



Recent post-release evaluations of weed biocontrol programmes in South Africa: a summary of what has been achieved and what can be improved

Iain D. Paterson · Samuel N. Motitsoe · Julie A. Coetzee ·
Martin P. Hill

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Abstract Biocontrol is widely considered an effective management solution for mitigating the negative impacts of invasive alien plants (weeds). Globally, post-release evaluations to assess individual biocontrol programmes are generally lacking and there have been persistent calls within the biocontrol of weeds literature to increase the quantity and quality of post-release evaluation studies. South African biocontrol researchers have prioritised post-release evaluation studies, with a significant proportion of funding dedicated to this purpose. In this study we review post-release evaluations of weed biocontrol programmes in South Africa that have been published in the last ten years, discuss the different ways these evaluations have been conducted, and identify gaps for

future research. Post-release evaluations have been conducted at different scales, including physiological changes within individual plants, plant growth parameters, plant population dynamics and landscape level changes. In most cases, the results of these studies indicated that biocontrol has reduced invasions according to these metrics. While the reduction in the invasion is assumed to alleviate negative ecological and socio-economic impacts, this is usually not directly measured. Evaluations of the socio-economic and ecosystem level benefits of biocontrol were limited to just a few examples on aquatic weeds. More studies that investigate the landscape, socio-economic and ecosystem level changes due to biocontrol are required, especially for terrestrial weeds, if the true scale of the benefits provided by biocontrol are to be understood.

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I. D. Paterson (✉) · S. N. Motitsoe · M. P. Hill
Centre for Biological Control, Department
of Zoology and Entomology, Rhodes University,
Makhanda (Grahamstown) 6140, South Africa
e-mail: i.paterson@ru.ac.za

S. N. Motitsoe
e-mail: samy4045@gamil.com

M. P. Hill
e-mail: m.p.hill@ru.ac.za

J. A. Coetzee
Centre for Biological Control, Department of Botany,
Rhodes University, Makhanda (Grahamstown) 6140,
South Africa
e-mail: julie.coetzee@ru.ac.za

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Introduction

Invasive alien plants (IAPs), also referred to as weeds, have significant negative impacts to indigenous ecosystems and the communities of people who rely on the services provided by these ecosystems (Vilà et al. 2004; Pyšek et al. 2020). The negative consequences of these invasions have resulted in

considerable resources being used for their control (Richardson and van Wilgen 2004; Blackburn et al. 2014). Biological control (biocontrol), the use of host specific natural enemies from the indigenous distribution of the IAP, is regarded as a safe and effective management option for many IAP species (McFadyen 1998). A typical biocontrol programme against an IAP is comprised of pre-release components, such as surveys for potential agents in the indigenous distribution and host specificity testing; and post-release components such as mass-rearing, redistribution of agents, and post-release monitoring and evaluation of success (Schaffner et al. 2020).

In South Africa, 90 weeds have been targeted for biocontrol using 136 agents, of which 92 are established on 66 target weeds (Zachariades 2021). A broad assessment of the success of these agents reports that 72% of the agents inflict some level of damage to the host plant, and 35% inflict extensive damage (Zachariades 2021). Moran et al. (2021) also evaluated the success of biocontrol on weeds in the country that have had agents released on them for long enough for biocontrol to have reached its full potential. Of the 54 targeted weeds considered, 39 have been reduced below pre-biocontrol levels for at least one of the metrics evaluated (density, biomass, area, rate of spread), and 15 have been reduced permanently to levels where they no longer have any negative impacts (Moran et al. 2021). These broad assessments of biocontrol success are extremely valuable but must be supported by quantitative studies of individual target weeds to make them robust and convincing. A fair proportion (65%) of the assessments of changes to weed growth parameters reported in Moran et al. (2021) are supported by quantitative data, but there is room for improvement by increasing the number of species included in studies, and, more importantly, in the way in which these studies are conducted and what parameters are measured.

Studies to evaluate the success of biocontrol programmes are referred to as post-release evaluation studies. There are several different designs for post-release evaluations, including measuring parameters before and after the release of the agent, comparing sites with and without the agent, and manipulative experiments (such as agent exclusion experiments) (Morin et al. 2009). Post-release evaluations can also be conducted on different scales, from physiological changes within the target weed, to changes in

individual plant parameters, population level changes and landscape level changes. Selecting the most appropriate parameters to measure in post-release evaluations is important as some require much less time, effort, and resources to measure, such as agent establishment or damage to the plant, while others, such as changes to the provisioning of ecosystem services, are much more difficult to measure (Schaffner et al. 2020). Ideally, a whole suite of relevant parameters should be measured that assess the success of the biocontrol programme at multiple scales.

