The initiation of biological control programmes against *Solanum elaeagnifolium* Cavanilles and *S. sisymbriifolium* Lamarck (Solanaceae) in South Africa

T. Olckers[1], J.H. Hoffmann[2], V.C. Moran[2], F.A.C. Impson[2] & M.P. Hill[3]

[1]*ARC - Plant Protection Research Institute, Private Bag X6006, Hilton, 3245 South Africa*

[2]*Zoology Department, University of Cape Town, Rondebosch, 7700 South Africa*

[3]*ARC - Plant Protection Research Institute, Private Bag X134, Pretoria, 0001 South Africa*

Two herbaceous *Solanum* species, *Solanum elaeagnifolium* Cavanilles and *S. sisymbriifolium* Lamarck have become problematic weeds in South Africa. A biological control programme was initiated against *S. elaeagnifolium* in the 1970s when a fruit-galling gelechiid moth, *Frumenta nephelomicta* Meyrick, was released on the weed but failed to establish. Subsequently, two chrysomelid species, *Leptinotarsa texana* Schaeffer and *L. defecta* Stål, were released on *S. elaeagnifolium* during 1992 and a third chrysomelid, *Gratiana spadicea* (Klug), was released on *S. sisymbriifolium* in 1994. Releases of the three beetle species were approved even though laboratory-based host-specificity studies showed that each was able to feed and develop on several native *Solanum* species and on a crop, *S. melongena* Linnaeus (eggplant). The rationale used to justify the release of these species, all of which have since become established, is discussed. *Leptinotarsa texana* reaches very high population densities on *S. elaeagnifolium* and causes considerable damage, stunting vegetative growth and fruit-production capacity. Early indications are that *L. texana* has the potential to contribute substantially to the biological control of *S. elaeagnifolium.* Conversely, *L. defecta* has remained localized and relatively scarce, with no obvious impact on the weed. *Gratiana spadicea* has become established on *S. sisymbriifolium* at a few release sites, but extreme winter temperatures and frequent 'veld' fires seem to have kept the beetle populations at low levels. After a slow start, the biological control programmes against *S. elaeagnifolium* and *S. sisymbriifolium* have made encouraging progress. Further studies are needed to determine the effect of *L. texana* damage on the population density of *S. elaeagnifolium* and to explain the limited abundance of *L. defecta* and *G. spadicea.*

Key words: biological weed control, *Gratiana spadicea, Leptinotarsa defecta, Leptinotarsa texana, Solanum elaeagnifolium, Solanum sisymbriifolium.*

The biological control campaign against weeds of the genus *Solanum* (Solanaceae) was initiated in the early 1970s when it became apparent that other control methods were largely ineffective against species such as *Solanum elaeagnifolium* Cavanilles (silverleaf nightshade, satansbos; Fig. 1) (Olckers & Zimmermann 1991). This North American plant is a major weed of agriculture and has invaded both arable and pastoral lands in many regions of South Africa (Wassermann *et al.* 1988; Fig. 2). Propagation is mostly vegetative and the ability of the weed to regenerate from small fragments of root had confounded attempts at mechanical or herbicidal control.

In an earlier review, Olckers & Zimmermann (1991) discussed the merits of a suite of potential agents that might be useful for biological control of *S. elaeagnifolium.* They noted several factors that have slowed progress with the programme against *S. elaeagnifolium.* In the mid 1980s, two weeds of South American origin, *Solanum mauritianum* Scopoli and *S. sisymbriifolium* Lamarck, were also targeted for biological control in South Africa. The programme against *S. mauritianum* was reviewed by Olckers & Zimmermann (1991) and is updated in this issue, while that against *S. sisymbriifolium* is reviewed here for the first time.

Solanum sisymbriifolium (wild tomato, sticky nightshade; Fig. 3), a native of warm climes in temperate South America, has been present in South Africa for around 100 years, but only during the last decade has it been recognized as a troublesome invader of agricultural lands and forestry plantations (Hill *et al.* 1993; Hill & Hulley 1995).

