

Improved prospects for biological control of three solanum weeds in South Africa

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Abstract. Numerous species of *Solanum* (Solanaceae) are weeds in many countries world-wide but, outside of South Africa, none have been deliberately subjected to biological control. *Solanum* weeds are difficult targets for biocontrol because the genus also includes some important cultivated species, a feature aggravated by the expanded host-ranges often displayed by candidate agents under cage conditions. Despite this, projects were launched on three introduced solanum weeds in South Africa, two of which have involved releases of agents. Following more than two decades of research on *S. elaeagnifolium* (silverleaf nightshade), two defoliating beetles, *Leptinotarsa texana* and *L. defecta* (Chrysomelidae), were released in 1992. This case was unprecedented in South Africa because a unique form of risk assessment was used to overrule the results of host-specificity tests which suggested that cultivations of eggplant (*S. melongena*) could be at risk. The beetles are currently inflicting appreciable damage to the weed at the release sites and may make a significant contribution to integrated control strategies. A more recent project against *S. sisymbriifolium* (wild tomato) culminated in the release of a defoliating beetle *Gratiana spadicea* (Chrysomelidae) in 1994. Both projects are currently focused on field evaluations, while that against *S. mauritanum* (bugweed) is concentrated on host-specificity tests. Trials on five defoliating species of beetles (*Platyphora* spp.: Chrysomelidae) again revealed expanded host-ranges, including cultivated species not known to be hosts in their native countries. None of these beetles were considered for release on *S. mauritanum* and testing is focused on five new agents which show greater promise. Despite the problems associated with solanum weeds, prospects for biological control are encouraging.

Introduction

The genus *Solanum* (Solanaceae) has several species that are of major agricultural importance world-wide and includes both cultivated and weedy species. Outside of South Africa, none of the weedy species have been deliberately subjected to biological control. Although surveys for natural enemies have also involved scientists from the United States of America (Goeden 1971) and Australia (Wapshere 1988), South Africa is currently the only country which has imported, tested and released biological control agents on solanum weeds. The dearth of biocontrol programmes within the Solanaceae (Julien 1992) has probably been influenced by perceived risks relating to the large number of cultivated species within the family.

Besides the species that have become naturalized in South Africa, the genus *Solanum* also includes two cultivated species, *S. tuberosum* L. (potato) and

S. melongena L. (eggplant, aubergine), at least 30 native species and a number that are grown as ornamentals. Despite these potential conflicts of interest, pioneering research on biocontrol has been undertaken in South Africa because three alien *Solanum* species already pose a threat to agricultural lands, forestry plantations and conservation areas.

Progress on biological control has been slow because of problems experienced during routine host-specificity tests in quarantine (Neser *et al.* 1990; Olckers and Zimmermann 1991, 1995; Olckers *et al.* 1995). Despite this, considerable advances with at least one of the problem species have provided the impetus for continued research on this group of weeds.

Importance of biocontrol in the solanum programme

The biocontrol campaign against solanum weeds was initiated in the early 1970s because of increasing

problems with *S. elaeagnifolium* Cav. (silverleaf nightshade, 'Satan's bush'). This plant is indigenous to the southern USA, Mexico and Argentina (Goeden 1971; Boyd *et al.* 1983), but has also become naturalized in India, Australia, Chile, north Africa, Mediterranean countries and some North American states (Wassermann *et al.* 1988). *Solanum elaeagnifolium* is a major weed of agriculture in both summer- and winter-rainfall regions of South Africa, where it has invaded arable and pastoral lands. The weed's ability to regenerate from an extensive and deep root system had confounded intensive chemical and mechanical control operations (Olckers and Zimmermann 1991, 1995) and this prompted the shift towards biocontrol.