Post-release evaluations are widely regarded as essential, yet neglected, parts of biocontrol programmes (Morin et al. 2009; Schaffner et al. 2020). The primary reason why post-release evaluations are often neglected is an unwillingness of funders to support long-term and sometimes expensive projects that evaluate impacts, but do not necessarily result in better control (Morin et al. 2009). In South Africa, the largest funder of weed biocontrol research, the Department of Forestry, Fisheries and Environment (DFFE), is mandated to evaluate the success of the management interventions that they support and fund. The weed biocontrol community in South Africa has therefore dedicated a large proportion of its capacity and resources towards post-release evaluations.

Here we review recent post-release evaluation efforts for weed biocontrol programmes that have been conducted in South Africa. The special issue on ‘Biological Control of invasive alien plants in South Africa (2011–2020)’, published in *African Entomology* in December 2021, was searched for any post-release evaluation studies that were either directly reported in the review articles or any relevant studies that were referenced. Articles were limited to those published in the last ten years (from 2013) and post-release assessment that only measured agent parameters, rather than plant parameters, were excluded. This resulted in 38 articles covering 23 target weeds (Table 1). Searches of online databases using keywords consistently resulted in a high number of irrelevant papers and failed to locate several relevant ones, while no relevant papers were found in searches of online databases that were not included in the *African Entomology* Special Issue. The different studies were then categorised in terms of the level of post-release evaluation, with each study being allocated to one of six categories (weed physiology, weed

Table 1 Recently published (from 2013) post-release evaluation studies from South Africa divided into the different levels of the assessment for each target weed. The numbers in each

column are the relevant references, which are provided below the table. Plant species are listed in alphabetical order.

Plant	Weed physiology	Weed growth	Weed population dynamics	Landscape level impacts *	Socio-economic returns	Eco-logical returns
<i>Acacia cyclops</i>			12	10		
<i>Acacia mearnsii</i>			13	10		
<i>Acacia saligna</i>			37	10		
<i>Ageratina adenophora</i>		3				
<i>Azolla filliculoides</i>				10	20	
<i>Campuloclinium macrocephalum</i>		30; 36				
<i>Cardiospermum gradiflorum</i>		32				
<i>Cereus jamacaru</i>			34			
<i>Chromolaena odorata</i>		38				
<i>Cylindropuntia fulgida</i>			17			
<i>Dolichandra unguis-cati</i>		16				
<i>Hakea sericea</i>		18				
<i>Lantana camara</i>		15; 26; 27; 31				
<i>Myriophyllum aquaticum</i>	2		5	10	20	
<i>Opuntia monacantha</i>		29				
<i>Opuntia stricta</i>	36		11			
<i>Parthenium hysterophorus</i>	7	33				
<i>Pereskia aculeata</i>		16				
<i>Pistia stratiotes</i>	2			10	20	4
<i>Pontederia crassipes</i>	2; 21; 23; 28; 35	14	24	6; 10	1; 9; 20	
<i>Salvinia molesta</i>	2		22	10	20	25
<i>Solanum mauritianum</i>	8					
<i>Tecoma stans</i>		19				

*Henderson and Wilson (2017) included all regulated plant species in their analysis, but the impact of biocontrol was only investigated for Australian *Acacia* species and water weeds

Arp et al. (2017)¹, Baso et al. (2021)², Buccellato et al. (2021)³, Coetzee et al. (2020)⁴, Coetzee et al. (2021)⁵, Coetzee et al. (2022)⁶, Cowie et al. (2016)⁷, Cowie et al. (2018)⁸, Fraser et al. (2016)⁹, Henderson and Wilson (2017)¹⁰, Hoffmann et al. (2020)¹¹, Impson et al. (2021a)¹², Impson et al. (2021b)¹³, Jones et al. (2018)¹⁴, Katembo et al. (2020)¹⁵, King et al. (2021)¹⁶, Klein et al. (2020)¹⁷, Lyons et al. (2021)¹⁸, Madire and Netshiluvhi (2021)¹⁹, Maluleke et al. (2021)²⁰, Marlin et al. (2013)²¹, Martin et al. (2018)²², Miller et al. (2019)²³, Miller et al. (2021)²⁴, Motitsoe et al. (2020)²⁵, Mukwevho and Mphephu (2020)²⁶, Mukwevho et al. (2017)²⁷, Paper et al. (2023)²⁸, Paterson et al. (2021)²⁹, Ramanand et al. (2016)³⁰, Simelane et al. (2021)³¹, Simelane and Mawela (2019)³², Strathie et al. (2021)³³, Sutton et al. (2018)³⁴, Venter et al. (2013)³⁵, Venter et al. (2022)³⁶, Wood and Den Breeÿen (2021)³⁷, Zachariades et al. (2021)³⁸

growth, weed population dynamics, landscape level impacts, socio-economic returns, and ecosystem returns). We review the outcomes of post-release

evaluation at each scale and identify gaps where post-release evaluation efforts should be focused in future.

