100 years of biological control of invasive alien plants in South Africa: History, practice and achievements

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How it all started

On 26 June 1906, the fourth Parliamentary Select Committee on Agricultural Cooperation met in Cape Town to debate the apparently intractable scourge to agriculture, and the wider community, of dense infestations of sweet prickly pear (*Opuntia ficus-indica*) in the Eastern Cape and Karoo.[1,2] Originating from Central America, this plant had been in South Africa since at least the 1750s, and by the 1890s had invaded an estimated 314 000 ha, which increased to about 1 million ha by the 1950s.[1] Dr G.H. Maasdorp, a member of the Legislative Assembly of the Cape and a medical practitioner in Graaff-Reinet,[3] which was literally in the thick of the prickly pear problem at the time, presented his perceptive views to the Committee[1,4]:

> *...I think we should find out what are the conditions in those countries in which* [the prickly pear] *is indigenous whether it is in the nature of a pest there or not...it may possibly be that in those countries this plant has some natural enemy for keeping* [it] *within bounds. ...and whether it would not be possible to transport that natural enemy to this country. It is a difficulty I think with all imported plants...that where they do not meet their natural enemies they...become a pest.*

Dr Maasdorp had succinctly explained the fundamental principles of weed biological control (WBC) (i.e. the use of imported plant-feeding or plant-damaging organisms, 'natural enemies', also called WBC agents, to suppress problematic plants). However, a crucial point had apparently been missed: WBC is effective only because the imported natural enemies themselves are devoid of their own natural enemies and thus have the potential for rapid population expansion on the targeted weeds in the country of introduction. In any event, a quarter of a century of political prevarication ensued because sweet prickly pear has several beneficial attributes (it bears copious quantities of edible fruits, and spineless varieties had long been cultivated as a drought-fodder crop) and it was only in 1933 that permission was ultimately granted to release a biological control agent against sweet prickly pear in South Africa[1,5] – the now-famous cactus moth, *Cactoblastis cactorum*.

Perhaps unbeknown to the Select Committee was the fact that, during the late 18th century, India had inadvertently illustrated the efficacy of WBC. In an attempt to obtain the commercially valuable dye-producing cochineal insect, *Dactylopius coccus*, entrepreneurs had erroneously imported another species, *Dactylopius ceylonicus*, from South America. This mistake resulted in the decimation of large areas of an extremely problematic cactus, called drooping prickly pear (*Opuntia monacantha*) between 1796 and 1809. *Dactylopius ceylonicus* was subsequently introduced into Ceylon (Sri Lanka) where it also successfully controlled the drooping prickly pear.[6]

Seemingly, news of this 'Deadly Indian Cochineal' reached South Africa only in 1910[1,7] and, in 1913, in South Africa's first venture in WBC, *D. ceylonicus* was imported and released as a biological control agent against drooping prickly pear, which, at the time, was highly invasive along the coast from the Western Cape to Durban. Lounsbury[7] recorded that

> [in] *about September, 1913, ...some material of the Indian species* [of cochineal was placed] *in a clump of Monacantha* [sic] *prickly pear growing* [near] *Pietermaritzburg. ...The insect soon spread...and in the following winter only the trunk-like stems were standing. The joints had blighted and fallen down...in masses...presenting a most miserable spectacle.*

The cochineal insects were then more widely distributed to other parts of the country, and within a few years drooping prickly pear had been completely controlled and has remained so ever since. Unfortunately this extraordinary precedent carries the misleading connotation that WBC is quick and easy, when in fact, in the majority of cases, WBC requires protracted research, success is not assured, and the benefits are often manifested only after many years have elapsed.