Fig. 1
Solanum elaeagnifolium.
(Drawn by A. Walters, National Botanical Institute, Pretoria.)

Although the weed has a limited distribution in South Africa (Fig. 2), there are several localized dense infestations, particularly in the high-lying regions along the eastern escarpment of Mpumalanga. Propagation, which occurs largely through seeds, is enhanced by high fruit production, dispersal by frugivorous birds and a resilient seed-bank. However, the weed can also propagate vegetatively and coppices readily after mechanical clearing which, despite offsetting fruit production, provides inadequate control. Only one herbicide, Garlon 4 (triclopyr), is registered for use against the weed. A biological control programme against *S. sisymbriifolium* was opportunistically initiated during 1989 (Hill & Hulley 1995). At the time, the natural enemies associated with *S. mauritianum* in South America were being surveyed by South African entomologists and the opportunity was taken to collect natural enemies on *S. sisymbriifolium.*

In this paper, we review the status of the biocontrol programmes against *S. elaeagnifolium* and *S. sisymbriifolium* in South Africa and describe the events that permitted the releases of seemingly non-specific agents. These projects are the first biological control programmes against solanaceous weeds anywhere in the world and as such are unique.

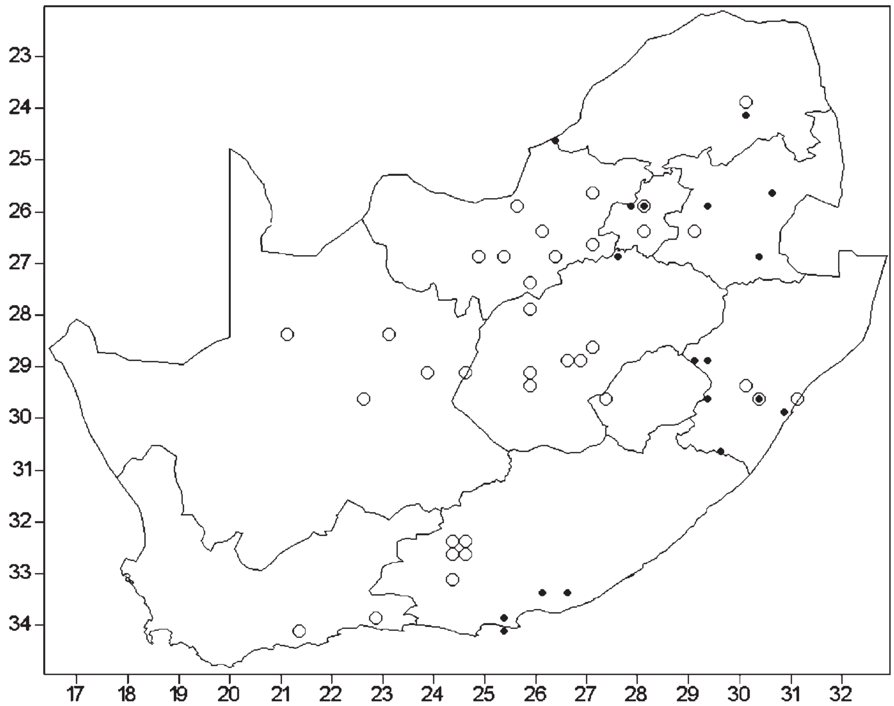

Fig. 2

Distribution of *Solanum elaeagnifolium* (○)and *S. sisymbriifolium* (●)in South Africa.

(Drawn by L. Henderson, Plant Protection Research Institute, Pretoria.)

EXPANDED HOST RANGES OF CANDIDATE AGENTS

The selection and introduction of potential biocontrol agents on *S. elaeagnifolium* and *S. sisymbriifolium* has been hampered by problems in determining the host specificity of the agents. Almost all of the agents tested so far have displayed expanded host ranges under confined experimental conditions and have fed on closely related plant species that are never attacked under natural conditions (Neser *et al.* 1990; Olckers & Zimmermann 1991; Olckers 1996). Additional complications have been the large number of agronomic crops in the family Solanaceae, two of which (potato and eggplant) also belong to the genus *Solanum,* and the presence of at least 30 indigenous species of *Solanum* in South Africa.