Recent post-release evaluations in South Africa

Weed physiology

Fluctuations in weed populations can be caused by a variety of factors, including seasonal fluctuations, drought cycles and nutrient availability, and it is often difficult to isolate the impact of a biocontrol agent. However, there have been studies in South Africa that have shown significant reduction in photosynthetic output and associated growth responses of several weeds, but most notably *Pontederia crassipes* Mart. (Pontederiaceae) to feeding by several of its biocontrol agents in South Africa (Marlin et al. 2013; Miller et al. 2019). Venter et al. (2013) showed that feeding by adult *Neochetina eichhorniae* (Warner) (Coleoptera: Curculionidae) on the leaves of *P. crassipes* accounted for only 50% of the total reduction in photosynthesis of the weed and the other 50% was due to opportunistic microbes carried around by the weevil. Significant reductions in photosynthesis due to damage by biocontrol agents have also been recorded for *Parthenium hysterophorus* L. (Asteraceae) and *Solanum mauritianum* Scop. (Solanaceae) (Cowie et al. 2016, 2018). Damage to *P. hysterophorus* by the beetle *Zygogramma bicolorata* Pallister (Chrysomelidae) resulted in a 36% reduction in photosynthesis on damaged leaves, but adjacent leaves that remained undamaged up-regulated photosynthesis by about 11%, reducing the overall damage, but not mitigating it completely (Cowie et al. 2018). Microbes were also thought to play an important role in the physiological damage caused by *Z. bicolorata*, but the relative contribution of damage from the agent and from microbes has not been measured (Cowie et al. 2018). The removal of chlorophyll by the sap-sucking bug *Gargaphia decoris* Drake (Tingidae) resulted in a reduction in photosynthetic rates of the target weed *S. mauritianum*, which resulted in a 52% reduction in transpiration rates (Cowie et al. 2016). Plants growing in direct sunlight were impacted significantly more than those in the shade due to heat stress, as evaporative cooling is reliant on transpiration (Cowie et al. 2016). These studies improve our understanding of how the agents impact their target plants and can help explain variations in biocontrol efficacy in the field, as well as

inform management of the most appropriate release sites for different agents.

Recent studies have evaluated the physiological response of weeds to biocontrol under elevated carbon dioxide (CO₂) concentration, which could have implications for biocontrol programmes. Baso et al. (2021) investigated the effect of elevated CO₂ concentration of 800 ppm *versus* the current 400 ppm, on the biocontrol of four aquatic weeds that are considered to be under complete biocontrol in South Africa, i.e., *Pistia stratiotes* L. (Araceae) (water lettuce), *Salvinia molesta* D.S. Mitch. (Salviniaceae) (giant salvinia), *Myriophyllum aquaticum* (Vell. Conc.) Verdr. (parrot's feather), and *Azolla filiculoides* Lam. (Azollaceae) (red water fern). The results of this study indicated that biocontrol of floating aquatic weeds may be more challenging under future climatic conditions, because elevated CO₂ concentration (800 ppm) resulted in an increase in plant biomass, an increase in leaf carbon to nitrogen ratio, and a reduction in feeding damage by biocontrol agents (Baso et al. 2021). Similarly, Paper et al. (2023) investigated the role of current (400 ppm) and projected (800 ppm) CO₂ concentration on another free-floating aquatic weed, *P. crassipes*, growth with and without two of its biocontrol agents, the leaf-chewing *Cornops aquaticum* Brünner (Orthoptera: Acrididae) and the phloem-feeding *Megamelus scutellaris* Berg (Hemiptera: Delphacidae). The study showed that herbivory by *C. aquaticum* was consistent across CO₂ conditions, but the feeding by *M. scutellaris* increased at the elevated CO₂ level suggesting that, at predicted elevated CO₂ concentrations, the successful biocontrol of *P. crassipes* might rely on phloem-feeding insects (Paper et al. 2023). In contrast, the sap-sucking bug *Dactylopius opuntiae* Cockerell (Dactylopiidae) had reduced fitness under elevated CO₂ which resulted in the target weed, *Opuntia stricta* Haw. (Haw.) (Cactaceae), taking on average three weeks longer to die than plants exposed to the same initial density of the agent at current CO₂ concentration (Venter et al. 2022). The efficacy of biocontrol of *O. stricta* in South Africa may therefore be reduced in future (Venter et al. 2022). The physiological impacts of agents under different climate change scenarios could have important management implications and is an understudied area of research where more effort is warranted.