It is also tempting to conclude from these early records that South Africans were pioneers in WBC. That is not the case, but they were not far behind. The first research-based WBC project commenced in 1902 in Hawaii where several insect species were released as biological control agents against lantana, *Lantana camara*, but with little success.[8] In 1903, the Australians deliberately imported cochineal insects from India against drooping prickly pear[6] (and they provided the initial culture of *D. ceylonicus* that was imported into South Africa in 1913[7]). The 1903 attempt in Australia failed but further releases in 1914 were a resounding success. This success motivated the Australians to mount, in 1920, what was to become recognised as the most extensive and accomplished of any WBC project in the world: that against a devastatingly problematic cactus, the 'pest [prickly] pear', *Opuntia stricta.*[9,10]

The purpose of this synoptic account is to provide a perspective on the problem of invasive alien plants in South Africa, to elaborate on the basic principles and procedures in WBC, to summarise our achievements, and to commemorate some attributes that have incrementally gained the country a reputation for innovation and success in this field of endeavour.

Invasive alien plants in South Africa: A WBC perspective

In common with other countries that have a long colonial history,[11] several thousand species of alien plants have been introduced into South Africa. Many of these have become naturalised and, some, following a long 'lag' phase which may last many decades, suddenly increase in abundance and become invasive weeds. In this country, introductions which started in the 1600s and peaked in the 1800s[12] have resulted in about 200 species now being listed as damaging in an agricultural or pastoral context or in natural and conserved ecosystems.[13-16] Many are also responsible for decreasing water run-off and groundwater reserves at rates that are far in excess of water usage by the natural vegetation types, which is especially problematic in this water-scarce country.[17]

South Africa is recognised as having severe difficulties with the sheer numbers of species of invasive plants. For example, Richardson and Rejmánek[11], in a recent global review, listed 63, 90, 105 and 117 species of invasive trees in South America, North America, Australia and 'southern' (i.e. south of 20°S) Africa, respectively. Henderson[18] lists 93 species of invasive trees in South Africa. In comparison to other continental regions, and expressed in relation to total land surface areas, South Africa has several times more invasive alien species of trees per square kilometre than anywhere else. While this means little in terms of measures of distributions, density or impact, South Africa, in respect of damaging invasions by alien plants, is clearly an unfortunate outlier.

Taking an overall and approximate view of the most important of the declared weeds in South Africa,[13-19] from the perspective of a WBC practitioner thinking about the impact and management of these invasive species, there are some generalities that become apparent.

Firstly, there are virtually no permanent open waters (lakes) in South Africa (the surface area of water is less than about 0.4% of the country's total area) yet a succession of floating alien weed species have imposed enormous damage and costs. Ironically, over recent decades, as WBC has significantly reduced the problem of floating weeds in South Africa, a suite of submerged aquatic weeds that have proved to be invasive elsewhere in the world have moved into the open water bodies, presenting the next major challenge for WBC in this country.[20]

Secondly, perhaps even more badly affected are our riparian habitats which have been transformed and degraded by alien tree species such as black wattle (*Acacia mearnsii*) and gums (*Eucalyptus* spp.). 'Few if any river systems [in South Africa] have not been extensively invaded'[13].

Thirdly, terrestrial ecosystems in higher rainfall regions harbour the majority of alien plant species. The Cape Floristic Region is dominated by Australian *Acacia* and *Hakea* species and, increasingly, by pines (*Pinus* spp.).[16] The subtropical eastern regions have the dubious distinction of hosting the most varied assortment of invasive plant species, including many tree species and environmentally damaging shrubs such as triffid weed (*Chromolaena odorata*) and the many very closely related *Lantana camara* taxa. As with the water weeds, when WBC gains the ascendancy against particular invasive species in terrestrial habitats, 'replacement' species sometimes proliferate, creating further challenges and a need for intervention.

Lastly, In South Africa's drier regions, the alluvial plains and the ephemeral watercourses are severely impacted by *Prosopis* species (mesquite) hybrids, a limited number of other woody invaders, and by cacti and shrubs.[13]

This broad perspective is anything but static. Potentially devastating invasive plants such as pompom weed, *Campuloclinium macrocephalum*, and the noxious parthenium weed *Parthenium hysterophorus*, also known as 'famine weed' in South Africa, are rapidly increasing in importance, and there are many other incipient or emerging weed species in this country,[21] some of which have already proved to be very damaging elsewhere in the world.

