

Biological control of *Solanum mauritianum* Scop. (Solanaceae) in South Africa: will perseverance pay off?

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Solanum mauritianum Scop. (Solanaceae), a fast-growing tree with a high reproductive capacity, threatens several commercial activities and natural habitats in the higher rainfall regions of South Africa. Biological control efforts spanning 26 years have previously been confined to South Africa, but have recently been extended to New Zealand. The weed is a particularly challenging target for biological control, largely because of its taxonomic relatedness to economically important and native plant species which resulted in the rejection or shelving of the majority of candidate agents tested thus far. Despite these problems, two insect agents, the sap-sucking *Gargaphia decoris* Drake (Hemiptera: Tingidae) and flowerbud-feeding *Anthonomus santacruzi* Hustache (Coleoptera: Curculionidae), have been released in South Africa. *Gargaphia decoris* was first released in 1999 and has become established in several regions of the country. Although large outbreaks and extensive damage have been observed in the field, to date these have been erratic and insufficient to inflict meaningful damage on the weed populations. *Anthonomus santacruzi* was released in early 2009 and so far appears to have established at two sites in KwaZulu-Natal. This paper is a review of the biological control programme against *S. mauritianum* in South Africa, including (i) aspects of the weed that are pertinent to its invasiveness and management, (ii) the current status of the two prominent insect agents, and (iii) the direction of future research efforts.

Key words: *Anthonomus santacruzi*, bugweed, *Gargaphia decoris*, weed biological control, woolly nightshade.

INTRODUCTION

Solanum mauritianum Scop. (Solanaceae) is a branched shrub or small tree that has become invasive in several tropical, subtropical and warm temperate regions worldwide (Roe 1972; ISSG 2006). Known by several common names, most notably bugweed, tree tobacco and woolly nightshade, the plant has emerged as an important economic and environmental weed in many countries (Florentine *et al.* 2003; ISSG 2006; PIER 2010). The problem is particularly acute in South Africa, where several features, notably self compatibility, rapid growth rates, prolific fruiting, an abundance of native frugivorous birds, and extensive seed banks, have promoted the invasion of agricultural lands, forestry plantations, riparian zones and conservation areas (Henderson 2001; ISSG 2006; Witkowski & Garner 2008).

Biological control was first considered in South Africa in the mid-1980s because of the ineffectiveness or non-sustainability of conventional control methods (Olckers & Zimmermann 1991; Olckers 1999). Mechanical control usually fails because felled plants coppice rapidly unless the plants are

cut low enough and the cut stumps are treated with herbicides (Witkowski & Garner 2008). Clearing operations also dislodge the fine irritating trichomes that cover the foliage, posing a health risk to labourers (Henderson 2001; ISSG 2006). Although chemical control is more effective, using herbicides such as glyphosate, imazapyr and triclopyr that are registered for use against *S. mauritianum* in South Africa, it is confounded by the extent of existing infestations, extensive seed banks and seed dispersal by birds, which allow rapid reinvasion of cleared areas by seedlings (Witkowski & Garner 2008).

South Africa is currently the only country to have implemented a biological control programme against *S. mauritianum*. Based on achievements in South Africa, New Zealand has recently launched a biological control programme against the weed (Hayes 2009). Biological control initiatives undertaken until 2007 have been reviewed in three earlier contributions (Olckers & Zimmermann 1991; Olckers 1999, 2009). In brief, the aim of establishing a complex of agents that can reduce the



Fig. 1. *Solanum mauritianum*. (Drawn by G. Condy; first published in Olckers & Zimmermann (1991), South African National Biodiversity Institute, Pretoria.)

weed's high seed output as well as its rapid growth rate has been constrained by difficulties in demonstrating the host specificity of candidate agents during routine quarantine testing procedures. *Solanum mauritianum* has proved to be a difficult target for biological control because of its relatedness to several *Solanum* species (Solanaceae) that are either native to or cultivated in South Africa. This coupled with the common problem of expanded host ranges during host-specificity tests (e.g. Briese 2005), has resulted in the rejection or shelving of the majority of candidate agents tested so far (Olckers 1999, 2009). Despite these problems, two insect agents were eventually cleared for release, one in 1999 and the other in 2009, and both have become established in South Africa.

The biological control programme against *S. mauritianum* in South Africa has been characterized by several successes and setbacks during its 26-year history, with the programme being suspended and then resurrected on two occasions. The aim of

this paper is to document these efforts, including (i) aspects of the weed that are pertinent to its invasiveness and management, (ii) the current status of the two prominent insect agents and (iii) the direction of future research efforts.

