------|
| Seedling density/m$^2$      | Treatment        | 1, 18| 0.07    | .78     |
|                             | Season           | 8, 144| 14.42  | <.001   |
|                             | Treatment × Season| 8, 144| 0.03    | .99     |
| Plant canopy cover (m$^2$)  | Treatment        | 1, 18| 0.19    | .66     |
|                             | Season           | 8, 144| 29.89  | <.001   |
|                             | Treatment × Season| 8, 144| 0.27    | .97     |
| Plant height (m)            | Treatment        | 1, 36| 0.009   | .92     |
|                             | Season           | 8, 288| 38.81  | <.001   |
|                             | Treatment × Season| 8, 288| 0.60    | .77     |
| Leaf damage (%)             | Treatment        | 1, 36| 0.43    | <.001   |
|                             | Season           | 8, 288| 40.24  | <.001   |
|                             | Treatment × Season| 8, 288| 0.94    | .48     |
regions (Mukwevho et al., 2017). A study conducted in the coastal regions of KwaZulu-Natal has reported significant reductions in the reproductive output of lantana, i.e. seed production, by 95%, largely attributable to the flower-galling mite, *A. lantanae* (Mukwevho et al., 2017).

Generally, lantana biocontrol agents perform well under maritime climatic conditions compared to those in the inland regions (Cilliers, 1987; Katembo et al., 2020; Mukwevho et al., 2017), largely due to the more humid and frost-free conditions, which are conducive to most biocontrol agents (Cowie et al., 2016; Urban et al., 2011; Zalucki et al., 2007). The preference for wetter areas is common with many biocontrol agents, whose target weeds originate from subtropical and tropical regions. For example, the control of

### Table 2. Correlation coefficient matrix (*R*) for percentage increase in plant canopy cover, plant height, leaf damage and the percentage reduction in seedling density.

|              | Correlation coefficient matrix (*R*) for percentage increase in plant canopy cover, plant height, leaf damage and the percentage reduction in seedling density. |
|--------------|---------------------------------------------------------------------------------------------------------------------------------|
| Canopy cover | Seedling density | Plant height | Leaf damage |
| Canopy cover | 1.00              |              |             |
| Seedling density | 0.72              | 1.00         |             |
| Plant height | 0.12              | −0.05        | 1.00        |
| Leaf damage | 0.26              | −0.15        | 0.59        | 1.00 |

The underlined correlation is significant (*P* < .05).

![Graph showing the reduction in Lantana camara seedling density as a function of an increase in plant canopy area cover.](image)

*y = −0.07 + 1.83 * x; R^2 = 0.52; P = 0.03*

**Figure 3.** Reduction in *Lantana camara* seedling density as a function of an increase in plant canopy area cover (data were arcsine-transformed) over nine seasons (summer 2013 to summer 2015) along the Sabie River in Mpumalanga province, South Africa. Percentage change (reduction or increase) was calculated from differences in mean values between biocontrol and exclusion treatments per season for all nine seasons.
Chromolaena odorata (Asteraceae) by the gall fly, Cecidochares connexa (Diptera: Tephritidae), was largely considered unsuccessful in drier compared to wetter provinces in Papua New Guinea (Day & Bofeng, 2007). In South Africa, the two C. odorata leaf-feeders, Pareuchaetes insulata Walker (Lepidoptera: Arctiidae) and Calycomyza eupatorivora Spencer (Diptera: Agromyzidae), have also been found to perform well under coastal, warm and wet conditions (Zachariades et al., 2017). Lantana has many genotypes that differ in their adaptability to varying climatic conditions (Day et al., 2003), and thus requires a suite of biocontrol agents to cope with the climatic extremes within the weed’s invasive distribution range. Currently, agents collected from regions of the native range that better match the South African inland climatic conditions are required.

The observed low impact of the current suite of agents on lantana seedling recruitment seems to have been further reduced by the plant itself. While lantana is reported to possess allelopathic compounds, namely triterpenes, which can inhibit seed germination (Duggin & Gentle, 1998; Gentle & Duggin, 1997; Parsons & Cuthbertson, 2001), seedling survival and/or plant growth of other species occurring in its vicinity (Achhireddy et al., 1985; Sharma et al., 2005), it remains unclear whether or not this exclusion behaviour can be equally detrimental to the weed itself. At a population level, studies in Australia have shown that in open canopy systems such as farm or disturbed land, lantana growth pattern displays bimodality, which is expressed as the suppression of smaller plants by larger ones (Osunkoya et al., 2012). Bivariate results of seedling recruitment and plant canopy cover in the present study seem to suggest that lantana self-limits its own seed germination, and/or reduces seedling recruitment through light deprivation (Duggin & Gentle, 1998; Vivian-Smith & Panetta, 2009), as evidenced by the relationship between plant canopy cover and reduction in seedling density. Consequently, it was observed that instead of declining, seedling recruitment was slightly higher under biocontrol compared to exclusion plants – implying that biocontrol agents may have indirectly promoted seedling recruitment by opening the plant’s canopy. This indirect promotion of seedling recruitment could in fact result in soil seedbank depletion (Vivian-Smith & Panetta, 2009) as an unexpected and indirect effect. Such an approach (promotion of seedling recruitment as a way of depleting the soil seedbank) can only be effective, if follow-up interventions such as seedling removal or spraying (Beater et al., 2008; McConnachie et al., 2012) is accompanied by the active planting of indigenous vegetation, including grasses, shrubs and trees.