These matters have long had the attention of various government departments and, crucially, since 1995, the Working for Water Programme (previously in the Department of Water Affairs, now in the Department of Environmental Affairs) has expended more than R3 billion on mechanical and chemical control operations. At best, this investment has just managed to retard, rather than reverse, the invasions. There is now wide recognition that more needs to be invested in research and implementation of WBC if the situation is to be at least stabilised, or improved.[22,23]

The practice of weed biological control

Conceptually, the practice of WBC is deceptively straightforward but, as is often the case, the devil is in the detail. In fact, there are considerable research and practical challenges (Table 1). Besides the accurate identification of the target weeds and the collection and importation of suitable candidate agents into quarantine, the main issue is to determine their safety for release and their potential to control the target weed. These findings form the basis of risk assessments for scrutiny by the relevant regulatory authorities who ultimately decide which agents may be released.

The determination of the host specificity of candidate agents has been paramount since the inception of concerted research into WBC at the beginning of the 1900s.[24] Single-host or multiple-host tests reveal the host-plant, feeding and egg-laying preferences of prospective agents to address the question that is always asked: 'What if the agent eliminates its intended host plant and then starts to damage beneficial or native plants?' Within all the major groups of plant-feeding insects, many species are monophagous (i.e. they are host specific and can survive on only one species of host plant) or are oligophagous and can survive only on a narrow range of closely related plant species.[25] Monophages are obviously the agents of choice for WBC. In certain circumstances, however, oligophages, such as some cactus-feeding species, may also be suitable for release because they are associated with host plant species that have no close relatives in the region where their releases are planned. Candidate agents in these categories, particularly those that have been tested, released and proven safe elsewhere in the world, require relatively short periods of confirmatory testing. Many prospective agents require much more elaborate and protracted testing (sometimes for as long as 9 years[26]) because they have never been previously tested or because they are intended for use against target weeds that are taxonomically related to important crops or to native plants. Examples of these WBC agents include candidates tested in South Africa for use against bugweed, *Solanum mauritianum*, which is in the same family as some important crops including potatoes and tomatoes.

Records from South Africa indicate that the average duration of specificity testing before WBC agents were released is nearly 4 years per agent tested.[26] Because of doubts about adequate specificity or because the agents did not seem to have the potential for sufficient impact on the target weed species, South African WBC research scientists have investigated and then rejected 64 species of candidate agents.[27] None of the WBC agents released in South Africa over the last 100 years have had any untoward or damaging consequences for beneficial or native plant species.[26,27]

What has been achieved?

Since 1913, South African entomologists and plant pathologists have considered 270 taxonomic entities (species or biotypes) of organisms including insects (87%), mites (2%) and pathogens (11%) that have the ability to feed and develop on, and thereby damage, their respective target weeds.[27] Of these, 106 were tested and released and 75 have become established as biological control agents on 48 species of invasive alien plants[27] (Table 2[1,28-31]). Six of the early South African projects, against four species of cacti, lantana and St. John's wort (*Hypericum perforatum*), were projects based on research and precedents from other countries. Since the late 1960s, South Africa has mounted independent research projects in WBC (although continuing to cooperate closely with other leading nations in biological control, namely Australia, the USA, New Zealand and Canada), targeting many weed species that have not been tackled anywhere else in the world. In recent years South Africa has been able to reciprocate previous generosity and goodwill by providing Australia and New Zealand with agents that have been developed entirely in this country.