THE TARGET PLANT

Description

Several published and electronic sources (Kissmann & Groth 1997; Henderson 2001; ISSG 2006; PIER 2010) provide a description of *S. mauritianum* (Fig. 1), which is an unarmed, evergreen shrub to small tree that varies from 2–10 m in height. Typical features include the densely pubescent foliage, caused by fine, whitish trichomes, and inflorescences of lilac blue flowers, which produce terminal clusters of green berries that ripen to a dull yellowish colour. Inflorescences bearing flowers, immature and mature fruits often are present on plants at the same time.

Origin and taxonomy

The native range of *S. mauritianum* includes northern Argentina, southern Brazil, Uruguay and Paraguay (Roe 1972; ISSG 2006). Synonyms for *S. mauritianum* include *S. auriculatum* Aiton, *S. carterianum* Rock, *S. tabaccifolium* Vell., *S. verbascifolium* L. forma *typicum* Hassl., *S. verbascifolium* L. ssp. *auriculatum* (Aiton) Hassl. and *S. verbascifolium* L. var. *auriculatum* (Aiton) Kuntze (ISSG 2006). Several closely related, and morphologically similar species, including *S. erianthum* D. Don, *S. granuloso-leprosum* Dun., *S. riparium* Pers. and *S. verbascifolium* L., coexist with *S. mauritianum* or occur further north in South America, even into North America (Kissmann & Groth 1997). Although not verified by DNA analyses, these may well be geographical forms of a widespread and variable species complex that includes *S. mauritianum*.

Solanum mauritianum has been introduced over a wide geographical range that includes several African countries, Australia, India, New Zealand and numerous islands in the Atlantic, Indian and Pacific oceans (ISSG 2006; PIER 2010). Pathways of introduction include accidental transfer by seafaring colonists, deliberate introductions for ornamental purposes, and dispersal (often between islands) by frugivorous birds (Roe 1972; ISSG 2006). Several countries, notably South Africa, several Pacific islands (e.g. Fiji, Hawaii and Tonga), New Zealand and some Indian Ocean islands (e.g. Madagascar, Mauritius and La Réunion) consider the plant to be invasive (ISSG 2006). Despite its use as a nursery plant to facilitate forest regeneration in tropical eastern Australia, there is evidence of *S. mauritianum* emerging as an invasive species in this region (Florentine *et al.* 2003), and this is probably also true of several other countries.

Introduction and distribution in South Africa

Although the precise date of introduction is unknown, *S. mauritianum* has been present in South Africa for at least 145 years, having first been recorded in KwaZulu-Natal in the early 1860s (Olckers & Zimmermann 1991). The pathway of introduction is unknown although the plant's secondary distribution has been linked with the Portuguese trade routes in the early 16th Century (Roe 1972). The plant has invaded all but the two driest of South Africa's nine provinces (Fig. 2), but is particularly widespread in the eastern, higher rainfall regions of the country, notably the East-

ern Cape, KwaZulu-Natal, Mpumalanga and Limpopo provinces. Of the most 'prominent' invasive weed species listed by the Southern African Plant Invaders Atlas (SAPIA), *S. mauritianum* is currently ranked sixth, with records of invasion from the Savanna Biome (748 records), Grassland Biome (530), watercourses and wetlands (419), forest habitats (97) and Fynbos Biome (86) (Henderson 2007).

Biology and ecology

The plant's biology and ecology (see Olckers & Zimmermann 1991; ISSG 2006; Olckers 2009 and references therein) predispose it to invasion. In particular, the plant produces flowers and fruit year-round, is pollinated by generalist pollinators, particularly bees, yet also is capable of self-pollination, allowing isolated plants to form new populations. In South Africa, several species of frugivorous birds, especially Rameron pigeons (*Columba arquatrix* Temminck) (Columbidae) (Oatley 1984), exploit the extremely large numbers of fruits produced and promote high levels of seedling recruitment in disturbed habitats, notably forestry plantations.