Weed growth

Impacts of biocontrol agents to individual plants are routinely assessed in post-release evaluations, especially for relatively recently released agents. The impact of a biocontrol agent on the target weed can be used to infer the more long-term impacts to the population level and is also important in linking the damage done by the biocontrol agent to any changes in the population of the target weed over time, thus excluding other possible reasons for weed population declines. Comparisons of plant parameters can be made before and after release, between sites where the agents are present or absent, and insecticides and cages can be used to exclude agents.

South African examples of weed growth level post-release evaluations include assessing the combined impact of all 16 biocontrol agents established on *Lantana camara* L. (Verbanaceae) by excluding the biocontrol agents from plots with insecticides. An overview and update of these studies is provided in a review of the biocontrol programme against *L. camara* (Simelane et al. 2021). Leaf damage was 44% greater in plots with agents and side-stem production was reduced by 16% in dry areas of the country (Katembo et al. 2020), while seed production was reduced by 94% in a similar study conducted in wetter areas (Mukwevho et al. 2017). Mukwevho and Mphephu (2020) showed that flower and fruit production of *L. camara* was significantly reduced on coppicing shoots due to the action of the biocontrol agent, *Aceria lantanae* (Cook) (Eriophyidae), suggesting that mechanical pruning combined with biocontrol may improve overall success.

Another insect exclusion study at the individual plant level showed an average reduction of 284 leaves m⁻² and 38% cover of the invasive vine *Pereskia aculeata* Miller (Cactaceae) due to the impact of the leaf-feeding flea-beetle, *Phenrica guerini* (Bechyne) (Chrysomelidae) (King et al. 2021). Although this insecticide exclusion study was conducted at a single site, by comparing the density of the agent and the damage (number of damaged leaves), inferences could be made that several other sites in the country had high enough *P. guerini* densities to cause similar impacts to plant parameters (King et al. 2021).

Jones et al. (2018) conducted an insecticide exclusion experiment to remove the biocontrol agents on *P. crassipes* on the Nseleni River, Kwa-Zulu Natal Province, compared to control sites with the biocontrol agents. This study showed that plants subjected to herbivory had significantly lower above and below water biomass and shorter petioles compared to insect free plants, but *P. crassipes* percentage cover was unaffected. In this example, although plant vigour was significantly reduced, an integrated approach with the use of herbicides was required to reduce the cover of the plant.

In biocontrol programmes where agents have recently been released, parameters have been measured before and after release. For example, after the release of *Liothrips tractabilis* Mound & Pereyra (Phlaeothripidae), the target weed, *Campuloclinium macrocephalum* (Less.) D.C. (Asteraceae), was significantly shorter, and had fewer nodes, fewer inflorescences, and fewer buds per inflorescence (Ramanand et al. 2016; Zachariades et al. 2021), indicating the impact of the agent in a short space of time. Another example of assessments of recently released agents is *Mada polluta* (Mulsant) (Coccinellidae) which resulted in a reduction in leaf density (82%–86%) and fruit production (90%–100%) of *Tecoma stans* (L.) Juss ex Kunth (Bignoniaceae) at two sites, but failed to establish at the vast majority of sites where it was released (Madire and Netshiluvhi 2021). Simelane and Mawela (2019) reported a reduction in seed set of *Cardiospermum grandiflorum* Sw. (Sapindaceae) by 32% after the release of the seed-feeding weevil, *Cissoanthonomus tuberculipennis* Hustache (Curculionidae).

Not all evaluations at this level have indicated that biocontrol has reduced weed growth parameters enough to control the target weed. The agents released against both *Hakea sericea* Schrad. & J.C. Wendl. (Proteaceae) and *Ageratina adenophora* (Spreng.) (Asteraceae) were found to reduce reproductive output but this impact was considered too limited to result in reductions to weed populations (Buccellato et al. 2021; Lyons et al. 2021) and long-term monitoring of sites where agents were established on *Dolichandra unguis-cati* (L.) L.G. Lohmann resulted in some indications of damage to late season leaf coverage, but generally very low levels of damage to the target weed (King et al. 2021).

Weed population dynamics

There are several examples of population level post-release evaluations of weed biocontrol success in South Africa. In some cases, population level parameters were measured over time from when the biocontrol agent was released, or even prior to release. In other cases, population demographics were used to show evidence of the current or future impact of biocontrol on the weed populations. Long-term monitoring of population level impacts requires repeated sampling events over long periods of up to decades depending on the life cycle of the target weed and the impact of the biocontrol agent, while population demographic studies can assess the impact of the biocontrol agent at the population level, and predict the changes to the target weed population that should occur in future, in a much shorter period of time (Paynter 2005).