The dilemma this has caused was exemplified by the programme against *S. elaeagnifolium* where, of eight potential agent species that were investigated between 1974 and 1991 (Olckers & Zimmermann 1991; Olckers 1996), only two were released. The problem was exacerbated by the fact that neither species became established when released (Olckers 1995). Similarly, of the nine insect species so far evaluated as candidate agents for *S. mauritianum,* only one species has proved host-specific and suitable for release (Olckers, this issue) and both insects evaluated for *S. sisymbriifolium* have displayed expanded host ranges.

During host-specificity tests, the candidate agents seldom survived on plants outside the genus *Solanum,* but some of the insect species developed on potato (*S. tuberosum* Linnaeus) and virtually all developed on cultivated eggplant (*S. melongena* Linnaeus) and certain native congeneric plants, particularly in starvation tests. These results indicated that, under the confined conditions of host-specificity tests in quarantine, very few solanaceous insects are likely to demonstrate their actual host specificity. Despite the lack of evidence of attacks on solanaceous crops, particularly eggplant, by the agents in their countries of origin and the selection of their natural hosts during choice tests, all applications for permission to release solanaceous agents were withheld until it was realized that conventional tests would never resolve the problem.

In the early 1990s, risk assessments were carried out on two leaf-feeding chrysomelid beetles,

Fig. 3
Solanum sisymbriifolium.
(Drawn by B. Connell, National Botanical Institute, Pretoria.)

Leptinotarsa texana Schaeffer and *L. defecta* Stål, which at the time were regarded as the most promising agents for biological control of *S. elaeagnifolium.* The risk to eggplant cultivations in South Africa was assessed by evaluating cultivation practices, damage inflicted by native solanaceous insects on the crop and the nature of crop-protection procedures (Olckers & Hulley 1994). The results provided convincing evidence that eggplant crops were not threatened by the two *Leptinotarsa* species (Olckers & Hulley 1994; Olckers & Zimmermann 1995; Olckers 1996). In particular, observations that several South African solanaceous insects feed on cultivated eggplant but cause negligible damage relative to generalist pests implied that imported agents were not a significant additional risk. Furthermore, the intensive pesticide regimes needed to secure the crop against other pests provides a ready-made deterrent to the introduced biocontrol agents.

Despite native *Solanum* species not having the benefit of chemical protection, there was also sufficient evidence to indicate that these would not suffer more than incidental damage. Extensive surveys of both native and introduced *Solanum* species in South Africa (Olckers & Hulley 1989, 1991, 1995; Hill *et al.* 1993) showed that very few of the native insects attack any of the exotic, often abundant, solanaceous species, suggesting that imported agents are similarly unlikely to exploit native solanums to any extent. Other considerations included the fact that none of the native species are endangered or have any special aesthetic value and that several are regarded as minor weeds. Indeed, most native solanums are pioneer plants of disturbed areas and thus are more threatened by exotic *Solanum* species (which mostly occupy the same habitats) rather than by the imported agents. Incidental damage caused by imported insects was regarded as a fair 'trade off' for the possibility of controlling the weeds.

Ultimately, it was advocated that both *Leptinotarsa* species be released on *S. elaeagnifolium* (Olckers & Zimmermann 1995), a request that was eventually approved in 1992, some six years after work on these beetles was initiated (Olckers *et al.* 1995). The use of risk assessments to interpret the results of host-specificity tests was unprecedented in South Africa and later facilitated the release of an agent on *S. sisymbriifolium* (see below).

SOLANUM ELAEAGNIFOLIUM

Releases and establishment of *Leptinotarsa* spp.

Besides the host-specificity problems, Hoffmann *et al.* (1998) noted that: 'the prognosis for the biological control of *S. elaeagnifolium* was considered to be poor because: (i) the weed is primarily a problem in arable lands where continual disturbances (ploughing, harvesting, insecticides) mitigate against the insect agents (*e.g.* Reznik 1996); and (ii) *S. elaeagnifolium* plants are able to recover following severe defoliation because they have plentiful reserves in extensive root systems (Wassermann *et al.* 1988; Olckers & Zimmermann 1991).' In addition, Hoffmann *et al.* (1998) noted that: 'The choice of insect agents in this case was also challenging in that the beetle species, *L. texana* and *L. defecta* are very closely related to one of the world's most notorious insect pests, the Colorado potato beetle, *L. decemlineata* (Say).'