Seed production commences when plants reach a height of 1.5 m and increases linearly with height, with individual plants taller than 3 m capable of producing 100 000 to 200 000 seeds per year (Witkowski & Garner 2008). Although plants reproduce primarily through seeds, they are also capable of vegetative propagation as evidenced by suckering and vigorous coppicing when plants are cleared and the cut stumps are not treated, or incorrectly treated, with herbicides. Even when cut-stump treatments are applied, plants cut above 50 cm all recover and plants thus need to be cut considerably lower (<18 cm) to maximize mortality (Witkowski & Garner 2008). *Solanum mauritianum* also displays very rapid growth rates, reaching heights of several metres in 2–3 years, and is able to produce seeds within one year of germination. Although soil seed-banks persist for relatively short periods, with seed half-life ranging from 11–16 months (Witkowski & Garner 2008), seed germination is stimulated by various disturbances including fire, floods and clearing operations. Clearing operations often aggravate weed densities unless regenerating seedlings are targeted with regular and thorough follow-up herbicidal operations (Witkowski & Garner 2008).

The plant aggressively colonizes disturbed habi-

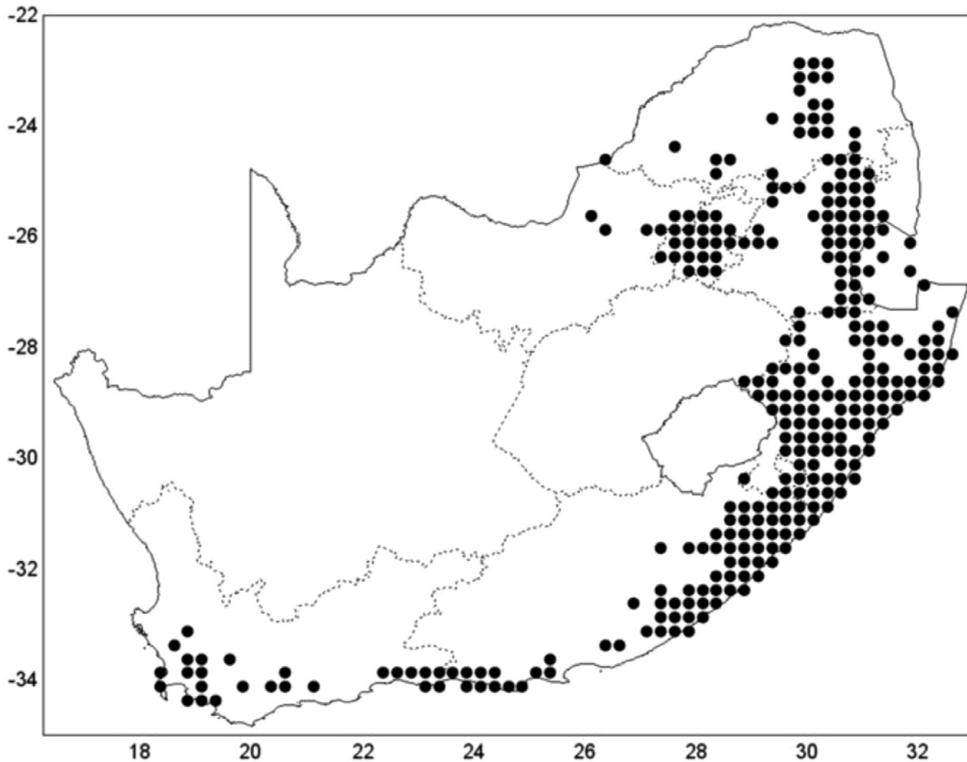


Fig. 2. Distribution of *Solanum mauritianum* in South Africa. (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria.)

tats, notably pastoral land, native forest margins, forestry plantations and urban areas, forming dense stands that overcrowd and shade out native plants or young forestry plants. Consequently, South African weed legislation lists the plant as a 'transformer' species, meaning that extensive stands are able to 'dominate or replace any canopy or sub-canopy layer of a natural or semi-natural ecosystem thereby altering its structure, integrity and functioning' (Henderson 2001). Besides the ripe fruits, the plants are unpalatable to wild and domestic animals since all parts are toxic to animals and to humans, particularly the alkaloid-rich green fruits (ISSG 2006). *Solanum mauritianum* is thought to be short-lived, with mature plants persisting for about 15 years in the field.

BIOLOGICAL CONTROL

Surveys for candidate agents commenced in 1984 and continued opportunistically for a decade until an officially-recognized biological control programme was inaugurated in South Africa in

1994. Extensive lists of the arthropods associated with *S. mauritianum* in South America are provided in earlier publications (Neser *et al.* 1990; Olckers *et al.* 2002; Pedrosa-Macedo *et al.* 2003). Given the plant's rapid growth and propensity for high seed production, a suite of agents, comprising defoliators, stem borers and flower feeders, were sought in order to maximize herbivore loads on photosynthetic, structural and reproductive tissues. In essence, the impact of these agents was intended to augment, rather than to replace, conventional control methods.