In as much as the number of germinable seeds was high in germination trials, it (the number) did not translate into a higher seedling density in the field, probably because of seed dormancy (Osunkoya et al., 2013; Sharma et al., 2005; Vivian-Smith & Panetta, 2009) and predation. In addition, since germination rates are generally higher under laboratory compared to field environmental conditions (Kelly et al., 2010; Osunkoya et al., 2013), any extrapolation of laboratory results into field situation has to be done with caution. Furthermore, because lantana appears to be a gap coloniser, the lack of sufficient light underneath plant canopies will negatively affect seed germination as well as the germination to seedling transition.

Topographic disturbances caused by flood events are a major driver of invasions along rivers in South Africa, mostly promoting plant species belonging to the genera Acacia, Eucalyptus, Populus and Salix (Hill et al., 2020), but also understorey plant species in the genera Solanum, Rubus and Lantana (Beater et al., 2008; Katembo, 2018). In 2005,
in the same study area, large numbers of small (1–2 m tall) and medium size (2–5 m tall) lantana plants emerged from within the gaps and bare patches caused by the major flood of 2000 (Beater et al., 2008; Foxcroft et al., 2008). Other studies have shown that canopy gaps resulting from disturbances provided favourable establishment sites for lantana invasions (Day et al., 2003; Raizada et al., 2008). The inference from these results is that constant and multifaceted control interventions of lantana are essential, especially during the weed’s early invasion/reinvasion stages, when annual growth is reported to increase in excess of 700% (Osunkoya et al., 2010).

As a side note, this study has for the first time reported on the seed recruitment potential of lantana in South Africa. Comparison, although not perfect considering numerous confounding abiotic (edaphic, vegetation type) and biotic factors (plant biotype, presence of biocontrol agents) specific to different areas, can be drawn with results reported elsewhere. For example, soil seedbank density was reported to range between 5 (Gentle & Duggin, 1998) and 98 seeds m\(^{-2}\) (Vivian-Smith et al., 2006) in Australia, 43 seeds m\(^{-2}\) in Ecuador (Myster, 2004), 2–657 seeds m\(^{-2}\) in Zimbabwe (Muvengwi & Ndagurwa, 2015) and between 1049 and 2690 m\(^{-2}\) in Ghana (Oppong et al., 2003), compared to 115 seeds m\(^{-2}\) in the present study. It is worth noting that soil seedbank was estimated through the germination method, which does not always account for the impending seed dormancy (Osunkoya et al., 2013; Sharma et al., 2005); and thus it may have been underestimated. Fensham et al. (1994) recorded 10–25 seedlings m\(^{-2}\) in Australia compared to just two seedlings m\(^{-2}\) in the present study, which is very low considering the amount of seeds produced per plant. The number of seeds produced per plant in India and Florida (U.S.A.) is reported to be 12,000 (Priyanka & Joshi, 2013) compared to 6717 seeds plant\(^{-1}\) in the present study, which almost corresponds to the one reported in Australia (1049–7409) (Osunkoya et al., 2012). The number of seeds per infructescence was reported to be eight in Australia (Barrows, 1976), between 25 and 28 in India (Sharma et al., 2005), and averaging 16 in the present study. Reports from India (Priyanka & Joshi, 2013; Sharma et al., 2005) suggest that lantana fruits are two-seeded, which is inconsistent with findings in the present study, where fruits were found to encapsulate a single seed. In comparison to other places in the world, lantana seed output in this study appears to be rather low, but still high enough to explain the considerable recruitment potential of the plant.

In conclusion, biocontrol programmes for IAPs with large seedbanks, such as lantana, should focus more on reducing the plant’s regenerative capacity, such as seed production and seedling recruitment (see Hill et al., 2020 for other South African examples). Projection studies conducted in Australia showed that unless seed production, germination and seedling growth are reduced by at least 95%, probably with the help of herbicides, the weed’s population growth will not significantly decline (Osunkoya et al., 2010). Results suggest that the suite of biocontrol agents in this inland region of the country has minimal impact on the recruitment potential of lantana, emphasising the need to adopt an integrated weed management approach, using a combination of agents, manual clearance and herbicide application, for an effective control of the weed. Finally, an additional introduction of biocontrol agents best suited to the colder and dryer climatic conditions, typical of inland higher altitude regions is required to increase the impact of the existing cohort of agents.
Disclosure statement

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