Table 1: Sequential phases and processes involved in weed biological control (WBC) and associated challenges

Main phases in WBC	Research procedures	Comments and challenges
Determine identity of target weed species	Undertake taxonomic, phylogenetic and molecular genetic studies	Accurate identity often very complicated (cryptic species, varieties, hybrids, cultivars)
Determine origin of target weed species	Perform herbarium and literature searches; explore area; search historical records	Many failures in WBC relate to exploration in the wrong region
Explore for suitable plant-feeding agents in area of origin of target weed	Identify candidate agents; explore indications of host ranges; study biology of agents and of close taxa elsewhere	Foreign exploration expensive, difficult and sometimes dangerous; expedite process through formal involvement of local research institutions
Export candidate agents from country of origin to country where releases are intended	Determine optimal conditions for maintenance and transportation	Permits to export agents from foreign countries sometimes impossible to obtain; quarantine facilities are required to receive and rear agents
Perform studies to confirm that agents are suitable and safe for release	Determine host ranges (safety) of candidate agents under quarantine conditions; assess potential efficacy by type and extent of damage caused	Choose test plants, usually by taxonomic relatedness to target weed, including native plants and crops; climate-controlled, quarantine facilities are specialised and very expensive
Apply for permits to release agents	Analyse research findings on host range and potential efficacy of agents; prepare motivations for release	Research results subject to peer review; cultures of agents that fail safety tests or may not be effective are destroyed; final approval often protracted
Mass rear approved agents	Develop techniques to maintain large colonies as a source of agents for field releases onto the target weed	Hygienic conditions required to avoid overcrowding and disease; retain genetic integrity of agent cultures
Release approved agents onto the target weed in the field	Determine optimal release techniques to improve chances of agent establishment	Timing, condition of target plant, and number of agent individuals released are important factors
Determine whether populations of agent have established on target weed	Monitor persistence and fluctuations in numbers, as well as spread of agents on target host	Several releases of agents at many sites may be necessary
Enhance distribution of agents in the field	Determine where agent populations are thriving and use for wider distribution	Some agents are slow to disperse and require repeated manual interventions (re-distribution)
Assess direct impact of agents on target weed	Quantify in detail the damage caused to different parts of the plant	Frequent monitoring of damage levels required over several seasons
Evaluate effects of agents on weed population dynamics	Determine changes in density and dispersal patterns of target weed before and after agents have established	Studies required over several decades on agent/plant interactions, seed dynamics and plant ecology
Integrate WBC with other control practices	Determine optimal use of WBC as a supplement or replacement for other control strategies	In some cases WBC is exclusively employed, but often WBC is used together with mechanical or chemical control
Perform cost: benefit analyses	Determine long-term costs of research and implementation of WBC; estimate benefits and economic viability of WBC	Compare costs and benefits with other forms of weed suppression; consider risks and costs of not using WBC

Table 2: Invasive alien plants (weeds) on which biological control agents (species or biotypes) have become established in South Africa over the last 100 years