Between 1984 and 1998, a total of 15 insect species was imported into quarantine in South Africa for screening as candidate agents (Olckers 2009). Of these, nine were rejected, because of a lack of demonstrable host specificity, whereas four were dropped from further consideration, largely because of culturing difficulties that precluded testing (Olckers 1998, 1999, 2000a, 2004, 2009; Olckers *et al.* 2002; Pedrosa-Macedo *et al.* 2003). In particular, acceptance of cultivated eggplant, *Solanum melongena* L. (Solanaceae), and some

native *Solanum* species, by many of the insects, disqualified them as agents. Two insect species were cleared for release, namely the leaf-sucking lace bug *Gargaphia decoris* Drake (Hemiptera: Tingidae) in 1999 and the flowerbud weevil *Anthonomus santacruzi* Hustache (Coleoptera: Curculionidae) in 2007. Both have become established in the field.

Slow progress in South Africa, caused largely by the difficulties associated with host-specificity testing and obtaining clearance for the release of agents, resulted in the programme being suspended during the early 1990s, resurrected in 1994 and then suspended again in 2003. However, the granting of permission to release *A. santacruzi* coupled with some recent evidence of extensive damage by *G. decoris* in the field, has revived the programme. Additional genetic material of the two released agents has been imported in recent years, but there have been no introductions of new agents since 1998.

Gargaphia decoris

Gargaphia decoris was first imported from a small founder colony collected at a single locality near the Iguazu Falls (25.41.22S 54.27.26W) in Misiones, Argentina, in 1995. Attempts to introduce additional genetic material from Argentina failed because the insect was not encountered during subsequent collecting trips (Olckers *et al.* 2002) and appeared to be rare in its countries of origin. However, in 2002, new stocks of the insect, from a much larger founder colony and collected from two sites, Bosque Alemão (25.24.20S 49.17.15W) and Parque Tanguá (25.22.46S 49.16.57W), around Curitiba on the First Plateau of Paraná, a high-altitude region in southern Brazil, were introduced into South Africa (Pedrosa-Macedo *et al.* 2003).

The biology and host range of *G. decoris* was first studied using the original Argentinean material. Aspects of the insect's biology, notably long-lived adults, high rates of oviposition, a relatively quick life cycle, and high rates of sap sucking by the adults and immature stages suggested considerable potential as a biological control agent (Olckers 2000b). Despite feeding on eggplant and a few native South African *Solanum* species during host-specificity tests, there was considerable evidence to suggest that the risk of non-target effects in the field was very low and *G. decoris* was cleared for release in February 1999. Additional host-specificity tests, using both the original

Argentinean stocks (Withers *et al.* 2002) and the new Brazilian stocks (Olckers & Borea 2009), confirmed that the insect was suitable for release in New Zealand. To preclude the complications of different biotypes of *G. decoris*, with differing host ranges, an additional study confirmed that the host ranges of the Argentinean and Brazilian stocks were the same (Hope & Olckers 2011). The insect was cleared for release in New Zealand in September 2009 (Hayes 2009) and a large founder population that was collected in the field in Pietermaritzburg, KwaZulu-Natal was shipped to New Zealand in July 2010.

During 1999–2003, extensive releases of *G. decoris* were carried out using the Argentinean stocks. Initially, these were concentrated in KwaZulu-Natal but were later extended to the Eastern Cape, Gauteng, Mpumalanga and Limpopo provinces (Table 1; Fig. 3). Mass-rearing and releases were originally undertaken by the Agricultural Research Council-Plant Protection Research Institute (ARC-PPRI) (Pietermaritzburg), but the inauguration of the National Biological Control Implementation Strategy (NBCIS) in 2000 led to the involvement of additional implementing agencies (Olckers 2000c), notably the *Working for Water* Programme and Sappi Forests. Large State-funded mass-rearing facilities ensured the release of over one million insects at some 82 sites countrywide (Table 1). However, in some provinces, information on release sites, numbers released and establishment success is incomplete. Releases were scaled down in the mid-2000s because of perceptions that the insect had not established or had not proliferated at many sites. However, during 2002–2007 some 34 000 insects were released in the KwaZulu-Natal midlands using the Brazilian stocks (Table 1) because it was hoped that they would be better adapted to the warm temperate regions of South Africa where *S. mauritanium* is particularly problematic.