Nevertheless, the beetles have become established on *S. elaeagnifolium* throughout its range in South Africa (Table 1), becoming the first insect agents to be deliberately established on a solanaceous weed anywhere in the world. Although *L. defecta* remains localized and relatively scarce at a few release sites, *L. texana* has proliferated and become abundant on the weed at several sites.

Under some circumstances, *L. texana* reaches extraordinarily high densities on its host plants, a phenomenon noted in other leaf-feeding chrysomelid species that have been used for biological control of weeds (*e.g.* Blossey 1995; Schöps *et al.* 1996; Syrett *et al.* 1996). Hoffmann *et al.* (1998) noted that: 'In the case of *L. texana*, this happens because the beetles are reluctant to disperse and, although they have well-developed wings, the adults seem to be unable to fly or, at least, are disinclined to do so. The beetles tend to remain in an area for as long as food is available but eventually the populations become so crowded that the host plants are stripped of all edible parts. The beetles then disperse in search of food and, as they migrate, they accumulate in large numbers on healthy host plants which in turn are rapidly stripped, so that the beetles are continually forced to move onto adjacent plants. In so doing, they crawl *en masse* through the infestations of the weed, forming extensive aggregations of beetles in distinct, relatively narrow bands, a phenomenon which has been recognized elsewhere in chrysomelid species released for biological control purposes and which has been described as a "solitary population wave" (Kovalev 1988).'

Hoffmann *et al.* (1998) showed that under these circumstances *L. texana* strips the leaves, flowers and epidermal tissues from the *S. elaeagnifolium* plants, leaving only skeletonized stems and branches bearing the inedible fruits. Furthermore, even at moderate population densities, sustained feeding damage by the adults and larvae of *L. texana* severely stunted the vegetative growth and fruiting capacity of the plants (Hoffmann *et al.* 1998).

These studies have demonstrated that, contrary to expectations, *L. texana* has considerable potential as a biological control agent of *S. elaeagnifolium* in South Africa. Additional studies on the effects of the beetles on the population dynamics of the weed are now needed to demonstrate the effectiveness of this biological control agent under different crop-management regimes. Furthermore, surveys of cultivated and native *Solanum* species are also needed to determine whether pre-release predictions on the safety of the beetles have been realized, as this will be of considerable importance in justifying releases of agents on other *Solanum* weeds.

Other agents

Two gall-forming moths of the genus *Frumenta* (Gelechiidae) are to date the only agents that have proved host-specific in quarantine tests. The fruit-

Table 1

Releases of adults of *Leptinotarsa texana* and *L. defecta* on *Solanum elaeagnifolium* in South Africa between 1992 and 1997.

Province and release site	Number of releases	Number released		Year(s) of releases
		L. texana	*L. defecta*	
Eastern Cape				
Adendorp, Farm Vroegroer	5	700[1,2]	200[2]	1993/94
Kendrew, Farm Wheatlands	1	1000		1997
Murraysburg, Farm Rietpoort	5	3000		1997
Murraysburg, Farm Kareebosch	1	100		1997
Murraysburg, Farm Misthoek	1	100		1997
Murraysburg, Farm Vleiplats	1	100		1997
Free State				
Winburg, Farm Junctionspruit	2	1000+[1]	100	1993/94
Gauteng				
University of Pretoria Experimental Farm	many	1000+[1]	1000+[1]	1992/94
Northern Province				
Warmbad, Farm Roodekuil	2	1200[1]	700	1994/95
Immerpan, Farm Rembrandt	2	1400	50	1995/96
Warmbad, Farm Saron	1	400		1995
Roedtan, Farm Bekend	1	3000	5	1997
North-West Province				
Wolmaransstad, Farm Rietpan	4	1600[1]		1995/97
Wolmaransstad, Farm Vlakpan	2	160		1995
Wolmaransstad, Farm Vaalboschbult	1	100		1995
Makwassie, Farm Roodepoort	1	150		1995
Western Cape				
Riversdale, Farm Soutmelksfontein	1	3000		1997