Some of the most problematic IAPs in Africa are invasive *Opuntia* and *Cylindropuntia* spp. (Cactaceae). Cochineal insects, *Dactylopius* spp. (Dactylopiidae), are generally used as biocontrol agents against *Opuntia* spp., and some are very effective, reducing weed populations to low levels at a much faster rate than biocontrol against most other plant taxa (Paterson et al. 2021). The rate at which complete control can be reached for these cactus weeds has made it possible to evaluate success by monitoring populations before and after release. The long-term monitoring of *Opuntia stricta* Haw. populations in the Kruger National Park was initiated in 1992, five years before the release of the effective biocontrol agent *Dactylopius opuntiae* (Cockerell) 'stricta', and was continued for 22 years until 2013 (Hoffmann et al. 2020). The number of cladodes (stem-segments) of *O. stricta*, as well as the number of fruits, were assessed annually along fixed transects over the 22 years of the study, and the results indicated a 90% reduction in plant biomass within six years of release of the agent (Hoffmann et al. 2020). This study not only recorded the decline in the *O. stricta* population due to biocontrol, it also provided a five-year pre-release assessment, and ten years of monitoring after control had been achieved, making it even more robust and valuable. This population level long-term monitoring programme provided the evidence to Kruger National Park management to change their policy with regards to weed management. This change reduced the

amount of herbicide used for the control of *O. stricta* and allowed the redeployment of labourers, who were previously responsible for herbicide applications, to mass-rearing and redistribution of the biocontrol agent (Foxcroft and Hoffmann 2000). Collecting pre-release data over several years may rule out target weed population level changes occurring that are independent of the impact of the biocontrol agent, while monitoring after release is important evidence that control is permanent.

Reductions in populations of another invasive cactus, *Cylindropuntia fulgida* (Engelm.) F.M. Knuth, after the release of the biocontrol agent *Dactylopius tomentosus* (Lamarck) 'cholla', were reported by Klein et al. (2020). Two different varieties of the cactus were included in this post-release evaluation, and the results indicated that control of one of the varieties (var. *fulgida*) required large plants to be felled two years after release, while for the other variety (var. *mamillata*), almost all the plants were dead within less than 18 months (Klein et al. 2020).

Another valuable long-term monitoring programme is the thirty-year study to evaluate the impact of the galling fungus, *Uromycladium morrisii* Doungsa-ard, McTaggart, Geering & RG Shivas (Raveneliaceae), as a biocontrol agent against the invasive tree *Acacia saligna* (Labill.) Wendel (Fabaceae). The population density of the biocontrol agent and target weed were monitored annually for 30 years (Wood and Den Breeÿen 2021). While 16 sites were included in the study overall, only three were consistently monitored for the full 30 years, with new sites added and sites falling away over time. The control of *A. saligna* was variable, with declines in density of over 80% at nine sites, and much lower levels of success at other sites (Wood and Den Breeÿen 2021). This post-release evaluation highlighted the importance of climatic conditions in understanding the variable success of the agent, as well as the importance of fire in controlling plants with long-lived seed banks.

The biocontrol of waterweeds has been successfully evaluated in South Africa (Coetzee et al. 2021), but these studies have mostly been species and site specific (e.g. Miller et al. 2021). However, in 2008 a programme was initiated to conduct quantitative post-release evaluations on the biocontrol programmes against waterweeds which involved annual visits to some 630 sites around South Africa where a series of plant and insect parameters, and weed population size

were measured. Although only the data for *S. molesta* and its agent *Cyrtobagous salviniae* Calder & Sands (Curculionidae) have been published to date (Martin et al. 2018), this programme has highlighted the need for long-term evaluation (in excess of ten years), consistency in what is measured, and continually returning to release sites where it appears that the weed has become locally extinct to detect any recruitment from long-lived seed banks, or replacement by other weeds.