Initially, establishment was only recorded at 18 % of the release sites in KwaZulu-Natal (Lotter 2004). Although monitoring of establishment has not been consistent throughout the country, field observations in KwaZulu-Natal since 2006 have revealed that *G. decoris* is considerably more widespread than previously thought (Table 1; Fig. 3), with establishment confirmed at several localities, including some where the releases were deemed to have failed. Similar reports have been received from Limpopo and Mpumalanga (Table 1; Fig. 3),

Table 1. Summary of releases of adults and nymphs of *Gargaphia decoris* against *Solanum mauritianum* in South Africa. Releases were largely carried out using the Argentinean stocks, but numbers in brackets indicate those that involved Brazilian material (see text). Release records were incomplete in one province (*). The establishment records include additional sites where releases were not carried out. QDS 'quarter-degree-squares'.

Years	Province	Number of sites	QDS covered	Total released	Establishment
1999–2007	KwaZulu-Natal	45 (8)	17 (2)	185 900 (34 100)	11 sites (4 sites)
1999–2003	Eastern Cape	21	10	214 500	Unconfirmed
1999–2001	Gauteng	4	4	23 700	Unconfirmed
1999–2000	Mpumalanga	4	3	4 200	3 sites
2000–2001	Limpopo	8	3	695 300*	4 sites
Total		82	37	1 123 600	18 sites

and populations of the insect are proliferating in at least three provinces. Initial monitoring of established *G. decoris* populations in the warm temperate KwaZulu-Natal midlands revealed that these fluctuate seasonally, with peaks in autumn (April–May), sharp declines during winter (June–July), and slow recoveries during spring and summer (T. Olckers, unpubl.).

These seasonal fluctuations led to assumptions that cold winter temperatures were suppressing

populations, and this resulted in the importation of fresh, presumably more cold-adapted, stocks of *G. decoris* from a colder region in southern Brazil (see above). However, temperature-tolerance experiments revealed that populations from both Argentina and Brazil are cold tolerant, with the Brazilian population able to tolerate lower temperatures (Barker & Byrne 2005). Confirmation that releases from both countries have resulted in establishment (Table 1) has suggested that clima-

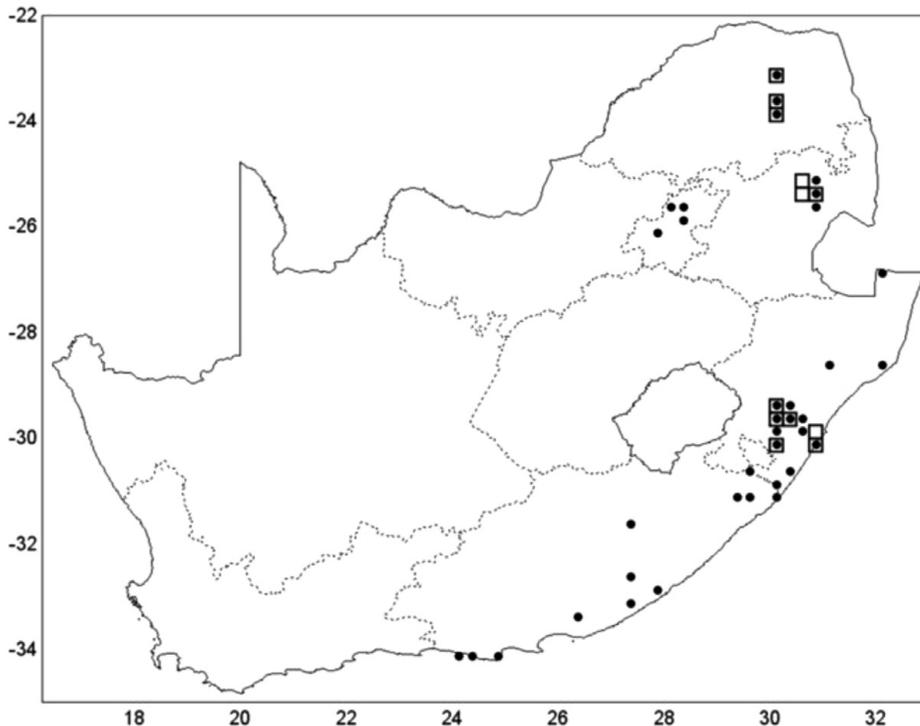


Fig. 3. Releases of *Gargaphia decoris* against *Solanum mauritianum* in South Africa (●); □ indicates confirmation of establishment. (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria.)

tic incompatibility does not pose a problem for *G. decoris*. Winter declines may be caused by decreases in host plant quality during the dry winters of the summer rainfall regions where *S. mauritianum* is particularly abundant. Field observations also have indicated that the insects display preferences for plants growing in shaded and semi-shaded habitats rather than in full sun, and this was supported by the results of a field trial that assessed the insect's persistence in, and preference for, habitats with varying shade conditions (Patrick 2009).