Around 1984, the programme was extended to include *S. mauritianum* Scop. (woolly nightshade, bugweed). Indigenous to warm temperate South America, this plant has also become naturalized in Australasia, India and islands of the Atlantic, Indian and Pacific oceans (Roe 1972). In South Africa, *S. mauritianum* has invaded agricultural lands, forestry plantations and conservation areas, particularly in the higher rainfall regions (Olckers and Zimmermann 1991). Seed dispersal is enhanced by a very high fruit production. The fruit are extensively utilized by frugivorous birds which prefer these to their usual, indigenous fruit sources. The extent of current invasions and the rapid and continued recruitment of seedlings in cleared areas has made chemical control prohibitively expensive, despite the plant being easily killed by herbicides. Biocontrol was thus considered with a view to augmenting conventional control methods.

In the interim, a third species, *S. sisymbriifolium* Lam. (sticky nightshade, wild tomato) has increased in importance as an invader of agricultural lands and forestry plantations in a number of regions. This species is indigenous to warm temperate South America, but has also been introduced to Australia, China and India (Hill *et al.* 1993). Biocontrol was considered because the weed is apparently in an early stage of invasion and is largely controlled mechanically. No herbicides are currently registered for use against it. Furthermore, surveys on *S. mauritianum* in South America provided the opportunity to search for natural enemies on this species and an opportunistic project was thus initiated and the first agents were imported in 1989.

Problems with biocontrol of solanum weeds

The programme against *S. elaeagnifolium* exemplifies the problems facing biocontrol of *Solanum* species. Between 1973 and 1989, a total of 15 potential agents were considered (Olckers and Zimmermann 1991) of which eight were evaluated (Table 1). However, only two species were released and neither became established (Olckers and Zimmermann 1991; Olckers 1995). During specificity tests, very few of the agents developed on plants from genera other than the Solanaceae, but a disturbing feature was the ability of most agents to develop on cultivated eggplant (*S. melongena*) and on certain native *Solanum* species (Table 1). These observations conflicted with the lack of host records of these agents on eggplant in North America (Olckers and Zimmermann 1991, 1995; Olckers *et al.* 1995).

When it was found that the two most promising agents, *Leptinotarsa texana* (Schaeffer) and *L. defecta* (Stål) (Chrysomelidae), developed on eggplant and on some native solanums, it became clear that prospects for biocontrol were limited. Indications that eggplant was a 'neutral host' for solanaceous insects implied that it was unlikely that host-specific agents would be found for any of the three solanum weeds. As a result, further importations of agents were suspended during 1989-1991 in favour of a thorough evaluation of the risks posed to eggplant cultivations in South Africa. The outcome of this study had a significant influence on the direction of the solanum programme (see below).

Initial research on agents for *S. mauritianum* also failed to identify any host-specific agents. Of the first three insect agents imported (Olckers and Zimmermann 1991), two were immediately rejected because of dubious host records in South America, while the third displayed a broad host-range during quarantine tests (Table 1). Agents for *S. mauritianum* proved more problematic than those for *S. elaeagnifolium* because, apart from development on eggplant and native solanums, their laboratory host-ranges also included potato. This was the recent experience with five defoliating beetle species in the genus *Platyphora* (Chrysomelidae) imported in 1992-1994 (Table 1). Lack of host records on cultivated species in South America again suggested that the extension of host-ranges was a laboratory artefact.

Similar problems occurred with *Gratiana spadicea* (Klug) (Chrysomelidae), a defoliating beetle which

Table 1. Candidate agents evaluated for biological control of *Solanum* weed species (bold type) in South Africa. Under 'status': 1 - accepted different genera within the Solanaceae; 2 - restricted to *Solanum* species but accepted potato, eggplant and many native species; 3 - accepted eggplant and some native solanums; 4 - not tested but rejected on the basis of host records.