In most cases, biocontrol takes many years, or even decades, before population level impacts are realised. Even programmes that take many decades before noticeable changes to populations are evident could be very successful because the trajectory of the invasion changes so that the invasion does not get worse, and the costs of the invasion are slowly, but permanently reduced (Hoffmann et al. 2019). It is important to quantify and predict the benefits of these biocontrol programmes in a relatively quick timeframe so that if further management interventions, including additional biocontrol agents or integrated control with other control methods, are required, they can be included at an early stage rather than waiting for decades while the success of the biocontrol programme is evaluated. Population demographic studies can be useful to predict future trends in target weed populations based on biocontrol impacts and therefore estimate changes to the invasion trajectory. In South Africa, a population demographics study was conducted on the long-lived invasive cactus species, *Cereus jamacaru* De Candolle, and the biocontrol agent, a galling mealybug, *Hypogeococcus* sp. (Sutton et al. 2018). The biocontrol agent causes a reduction in the number of fruits produced by mature plants, and kills small plants, but rarely kills large mature plants unless agent populations reach very high densities. Rather than measuring the impact of the agent before and after release, which would have taken several years of monitoring and repeated visits to multiple sites, a single monitoring event was conducted at multiple sites with varying levels of agent density. The evaluation was conducted during the fruiting season so that reproductive output could be assessed, and the age-structure of the populations was assessed. This once off sampling indicated that populations with high densities of the biocontrol agents had proportionally fewer young plants compared to old plants,

and that populations were in decline. By including the time since the agent established at the various sites, it was possible to predict that dense stands of *C. jamacaru* will be reduced to just a few individual plants after ten to 15 years (Sutton et al. 2018). In the past, significant funds have been spent on the control of *C. jamacaru* using herbicides in South Africa (van Wilgen et al. 2012) but the evidence from this post-release evaluation has resulted in a change of policy that biocontrol alone is utilised for control through active redistribution of the agent (Zachariades et al. 2017).

Population demographic studies, particularly quantification of seed rain and seed banks, have also been used for the evaluation of biocontrol success of invasive *Acacia* species in South Africa. *Acacia* species produce large amounts of seed and have persistent seed banks with some seeds remaining viable for over 50 years. Biocontrol has been limited to flower and seed attacking agents as the *Acacia* species are valued for firewood and timber, and some species are cultivated on a large commercial scale (Impson et al. 2021a). For one species with a relatively short-lived seed bank, *Acacia cyclops* A. Cunn. Ex G. Don., the flower galling midge and seed feeding weevil used for biocontrol have significantly reduced seed banks, resulting in a permanent reduction to plant populations in combination with mechanical control and, in particular, with fire (Impson et al. 2021a). Evidence from seed rain monitoring of other invasive *Acacia* species has shown that, although variable in space and time, generally sites with long-term biocontrol have consistently lower seed rain than sites without biocontrol or historical pre-biocontrol measurements (Impson et al. 2021a,b). The trajectory of the invasion of many invasive *Acacia* species has been changed so that the problem is slowly improving, rather than quickly getting worse, and this has undoubtedly substantially reduced the costs of *Acacia* invasions to South Africa (Hoffmann et al. 2019; Moran et al. 2021). There would be no evidence of this benefit without the detailed population level demographic studies that have been conducted. In most cases, densities of adult trees have not changed at all, so, without these post-release evaluations, we would be unaware of the magnitude of the benefits from the seed attacking biocontrol agents released against invasive *Acacia* in South Africa.

Landscape level impacts of biocontrol

The success of biocontrol is seldom assessed on a landscape level, despite biocontrol being a landscape level management intervention. Landscape level impacts have been assessed in South Africa using satellite imagery and monitoring broad distributions of IAP populations over time.

The South African Plant Invader Atlas is a long-term dataset of distributions of IAPs launched in 1994 (Henderson 1998) and is a valuable resource for evaluations of IAPs on a landscape level (i.e., country wide). An analysis that compared weeds under biocontrol to those without biocontrol agents indicated a significant reduction in the rate of spread of those with effective biocontrol agents (Henderson and Wilson 2017). When specific groups of weeds (Australian *Acacias* and aquatic macrophytes), were investigated more closely, it was clear that species under biocontrol had reduced rates of spread compared to those without biocontrol agents (Henderson and Wilson 2017). A disadvantage of relying on distributions as a method of assessing biocontrol success is that even plants that are reduced well below the tolerable threshold are still present in the ecosystem, so reductions in density, which are assumed to be linked to reductions in the negative impacts of the weeds, are overlooked.

Recent advances in drone (e.g., Yang et al. 2020; Kim et al. 2021; Lake et al. 2021) and satellite technology (Fletcher 2014) have improved our ability to measure landscape level changes in weed cover due to a biocontrol intervention. A recent study by Coetzee et al. (2022) showed the change in *P. crassipes* cover on a high elevation, highly eutrophic impoundment, Hartbeespoort Dam, in the north of South Africa, due to the biocontrol agent *M. scutellaris* between 2015 and 2021. Coverage of the weed was measured using Sentinel-2 MultiSpectral Instrument (MSI) satellite imagery at a 10 m ground resolution. The data provided an excellent up to the minute assessment of the percentage cover of the weed which allowed for timeous responses (augmentative releases of the agent) by the water resources managers.