1: establishment confirmed.
2: in addition, 100+ larvae also released.

galling moth *F. nephelomicta* Meyrick was released in large numbers on several occasions in South Africa between 1979 and 1985 but no establishment has been recorded (Olckers & Zimmermann 1991; Olckers 1995). An unidentified species of *Frumenta,* which causes both fruit- and stem-galls, was imported during 1989 and initially became established at an experimental release site at the Uitenhage Weed Laboratory (33.43S 25.26E) during 1990. However, a combination of parasitism and other unknown factors resulted in very low recoveries of galls during 1991 and 1992 and no recoveries have been made since 1993 (Olckers 1995). The reduction in fruit production on *S. elaeagnifolium* plants exposed to *L. texana* largely negates the need for fruit-feeding agents and there are no plans to reintroduce either *Frumenta* species.

Another chrysomelid, *Gratiana lutescens* (Boheman), was introduced into South Africa for biological control of *S. elaeagnifolium* during 1973 but was rejected because the beetles fed on eggplant and a native species of *Solanum* during specificity tests (Olckers & Zimmermann 1991). Following the release of the two *Leptinotarsa* species in 1992, *G. lutescens* was reintroduced from Argentina in late 1994 but was discarded when it was shown that the beetles developed on several native *Solanum* species that were not tested previously (Hill, in press) and reports were received that the species is a minor pest of both eggplant and potato in the USA.

Several other promising agents from North America and Mexico are available for introduction into South Africa (Olckers & Zimmermann 1991) but initial results with *L. texana* indicate that additional agents are not required at this stage. Introductions of other agents have thus been suspended until the impact of the two *Leptinotarsa* beetles has been clarified.

Table 2

Releases of *Gratiana spadicea* on *Solanum sisymbriifolium* in South Africa between 1994 and 1997.

Province and release site	Number of releases	Number released		Year(s) of releases
		Adults	Larvae	
Eastern Cape				
Grahamstown, along East London bypass	1	150	150	1994
Port Elizabeth, along Kragga Kamma Rd	2	500		1996
Port Elizabeth, along Seaview Rd	1	200		1997
Gauteng				
Kromdraai, Farm Jemcoh Holstein Stud	1	50	150	1995
Bryanston, roadside	1	20		1996
Mpumalanga				
Carolina, Farm Bankfontein	1	100		1994
Carolina, Farm Tevreden	2	500	500	1995
Breyton, Farm Goedverwachting	3	500[1]	500	1995
Carolina, Farm Witrand	1	100	100	1995
Carolina, Farm Buffelspruit	1	300[1]		1995
Badplaas, Farm Doornpoort	1	120		1995
Witbank, Amcoal Mines	3	350[1]		1995/96

1: establishment confirmed.

SOLANUM SISYMBRIIFOLIUM

Introduction and testing of agents

In 1989, *Gratiana spadicea* (Klug) (Chrysomelidae) was selected as a potential agent for biological control of *S. sisymbriifolium* in South Africa. *Gratiana spadicea* occurs in very high numbers on *S. sisymbriifolium* in Argentina, Brazil and Uruguay, where defoliation by both larvae and adults causes considerable damage and reduces the reproductive potential of the plants. Between 1989 and 1995, several shipments of *G. spadicea* were imported into South Africa from different regions of Argentina, Paraguay and Brazil (Olckers 1996).

Host-plant records and surveys in South America (*e.g.* Becker & Frieiro-Costa 1988) indicated that the beetle was 'strictly monophagous'. However, during host-specificity tests in quarantine the beetles developed to a limited extent on eggplant and eight native *Solanum* species (Hill & Hulley 1995). Following the successful case presented for the release of the two *Leptinotarsa* species against *S. elaeagnifolium*, similar arguments were used to promote approval for *G. spadicea* and the beetles were cleared for release in early 1994.