Gargaphia decoris appears to be negatively affected by native natural enemies in the field. Although no parasitoids have yet been recorded from the immature stages, all life stages are susceptible to foraging ants and several other generalist predators. In particular, predation of the eggs and early instars by several species of Miridae (Hemiptera) and Coccinellidae (Coleoptera) may be limiting population increases, but this has not been quantified. In outdoor trials with potted plants, several species of ants were observed removing the eggs, nymphs and adults, all of which appear to be poorly defended. Similar problems with ants were reported by implementing agencies involved with the mass-rearing of *G. decoris*, with starter colonies being lost in several instances.

Laboratory trials to determine the impact of sap sucking on *S. mauritianum* have yielded variable results. Initial experiments involving small plants revealed that high levels of feeding damage affected plant growth rates, causing stunting and biomass reductions of about 33 % relative to the undamaged controls (T Olckers, unpubl.). Longer-term trials in which plants in different size classes were exposed to varying levels of sap sucking indicated that *S. mauritianum* plants were tolerant of even high levels of damage, showing no signs of stunting, but displaying reductions in root biomass (Hakizimana 2008). With one notable exception (see below), high levels of damage have mostly not been realized in the field. Even though *G. decoris* has become more widespread in recent years, damage to weed populations in general has been only moderate because insect populations have remained at low densities and have not reached the outbreak levels that are needed to inflict severe damage. However, in April 2007, a massive outbreak of *G. decoris* was reported in an invaded forestry plantation near Sabie, Mpumalanga (25.08.66S 30.45.43E), which caused extensive

defoliation of *S. mauritianum*, reduced flowering and fruiting and even mortality of seedlings and larger trees (Witt 2007). Similar outbreaks were reported at other nearby sites (e.g. Rosehaugh; 25.17S 30.45E), but these were all destroyed by extensive and severe forest fires in the area in July 2007. In March 2010, a smaller outbreak was observed at a roadside infestation at Hillcrest, KwaZulu-Natal (29.47.50S 30.46.31E), but the levels of damage were less and no mortality of the plants was apparent. Outbreaks like these may well be sporadic and too inconsistent to inflict significant damage on *S. mauritianum* populations.

Gargaphia decoris displayed an ability to feed on some non-target *Solanum* species during laboratory host-specificity tests, but there is no evidence of non-target feeding in the field. Surveys at the original release site near Howick, KwaZulu-Natal (29.25S 30.13E) indicated that *G. decoris* did not colonize non-target *Solanum* species growing in close proximity to *S. mauritianum*, even those that were fed on during the laboratory trials (Olckers & Lotter 2004), thus justifying the decision to release the insect.

Anthonomus santacruzi

Flowerbud-feeding weevils of the genus *Anthonomus* Germar were considered to be the most promising agents for *S. mauritianum* because they occur throughout the plant's native range in South America and appeared to be largely responsible for the low levels of fruit set, which are typical of the plants in their natural range. Two species in particular, *A. santacruzi* and *Anthonomus morticinus* Clark, are commonly associated with plant populations in Argentina, Brazil and Paraguay, often coexisting at the same localities (e.g. Posadas in Misiones, Argentina; 27.30S 55.51W) (Olckers *et al.* 2002).

The weevils were introduced from northeastern Argentina into quarantine on several occasions during the late 1980s and early 1990s (the details and coordinates are no longer on record), but excessive mortality during importations and inadequate culturing procedures prevented culturing in quarantine. In 1995, a small founder colony of 18 adults collected near the Iguazu Falls in Misiones, Argentina (25.41.22S 54.27.26W) resulted in the first quarantine culture which was sustained for two years. Collections near Ituzaingo (27.33S 56.33W) and Posadas (27.30S 55.51W) in northeastern Argentina and near Juan O'Leary (25.25S

Table 2. Chronological record of releases of adult *Anthonomus santacruzi* against *Solanum mauritianum* in KwaZulu-Natal, South Africa.