Socio-economic returns

Globally, the direct and indirect costs of controlling IAPs are well documented and have been estimated to

be as high as US\$ 1.4 trillion per annum (about ZAR 26 trillion in South African currency), making IAPs one of the greatest threats to the global economy (Diagne et al. 2021). While there are older studies of the economic benefits associated with biocontrol of terrestrial weeds in South Africa (e.g., van Wilgen and De Lange 2011), publications from the last ten years are limited to aquatic weeds.

Fraser et al. (2016) and Arp et al. (2017) investigated the water loss savings due to the biocontrol of *P. crassipes* at two impoundments in South Africa. Both of these studies showed that the reduction of *P. crassipes* cover from 100% to less than 20% due to biocontrol translated to a significant reduction in water loss due to evapotranspiration by the weed. Maluleke et al. (2021) conducted a retrospective analysis over a twenty year period of the relative herbicide cost saving associated with the successful use of biocontrol for four aquatic weeds species (*S. molesta*, *Pistia stratiotes*, *Azolla filiculoides* and *M. aquaticum*) in South Africa. This study showed that the estimated cost (in 2020 values, discounted over 20 years at 8%) of the biocontrol programmes on all four aquatic weeds was about ZAR 7.8 million, while the estimated cost of chemical control to achieve the same level of control varied between ZAR 150 million and ZAR 1 billion, depending on the mode of application and number of follow-up herbicide sprays that were required.

Ecological returns

Reductions in weed density do not always result in improvements in terms of ecosystem services (Culliney 2005; Denslow and D'Antonio 2005), and there are very few studies that investigate the recovery of indigenous biodiversity after the management of IAPs globally (Reid et al. 2009). For example, from a global review on successful biocontrol projects, Denslow and D'Antonio (2005) observed a noticeable reduction in target weed cover and distribution, but very little quantitative evidence on the response of ecosystems after control. In a review that included 95 research papers that investigated ecosystem responses after IAPs control, 18 studies found no plant community recovery, and many of the studies that did report community recovery based these results on observations without data (Reid et al. 2009). As biodiversity recovery and improved ecosystem functioning is often the goal of a biocontrol programme, it is changes to

these parameters that should be used to evaluate success (Morin et al. 2009; Paterson et al. 2011).

In South Africa, ecosystem recovery after biocontrol has been quantified at a community level using aquatic macroinvertebrates as biological indicators. Case studies by Coetzee et al. (2020) and Motitsoe et al. (2020) clearly illustrated that biocontrol of *P. stratiotes* and *S. molesta* facilitates an increase in aquatic macroinvertebrate diversity in freshwater ecosystems. Furthermore, Motitsoe et al. (2022) showed that not only do aquatic macroinvertebrate communities recover following biocontrol, there is also an improvement in aquatic ecosystem processes, structure and functioning. When comparing biocontrol and other conventional methods, the biocontrol sites were completely different in terms of ecosystem structure, i.e., resource abundance, trophic diversity and food web complexity.

Identifying gaps in post-release evaluation efforts in South Africa

We included 38 post-release evaluation studies published for South African biocontrol targets over the last ten years in this review (Table 1). It is possible that some studies were missed in our literature search, but we are confident that the majority of the relevant published studies are included. These 38 publications cover 23 target weeds (Table 1). Four of the species included in this study (i.e., *Campuloclinium macrocephalum*, *Cardiospermum gradiflorum*, *Parthenium hysetrophorus* and *Tecoma stans*) were not included in the 54 weed species assessed by Moran et al. (2021) in their assessment of success of weed biocontrol in South Africa. So 19 species that were assessed by Moran et al. (2021) have post-release evaluations that were included in this review paper. Although this low number of post-release studies to support evaluations of success does indicate a need to expand post-release evaluation efforts to more target species, it is also important to note that some historical studies conducted prior to 2013 were excluded and that unpublished data was also included in the Moran et al. (2021) study. There are, however, several target weed species included in Moran et al. (2021) where assessments of success were made based on expert knowledge rather than data from formal studies, so post-release evaluation studies on these target weeds

would be of value, especially if they result in publications that are accessible to relevant stakeholders.

Most post-release evaluations focused on the three lower levels of assessments (weed physiology, weed growth and weed population dynamics), while very few studies have evaluated biocontrol at the landscape level (eight target weeds, but only two studies), at the socio-economic level (a single study of five aquatic weeds and two studies on water hyacinth), and ecological level (two studies on two aquatic weeds) (Table 1). While there are several studies published prior to 2013 that investigate the socio-economic benefits of weed biocontrol (van Wyk and van Wilgen 2002; McConnachie et al. 2003; van Wilgen and De Lange 2011), to the authors knowledge there are no studies investigating landscape or ecological level impacts. There is therefore a need to increase post-release efforts at these higher levels.