Agent	Year	Origin	Damage	Status
<i>S. elaeagnifolium</i>				
<i>Gratiana lutescens</i> (Boh.) (Chrysomelidae)	1973	Argentina, Texas	Defoliator	Rejected ³
<i>Arvelius albopunctatus</i> (De Geer) (Pentatomidae)	1974	Argentina	Seed feeder	Rejected ⁴
<i>Conotrachelus bisignatus</i> (Boh.) (Curculionidae)	1974	Argentina	Seed feeder	Rejected ¹
<i>Fruentia nephelomicta</i> Meyrick (Gelechiidae)	1976	Mexico	Fruit galler	Released; not established
<i>Ditylenchus phyllobius</i> (Thorne) Filip'ev (Nematoda)	1984	Texas	Leaf galler	Rejected ³
<i>Leptinotarsa texana</i> Shaeffer (Chrysomelidae)	1985- 1989	Texas	Defoliator	Released ³ ; established
<i>Leptinotarsa defecta</i> Stål (Chrysomelidae)	1985- 1987	Texas	Defoliator	Released ³ ; established
<i>Fruentia</i> spec. nov. (Gelechiidae)	1989	Texas	Fruit and stem galler	Released very locally; not established
<i>S. mauritianum</i>				
<i>Corythaica cyathicollis</i> (Costa) (Tingidae)	1984	Argentina, Brazil	Defoliator	Rejected ⁴
<i>Alcidion bicristatum</i> (Bates) (Cerambycidae)	1984 1995	Argentina, Brazil	Stem borer	Rejected ⁴ but reimported. In culture, untested
<i>Acrolepia xylophragma</i> (Meyrick) (Acrolepiidae)	1984	Argentina	Leaf miner	Rejected ²
<i>Platyphora</i> spp. (5) (Chrysomelidae)	1992- 1994	Argentina, Brazil	Defoliators	Rejected ²
<i>Anthonomus</i> sp. (Curculionidae)	1995	Argentina	Flowerbud feeder	In culture, showing promise
<i>Adesmus</i> sp. (Cerambycidae)	1995	Argentina	Stem borer	In culture, untested
<i>Conotrachelus</i> sp. (Curculionidae)	1995	Argentina	Stem borer	In culture, untested
Unidentified sp. (Tingidae)	1995	Argentina	Defoliator	In culture, showing promise
<i>S. sisymbriifolium</i>				
<i>Gratiana spadicea</i> (Klug) (Chrysomelidae)	1989- 1995	Argentina, Brazil	Defoliator	Released; established locally
<i>Metriona elatior</i> (Klug) (Chrysomelidae)	1992- 1994	Argentina, Brazil	Defoliator	Rejected ³

otherwise showed potential as an agent for *S. sisymbriifolium*. Although the beetles developed on eggplant and eight indigenous solanums, clear preferences for *S. sisymbriifolium* during choice tests and a lack of host records on eggplant in South America suggested that they were suitable for release (Hill and Hulley 1995). These findings further emphasized the importance of resolving the apparent risk to eggplant and to native solanums.

Assessing and resolving the risks

Concerns that imported solanaceous insects were a risk to eggplant cultivations in South Africa were addressed following an investigation of: (i) eggplant cultivation practices; (ii) damage to the crop by native solanaceous insects; and (iii) the nature of crop protection procedures (Olckers and Hulley 1994). The results of this study suggested that eggplant cultivations were not

at risk and it was advocated that biocontrol be implemented as a 'leap of faith' (Olckers and Zimmermann 1995). This culminated in an application for permission to release *L. texana* and *L. defecta* for the control of *S. elaeagnifolium* in 1991.

Both *L. texana* and *L. defecta* were cleared for release in South Africa during 1992 on the grounds that: (i) neither species was reported to feed on eggplant in their native habitats; (ii) many South African solanaceous insects feed on eggplant in cultivation but cause minor damage relative to polyphagous pests; and (iii) eggplant cultivations are very prone to insect attack and are thus subjected to intensive pesticide regimes which would kill any *S. elaeagnifolium*-biocontrol agent which might venture onto the crop (Olckers and Hulley 1994).

Although native South African *Solanum* species do not have the advantage of chemical protection, evidence that they would not suffer from incidental damage was supported by the fact that: (i) none of these native plants are endangered or have any special aesthetic value and many of them are regarded as minor weeds (Wells *et al.* 1986); and (ii) with few exceptions, they are all pioneer plants of disturbed areas and are thus more likely to be displaced by any one of the three solanum weeds which all occupy the same habitats (Olckers *et al.* 1995).