Releases of *Gratiana spadicea*

Gratiana spadicea was released at several sites in the Eastern Cape coastal region, Gauteng and Mpumalanga highveld between 1994 and 1997 (Table 2). Despite indications that the beetle populations were breeding and dispersing from several release sites in Mpumalanga during the 1994/95 and 1995/96 summer periods, the beetles were not recovered in the spring of the following years. Initially, it was suspected that *G. spadicea* was unable to tolerate the low winter temperatures (–10 °C) of the high altitude regions of Mpumalanga, where the most troublesome infestations of *S. sisymbriifolium* occur. The weed persists in these cold regions by dying-back in winter and coppicing from rootstocks and producing seedlings in spring. The adult beetles overwinter in cracks and crevices in rocks or in leaf litter at the base of the plants. In late 1997, populations of *G. spadicea* were found to have persisted at some of the release sites in Mpumalanga (Table 2), indicating that other factors may have hampered the initial progress of the beetles. In particular, the burning of *S. sisymbriifolium* infestations when the plants die back in winter could have destroyed or repelled the overwintering adult beetles.

Studies are needed to corroborate these suppositions and thus to implement corrective measures and create conditions that favour survival of the beetles. For example, should low winter temperatures prove to be important, then the introduction of cold-adapted 'strains' of *G. spadicea* from the colder regions of Argentina may provide a solution. Alternatively, rangeland management strategies could be modified to reduce the frequency and extent of fires in areas where the beetles are overwintering.

Gratiana spadicea seems to have failed to become established in the coastal regions of the Eastern Cape, but more extensive surveys are needed to confirm that the beetles are not present at low levels. Neither fires, which are less frequent, nor climatic conditions, which are considerably milder, could account for the failure of *G. spadicea* to establish in these coastal regions. However, *S. sisymbriifolium* behaves as a pioneer species in the coastal regions, persisting for relatively short periods in disturbed areas before being replaced by perennial weeds (notably Australian *Acacia* species) and native plants. The ephemeral nature of the weed infestations may make them unsuitable for *G. spadicea.* The situation needs to be monitored further to determine whether this is indeed the case and whether further releases in these areas are justified.

Other agents

Host-specificity tests were conducted on another chrysomelid, *Metriona elatior* (Klug), which was also opportunistically imported from Argentina and Brazil during 1992 and 1994. The tests showed that *M. elatior* was not host specific and it was considered to be unsuitable for release in South Africa (Hill & Hulley 1996).

The opportunistic nature of the biological control programme against *S. sisymbriifolium* has restricted the extent of the surveys for natural enemies. Despite this, several other herbivorous insect species have been identified as possible candidates for introduction into South Africa (Erb, unpubl.). The most promising of these is the flowerbud-feeding weevil, *Anthonomus sisymbrii* Hustache (Curculionidae), whose larvae develop in and destroy the flowerbuds, thereby preventing fruit set. Research currently in progress on a congeneric species, *A. santacruzi* Hustache, on *S. mauritianum* (Olckers, this issue), may facilitate the introduction and testing of *A. sisymbrii* in the future.

CONCLUSIONS

Early indications are that *L. texana* has considerable potential as a biocontrol agent of *S. elaeagnifolium* in South Africa. Although several additional agents are available, efforts should be made to determine the efficacy of *L. texana* and *L. defecta* in the medium to long term before the introduction of any other agents is considered. In particular, the effects of the two species on the population dynamics of *S. elaeagnifolium* needs to be measured under different crop or rangeland management regimes. Also, the impact of the beetles on cultivated and native *Solanum* species needs to be measured to confirm that the rationale for their introduction was sound.

The opportunistic nature of the programme against *S. sisymbriifolium* has limited its scope for success, but much might be achieved, with moderate additional effort, by creating favourable conditions for *G. spadicea* or by obtaining alternative agents.

Despite the slow start, the biological control programmes against *S. elaeagnifolium* and *S. sisymbriifolium* have made considerable progress recently and the prospects for the short to medium term appear promising.

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