WEEDS (Total number of agent species established)	1910s		1920s		1930s		1940s		1950s		1960s		1970s		1980s		1990s		2000s		2010s	
CACTI																						
Opuntia monacantha (2)	*																					
Opuntia ficus-indica (4)					*	*	*	*														
Opuntia aurantiaca (2)						*																
Opuntia engelmanii (2)						*																
Cylindropuntia imbricata (1)													*									
Cylindropuntia fulgida v. *fulgida* (2)													*							*		
Cylindropuntia leptocaulis (1)														*								
Opuntia stricta (2)															*			*				
Harrisia martinii (2)															*		*					
Cereus jamacaru/ hildmannianus (2)																	*					
Pereskia aculeata (1)																	*	*				
Harrisia bonplandii (1)																				*		
AGENTS ESTABLISHED ON CACTUS WEEDS: DATES UNKNOWN																						
Austrocylindropuntia subulata (1)													?									
Opuntia salmiana (1)													?									
Opuntia spinulifera (1)													?									
SHRUBS, HERBS AND CLIMBERS																						
Lantana camara (17)										*	*		*	*	*			*	*	*		
Hypericum perforatum (2)											*	*	*									
Solanum elaeagnifolium (3)														*			*					
Cirsium vulgare (1)															*	*						
Ageratina adenophora (2)															*	*						
Ageratina riparia (1)																*						
Solanum sysimbriifolium (1)																	*					
Caesalpinia decapetala (1)																		*				
Dolichandra unguis-cati (3)																		*		*		
Chromolaena odorata (2)																			*			
TREES																						
Hakea sericea (5)													*	*	*				*	*		
Sesbania punicea (3)													*		*							
Hakea gibbosa (2)														*					*			
Acacia longifolia (2)															*	*						
Acacia melanoxylon (1)																*						
Acacia pycnantha (2)																*	*			*		
Acacia saligna (2)																*			*			
Paraserianthes lophantha (1)																*						
Prosopis hybrids (2)																*	*					
Acacia cyclops (2)																	*		*			
Acacia mearnsii (2)																	*	*	*			
Acacia dealbata (1)																	*	*	*	*		
Leptospermum laevigatum (2)																	*	*				
Leucaena leucocephala (1)																		*				
Solanum mauritianum (2)																		*		*		
Acacia decurrens (1)																			*	*		
Acacia baileyana (1)																				*		
Acacia podalyriifolia (1)																				*		
WATER WEEDS																						
Eichhornia crassipes (6)													*	*	*	*	*	*				
Salvinia molesta (2)																*						
Pistia stratiotes (2)																*						
Myriophyllum aquaticum (1)																	*					
Azolla filiculoides (1)																		*				

Sources: The records are derived from three review volumes[28-30] and from personal communications for more recent developments.

The weeds are grouped in categories[18] and then listed chronologically, in 5-year intervals, by the date of the first release of an agent entity.[27] First and subsequent releases of the same or of different agent entities are indicated by asterisks. Dark grey shading indicates that complete control of the weed has been achieved; medium grey shading that substantial control has been achieved; and light grey shading that control is trivial or not determined.

Note: In the case of L. camara, three agent species were released and established 'pre-1961': these releases are indicated by an asterisk in the late 1950s period.

Following the release of a WBC agent, a period of several years may elapse before populations of the agents build up to levels where there is a noticeable impact on the distributions or densities of the target weeds. Of the weed species in South Africa on which agents have become successfully established, 23% have been completely controlled (i.e. no other control measures have been needed) and 38% are under substantial biological control (i.e. other control measures may be intermittently or routinely needed, but less effort or expenditure is required than would have been the case in the absence of the WBC agents; Table 2[1,28-31]). In most cases these benefits have been sustained for decades and will continue to accrue into the future.

It is clear from Table 2 that there has been a surge in activity (i.e. number of species targeted and WBC agents released) in recent years, but not enough time has yet elapsed for these WBC agents to have brought about a significant decrease in the abundance of the targeted weed populations. What cannot be determined from Table 2 is that there are at least 15 invasive alien plant species, including incipient or emerging weeds, that are currently the subject of active WBC research but which have not been listed because no agents have yet been released on them.[27]

Some factors that have enhanced WBC endeavours in South Africa

After 100 years of effort, it is instructive to record some of the reasons for the successes achieved and to consider the current vigour and prospects for expansion of the science of WBC in South Africa:

- The enormous negative consequences of invasive alien plant species in South Africa have provided a strong incentive for investment and innovation in WBC. More than half of the projects listed in Table 2, and nearly all of the current projects, are uniquely South African in that the target weeds have never been considered for WBC elsewhere.
- From the late 1960s, the Department of Agriculture, which had always been the main agency responsible for WBC, developed a team at the Plant Protection Research Institute (PPRI) to increase research activity. An important development at the time was a change in official political strategy which turned the focus of WBC away from the traditional targets of weeds in agricultural and pastoral settings and placed an emphasis on weeds in natural ecosystems and in conservation areas. This change in priority was spurred by the threat of invasive alien trees (Australian *Acacia* and *Hakea* species) in the Fynbos Biome.[16] Projects against these weeds led to innovative expedients to use agents that reduce seed production by feeding on the flowers, buds or seeds, or that induce gall-formation of the reproductive structures, and thus diminish the aggressiveness, but not the usefulness, of the targeted plants.[16]
- Traditionally, the PPRI has concentrated on all the procedures leading up to the release of WBC agents and the monitoring of their fate. From the early 1970s the PPRI encouraged cooperative ventures in WBC with staff at some universities. Although the lines are blurred, university researchers, in collaboration with their PPRI colleagues, have mostly concentrated on long-term projects to evaluate the effects of the WBC agents on the population dynamics of the plants and thereby to determine the levels of success achieved.[32-35] This pragmatic and collegial division of responsibilities between the PPRI (now in the Agricultural Research Council) and the universities has synergised national WBC endeavours against invasive alien plants. A manifestation of these interactions has been the production of a series of review volumes by the WBC research community in South Africa in 1991[28], 1999[29] and in 2011[30], which was preceded by two earlier reviews, one on sweet prickly pear[1] and the other on jointed cactus[31]. These reviews present a detailed record of all WBC attempts in South Africa over the past century and provide a platform for constructive reflection and planning.
- A key development in WBC research and implementation from 1995 has been the involvement of the Working for Water Programme which has generously supported WBC efforts politically and financially[22]; it has successfully integrated WBC to supplement its own substantial efforts (involving tens of thousands of people) concentrating on the mechanical and chemical control of invasive alien plants; and has enabled wider international cooperation and especially collaborative ventures into the rest of Africa.[22]
- In 1973, a fledgling WBC research meeting was held at Rhodes University, attended by five people. This meeting turned out to be the forerunner of annual conferences in this country which now attract 150 or more delegates. This escalation in participants is a direct tribute to the involvement of the Working for Water Programme which, besides financial and other support, had the insight to put money into developing capacity in WBC. Of note is their funding of a most successful WBC training programme at Rhodes University, which especially includes people from population groups who until 1994 had had little involvement in these sorts of activities. At the 2013 WBC conference, the majority of the attendees were persons from previously disenfranchised groups and both genders were about equally represented. A remarkably exciting and productive transformation has been achieved in a relatively short time.
- WBC research efforts in South Africa have enjoyed increasing political and public credibility, at least in part because of the involvement of personnel from the South African Council for Scientific and Industrial Research who have shown that WBC is highly cost effective and that it constitutes an essential supplement to other management practices that are aimed at the suppression of invasive alien plants in this country.[36,37]
- In 1996, South Africa hosted the IX International Symposium on Biological Control of Weeds and will host the 14th in this series of meetings in 2014 as part of our WBC centenary celebrations. In spite of a strong emphasis on research results from WBC projects on plants that are not problematic anywhere else in the world, South African publications in WBC have garnered several thousand citations. While this may be comparatively modest, it is clearly an encouraging measure of international recognition and the stage is set for an increase in productivity and success in the field of WBC in this country.
- Lastly, but by no means least, since the 1980s, the practice of WBC, both internationally and in South Africa, has suffered from an escalation in exaggeratedly risk-averse attitudes and restrictive political structures and processes for gaining formal approval for the release of newly tested WBC agents.[24,26] This situation has slowed and almost stopped WBC progress in South Africa, causing delays that have cost millions while agents are held in quarantine.[38] Fortunately, in this centenary year, the Directorate of Plant Health of the Department of Agriculture, Fisheries and Forestry, and the Department of Environmental Affairs assisted by the South African National Biodiversity Institute, has re-activated a peer-review process for assessing applications for the release of WBC agents in South Africa. Through this initiative, a protracted stalemate seems to have been broken and the positive significance of this development to our WBC efforts cannot be overstated.

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