Discussion

Biocontrol does not aim to eradicate the target weed, but rather aims to permanently reduce the invasion to the point that it is no longer a problem or can be managed far more effectively using other methods. For this reason, evaluations of success should not simply record changes to target plant population parameters but should rather evaluate changes in the magnitude of the negative impacts inflicted by the target weed. It is therefore essential that we improve our understanding of the negative impacts that target weeds have on ecosystems and society, and that these impacts are quantified. This would allow for direct quantification of changes in the negative impacts due to biocontrol interventions. It is also important that goals for biocontrol programmes are clearly stated before agents are developed and released so that success can be measured against these goals (Morin et al. 2009). This review found only four publications that directly measured a change in negative impacts of target weeds (socio-economic and ecological returns), and these were limited to aquatic ecosystems (Table 1). There is clearly a need to increase evaluation efforts to better quantify the benefits of biocontrol at these levels, especially in terrestrial ecosystem.

The return of ecosystem functioning to pre-invasion levels is often the ultimate goal of biocontrol interventions, but there is evidence that active

restoration of ecosystems in conjunction with biocontrol could reduce the time taken for ecosystem recovery and prevent invasion from another weed species (Holmes et al. 2020). Invasive alien plant species can result in legacy effects (abiotic or biotic barriers to restoration) on invaded ecosystems even after the densities of the IAPs have been reduced (Corbin and D'Antonio 2011; Schultz and Dibble 2012; Nsikani et al. 2018). For example, there is evidence that IAPs species alter water and sediment chemistry, thus changing the microbial composition of the ecosystem, which limits native plant seed establishment following weed control, with significant implications for ecological recovery (Elgersma et al. 2011; Vilà et al. 2011). Thus, case studies focusing on identifying barriers, i.e., soil sediment chemistry and microbial composition in a 'before-after control impact' designed experiments should be given attention, since they have implications for the re-establishment and success of native (and introduced) fauna and flora (Motitsoe 2020). Incorporating restoration into post-release evaluations, and quantifying the individual contributions of biocontrol and restoration in management strategies that combine these two methods, is under studied. There were no South African examples that included restoration within post-release evaluation, but the two studies that assessed ecological returns (Coetzee et al. 2020; Motitsoe et al. 2020) take the first steps towards understanding what restoration may be required.

Similar to integrating restoration in weed control strategies, in many cases, biocontrol must be integrated with mechanical and chemical control methods in order to reduce target weeds to acceptable levels. While post-release evaluations of biocontrol programmes can help inform management which target species require integrated control, quantifying the overall success of integrated control programmes, as well as quantifying the individual contribution of each control method, is a significant challenge. Although there are a few examples of studies that have evaluated the ecosystem benefits of integrated control programmes in South Africa (e.g., Gaertner et al. 2011; Le Maitre et al. 2022), these do not separate the contributions from different control methods, so the benefit of biocontrol to ecosystems under these conditions is not quantified.

South Africa has dedicated significant resources towards post-release evaluations, and the benefits

from these studies have far outweighed the costs of implementing them. In several of the examples discussed in this paper, management strategies have changed due to the evidence of biocontrol success from post-release evaluations. These changes have improved the level of control, reduced the use of harmful herbicides, and redirected resources so that they are better used. The real benefits to ecosystems and society are, however, usually not properly quantified and in most cases are inferred. A greater effort to directly quantify the real ecosystem level benefits, and benefits to society, is likely to reveal benefits of a much greater value. Quantifying these benefits is important to motivate for further investments in the implementation of biocontrol, and the development of new agents, so that biocontrol can benefit ecosystems and society further.

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Declarations

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Iain D. Paterson is an associate professor at Rhodes University, South Africa where he is a research scientist at the Centre for Biological Control. His research focus is biological control of invasive alien plants

Samuel N. Motitsoe is a research scientist at the Centre for Biological Control who is based at Wits University, South Africa where he holds a senior lecturer position. He specialises in research on aquatic weed biocontrol and restoration of freshwater ecosystem.

Julie A. Coetzee is a professor of Botany at Rhodes University, South Africa where she is a research scientist at the Centre for Biological Control. Her research focus is aquatic weed biocontrol and invasion ecology of aquatic ecosystems.

Martin P. Hill is a distinguished professor of entomology at Rhodes University, South Africa and director of the Centre for Biological Control. His research focus is biological control of invasive alien plants and agricultural pests.