Site no.	Town: site (Map reference)	Vegetation (disturbance)	First/last release dates	No. of releases	Total released	Outcome
1	Hilton: Nr Hilton Hotel (29.32.36S 30.17.59E)	Transformed (wasteland)	17 Dec 08 13 June 09	6	500	No signs of persistence
2	Umkomaas: Empisini Nature Reserve (30.12.07S 30.47.06E)	Forest in wetland	24 June 09 21 Oct 09	3	300	Population increasing
3	Hillcrest: St Hellier Road (29.47.50S 30.46.31E)	Transformed (roadside)	30 June 10	1	100	Population increasing

55.22W) in Paraguay in 1998 resulted in the importation of some 200 weevils which mostly comprised *A. santacruzi*, but also a few individuals of *A. morticinus*; the latter were subsequently removed and destroyed. Biology and host-specificity tests were carried out on these *A. santacruzi* stocks, which eventually died out in 2005. Fresh stocks of *A. santacruzi* were imported from sites near Santa Ana (27.21.25S 55.34.59W) and Wanda (25.57.55S 54.3.50W in Misiones, Argentina in 2007 (40 individuals) and from sites between Corrientes (27.28.10S 58.50.22W and Ituzaingo (27.35.15S 56.41.31W) in Corrientes, Argentina in 2009 (190 individuals) to facilitate additional trials, mass-rearing and releases.

Initial studies on the biology and host range of *A. santacruzi* were completed in 2002. Adults feed on the open flowers, flower buds and young leaves at the shoot tips and cause the abortion and abscission of floral material at high densities (Olckers 2003). Following oviposition in the floral material, the endophagous larvae develop inside the flower buds and destroy them during their development. Despite some non-target feeding and development on eggplant and some native *Solanum* species during host-specificity tests, several lines of evidence, notably host records, field surveys in South America, and a risk assessment, suggested that *A. santacruzi* was suitable for release (Olckers *et al.* 2002; Olckers 2003). An application for permission to release the weevil in South Africa was submitted in 2003 and after a four-year delay, and following some additional tests, *A. santacruzi* was cleared for release in 2007 (Olckers 2008). Further host-specificity tests are currently being conducted on cultivated and native *Solanum* species from New Zealand to confirm its safety for release in that country.

Results achieved thus far suggest that an application for the weevil's release in New Zealand could be submitted in 2011.

Following the importation of the most recent stocks of *A. santacruzi* in 2009 (see above), cultures were established at the University of KwaZulu-Natal, Pietermaritzburg, to facilitate releases. Mass-rearing for releases is labour-intensive and time consuming, because the endophagous larvae need to be dissected out and transferred to fresh buds to complete their development. Despite this, some 900 weevils have so far been released at three sites in KwaZulu-Natal, with founder colonies varying from 100 to 500 individuals (Table 2). Preliminary results are promising, with signs of population persistence and increases already apparent at the two coastal sites, one of which involved a single release (Table 2). Since there have been no indications of persistence at the colder inland site, where the highest number of weevils was released, further releases will focus on the coastal region to maximize the chances of establishment.

Besides the possible influence of climate, *A. santacruzi* may be negatively affected by native natural enemies. Although parasitism of the endophagous larvae may be less likely because there are no equivalent flowerbud-feeding beetle taxa associated with native *Solanum* species in South Africa (Olckers & Hulley 1995), predation of the adults seems more likely. In particular, spiders (Araneae: Thomisidae) that prey on pollinators are commonly associated with *S. mauritianum* inflorescences in the field and, when they are present in laboratory cultures, they have been observed to capture the weevils. Seasonal field surveys and predation experiments in the laboratory are currently in progress to determine the extent to

which generalist predators, particularly thomisid spiders, are likely to interfere with the weevil's establishment and success.

DISCUSSION

Although the biological control programme against *S. mauritianum* in South Africa has been plagued by slow progress, the establishment of two agents has provided some incentive to persevere with the project. The future of the programme depends upon the performance of these two agents over the next few years. In this regard, there are several aspects pertaining to the two agents that need to be clarified in order to determine the way forward.

Gargaphia decoris

Recent evidence that *G. decoris* is more widespread than previously thought suggests that a far higher proportion of the releases undertaken originally have resulted in establishment. Although several implementing agencies adopted this insect at the outset of the NBCIS (Olckers 2000c) and facilitated the release of high numbers throughout South Africa, there has been a lack of follow-up monitoring of the release sites in some provinces. Similarly, in some provinces, details of releases were not recorded consistently, making it difficult to link establishment success or failure with release efforts or environmental factors. Consequently, as a priority, comprehensive surveys of *S. mauritianum* populations should be undertaken in all the major regions (Figs 2, 3) to determine the status of *G. decoris*.