Similar arguments were later used to support a request for the release of *G. spadicea* on *S. sisymbriifolium*, which was subsequently granted in 1994 (Hill and Hulley 1995).

Releases and establishment of agents

Both *L. texana* and *L. defecta* have become established on *S. elaeagnifolium* at a number of sites in South Africa, with *L. texana* the more widespread of the two. Early evaluation studies revealed considerable defoliation by the beetles, resulting in reduced fruiting and a relatively slow rate of foliar regrowth compared with the rapid regrowth that usually follows conventional control methods. These observations have provided evidence that *L. texana*, at least, could have a substantial influence on the nature of integrated control strategies (Hoffmann 1995). The present evaluations will indicate the long-term prospects for this programme and whether or not additional agents are required (Olckers and Zimmermann 1991).

Although *G. spadicea* appeared to establish at several release sites, evaluations suggested the beetles

are unable to survive the low winter-temperatures typical of the high-altitude regions where *S. sisymbriifolium* is abundant. Current releases are centred around infestations in coastal and other low-lying regions, which are climatically better matched with the natural habitats of the imported stock. The long-term prospects for *G. spadicea* are thus uncertain at present.

Prospects for biocontrol of solanum weeds

The problems experienced with host-specificity testing will undoubtedly continue to plague the programme against solanum weeds in South Africa. However, prospects for biocontrol have improved considerably since the 'breakthrough' with *S. elaeagnifolium*, which occurred some 22 years after the programme was initiated. This case history, in which a holistic form of risk assessment was used to overrule the results of host-specificity tests, was unprecedented in South Africa and has increased the possibility of releases of agents on the other two solanum weeds and facilitated the release of the first agent on *S. sisymbriifolium*.

The programmes against *S. elaeagnifolium* and *S. sisymbriifolium* are currently under evaluation to determine the potential of the agents released so far and these evaluations will also reveal the accuracy of predictions about the impact of the agents on non-target species. No further introductions of agents for these two weeds are envisaged.

By contrast, the programme against *S. mauritanum* is focused on host-specificity tests, but is far more problematic because the expanded host-ranges in the laboratory have included potato, a phenomenon not observed with agents tested on the other two solanum weeds. Unlike the case with eggplant, these artefacts will be extremely difficult to defend because of the very high agronomic status of potato. Prospects for biocontrol of *S. mauritanum* are centred around five agents introduced from South America during late 1995, at least two of which appear promising (Table 1).

Current and future evaluations of agents imported for solanum weeds should concentrate on testing procedures that are less likely to produce ambiguous results. Up to now, the initial procedure has been to conduct larval and adult starvation tests followed by adult choice-tests involving species that supported development (e.g. Wapshere 1989). However, starvation tests are renowned for producing conflicting

results (e.g. Shepherd 1990) and have been the main cause of the ambiguous results observed so far for the solanum agents. Our problem is that survival on agronomic *Solanum* species during starvation tests carries the risk of compromising the agents at the outset, irrespective of the results of later choice-tests. As far as solanum weeds are concerned, it seems appropriate to reverse the procedure and concentrate on choice tests, with starvation tests confined to test species where no clear preferences were displayed. Clear preferences during choice tests which are backed up by favourable host-records from the country of origin should be the main criteria whereby agents for solanum weeds are evaluated. Indeed, it was these criteria which were used to overrule the results of the starvation tests in the case of the two *Leptinotarsa* species and *G. spadicca*, resulting in them being cleared for release.

The biocontrol programme against solanum weeds in South Africa has been ongoing for more than 25 years, although real progress has only been made during the last three years. The prospects for biological control are encouraging and will be enhanced by field evaluations of the established agents, as well as the selection of appropriate testing procedures which will reduce the danger of having potentially-suitable agents rejected.

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