Besides confirmation of establishment, population densities should be monitored at selected sites in order to determine whether insect numbers consistently fluctuate to the extent observed initially (e.g. rapid winter declines). The causes for the population fluctuations also need to be explored and could include climatic conditions, variations in host-plant quality, the apparent preference of the insects for shaded habitats, and predation of the immature stages. The ability of *S. mauritianum* to tolerate high levels of sap removal without visible signs of stress has raised the question of whether *G. decoris* will be able to inflict sufficient damage on field populations. So far, only one sustained insect outbreak has been observed to cause large-scale damage that drastically affected plant populations. This raises con-

cerns that such outbreaks may be sporadic events that are too inconsistent to contribute to biological control. Medium- to long-term monitoring of such outbreak sites, once detected, might resolve several uncertainties including: the initiation and duration of the outbreaks; dispersal patterns of the insect populations; and response of the plant populations.

Anthonomus santacruzi

Recent observations that founder populations of *A. santacruzi* are persisting and increasing in the coastal region of KwaZulu-Natal, within only one year of release, suggest that more resources should be invested in the wider redistribution of this agent in South Africa. Because *A. santacruzi* is considerably more difficult to propagate than the tingingid, *G. decoris*, the weevils are probably not suited for propagation by State-based mass-rearing centres that generally lack the specialized entomological skills. Instead, professional research institutions such as the South African Sugarcane Research Institute, which has recently proved to be highly efficient in the mass production of several weed biological control agents, may be better placed to mass-rear and release these agents. Efforts to increase weevil production also could involve research into the development of an artificial nutrient medium that will permit rapid development of the immature stages. However, given the difficulty of laboratory rearing, a preferred option would be to establish several nursery sites in the field, from which weevils could be redistributed to new field sites. Further monitoring of field populations will determine the point at which post-release evaluations should be initiated.

Impacts of *Gargaphia decoris* and *Anthonomus santacruzi*

Demonstrating significant impacts of biological control agents on plant populations (e.g. Hoffmann & Moran 1998) is the overall objective of any weed biological control programme. Unfortunately, many do not reach the post-release evaluation stage because the agents failed to proliferate and reach levels where significant impacts were measurable. Until the 2007 outbreak of *G. decoris*, the programme against *S. mauritianum* was considered to fall into this category, but a re-examination of this status seems appropriate. In particular, the availability of long-term study sites in Mpumalanga Province that have already generated considerable pre-release data on the seed production of

S. mauritianum populations (Witkowski & Garner 2008) has provided an opportunity to make quantified 'before-and-after assessments' of biological control. Releases of both *G. decoris* and *A. santacruzi*, alone or in combination, at experimental sites, with insect-free sites (possibly facilitated by chemical exclusion) maintained as controls, could provide useful long-term data on the efficacy of the two agents.

The need for additional agents

The performance of the two established agents will be the determinate of whether additional agents will be required to intensify herbivore stress on *S. mauritianum*. Because repeated surveys are unlikely to reveal any new, previously uncollected agents, any future efforts should be focused on species that have already been prioritized as promising agents (Olckers 1999, 2009). These include the congeneric flowerbud-feeding *A. morticinus*, the leaf-mining *Acallepitrax* sp. nov. (Coleoptera: Chrysomelidae), and the stem-boring *Conotrachelus squalidus* Boheman (Coleoptera: Curculionidae). In any event, it would be imprudent to release *A. morticinus* before the distribution and impact of *A. santacruzi* has been fully assessed. In particular, *A. morticinus* seems to be more abundant in the colder regions of *S. mauritianum*'s native range (Olckers *et al.* 2002; Pedrosa-Macedo *et al.* 2003) and may thus be considered if *A. santacruzi* fails to establish in the colder regions of South Africa. The undescribed leaf-mining flea

beetle *Acallepitrax* sp. nov. was tested but later shelved because of ambiguous host-specificity data (Olckers 2004). Any attempts to reconsider this species should be preceded by host-plant surveys and open-field host-range tests in South America to provide more compelling evidence of host specificity. The stem-boring weevil *C. squalidus*, may be the agent with the greatest potential, but it was shelved because, despite several introductions of healthy material, the insect could not be cultured in quarantine and no host-specificity testing was ever done. Field surveys and host-range studies in Brazil, involving a collaborating Brazilian institution, may be needed before the weevil is reconsidered for introduction into quarantine.

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