

Work Towards Biological Control of *Lantana camara*: Perspectives

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Abstract

The weed generally referred to as "lantana" or *Lantana camara* is one of the oldest biological control projects. Yet the level of biological control obtained, in the many countries where natural insect enemies have been imported, varies from "poor" to "excellent". Exploration for natural enemies (insects and pathogens) on *L. camara* and closely related lantana species have been done by Koebele early this century in Mexico and much later in Central and South America by mainly Australian entomologists. It is now well known that "*L. camara*" occurs as many different forms and that these forms should be regarded as cultivars that resulted from hybridization and that hybridization is still continuously occurring. "*L. camara*" thus becomes a complex of weeds. Those introduced insect natural enemies that became successfully established in many countries around the world are possibly quite often effective or not as control agents because of different lantana cultivars. The aim of this paper is to have a critical look at the possibilities for more satisfactory levels of lantana biological control.

Introduction

The plant generally referred to as "lantana", i.e., *Lantana camara* L. (*sensu lato*), originally from subtropical to tropical America, has been the subject of concerted biological control studies for over 85 years. During this time an array of insect species have been introduced to various countries all over the world, generally with variable results (Julien 1982). The plant appears to have remained a troublesome invasive weed in suitable habitats practically all over the world, and has been rated as one of the world's ten worst weeds (Holm *et al.* 1977).

The work done on the biological control of lantana in the past is very extensive, but active new work seems to have come to a virtual stand-still despite the magnitude of the problems caused by this weed. The aim of this paper is to look critically at the possibilities of more satisfactory levels of biological control of lantana in the light of what is now known of the identity and origin of the weed, and the latest information on its natural enemies. It is not our intention to make this a complete review of all the work done world-wide on the plant and its biological control. Reviews of the biological control of *L. camara* have been done by Fullaway (1959) for Hawaii, O'Conner (1960) and Kamath (1979) for Fiji, Greathead (1968) for East Africa, Haseler (1965) and Harley (1974) for Australia, Scheibelreiter (1980) for Ghana, and Oosthuizen (1964) and Cilliers (1983) for South Africa. General reviews have been made by Holloway (1964) and Goeden (1978) and in a CIBC Status Paper (1977). To reach a decision on the viability of further work and to try and identify areas or approaches that may be further exploited, brief attention is given to the origin and exact identity, history of exploratory work, the natural enemies considered for release, results achieved and possible reasons for failures in the past.

Origins, Exact Identity and Distribution

The plant generally referred to as "lantana" or "*Lantana camara*" is regarded as of tropical American origin (Mexico, Central America and South America as far south as northern Argentina; Swarbrick 1986). It has been reported as a weed from 47 countries (Holm *et al.* 1977).

"*L. camara*", the weed, occurs in many different forms; e.g., in respect of flower colour and shape, growth form and vigour, hairiness of leaves, presence of prickles on the stems (Haseler 1965, 1980, Smith and Smith 1982), chemistry and toxicity to livestock (Louw 1943, 1948, Watt and Breyer-Brandwijk 1962, Seawright 1965, Everist 1974, Hart *et al.* 1976), cytology and fertility (Spies and Du Plessis 1987, Spies and Stirton 1982*a,b,c*), and susceptibility to attack by certain biological control agents (Radunz 1971). It has often been stated that the different "forms" should be regarded as distinct cultivars, which are known to have resulted from deliberate hybridization and selection carried out in European glasshouses during the last century (Stirton 1977). In the past it was generally believed, according to Koshoo and Mahal (1967), that the plant reproduced apomictically and that this phenomenon explained the "stability" of the cultivars. Smith and Smith (1982) named and described 29 cultivars from Australia after comparing the biotypes present in that country with those in the countries of origin. Recent cytogenetic studies (Stirton 1977, Spies 1984, Spies and Stirton 1982*a,b,c*) have, however, demonstrated that the plant does actually reproduce sexually. They showed that the plant occurs in different levels of ploidy and with fertile intermediates, and that hybridization still occurs continuously, even between "sterile" (non-fruiting) plants or plants of different ploidy levels (Spies and Du Plessis 1987).

It is generally accepted that the parents of the plant are members of the *L. camara* complex of species which occurs from Mexico to northern Argentina, and that this complex includes various *Lantana* species, the exact identity of which has not been clearly defined (Stirton 1977).

Past Exploratory Work

The original exploration for natural enemies of lantana for use in Hawaii was made in Mexico by Koebele in 1902 (Perkins and Sweezy 1924). It is worth highlighting some of the aspects of this early work, as it was an extensive search. Also, many of the species that later established world-wide, resulted from the first releases in Hawaii, from where they were redistributed along various routes (Julien 1982).

Among the 318 insect species encountered by Koebele on four *Lantana* species (with *L. camara* occurring only sparingly), there were 21 which attacked flowers primarily and a large variety, with Coleoptera and Hemiptera predominating, which damaged peduncles, seeds, leaves, twigs, stems and roots. Of the 23 species introduced in 1902 by Koebele only eight became established in Hawaii. Losses during the long, hot journey of 7 to 8 d overland to San Francisco and then by sea were high. Also, the short life cycles of several species, notably chrysomelids and cecidomyiids in galls, made them unsuitable for shipment. Losses were aggravated by high levels of parasitism and incidence of disease en route, and lack of suitable equipment for breeding the insects.

Further major searches for natural enemies of lantana were made from about 1960 to 1978 by Australian entomologists, mainly in Brazil, but also in Mexico, central America, Peru and Colombia (Wilson 1960, Haseler 1965, Harley 1974, Diatloff 1977, Winder and Harley 1983, Winder *et al.* 1984). The studies in the five main geographical regions of Brazil (including more temperate climatic regions, yielded a total of 345 species. Of these about 13 were believed to be host-specific (Winder and Harley 1983), but not all were subjected to further studies. The main gains from these Australian initiatives, as far as establishment successes are concerned, were the leaf-mining hispines (*Octotoma scabripennis* Guérin-Mèneville, *Uroplata girardi* Pic; Coleoptera: Chrysomelidae) and the leaf-mining fly, *Calcomyza lantanae* (Frick) (Diptera: Agromyzidae) (Julien 1982).

Natural Enemies Established and Their Effect

Koebele contended that flower- and seed-attacking insects would be of greater value than leaf-feeders and regarded the latter as of little significance, except when the defoliation led indirectly to reduced seeding (Perkins and Sweezy 1924). *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae), which feeds mainly on young growth and inflorescences, and *Ophiomyia lantanae* (Froggatt) (Diptera: Agromyzidae), which develops in green berries,

were among the original introductions and both became established, practically wherever lantana got naturalized (Julien 1982, Harley and Kassulke 1971).

During the sixties and seventies the leaf-mining hispines became widely established (Harley 1973, Julien 1982), and during the seventies and eighties *C. lantanae* was introduced into and became established in coastal regions. The first introduction was in Queensland (Julien 1982, Harley and Kassulke 1974), and subsequently in coastal situations in South Africa where it also appears to make an increasing contribution to leaf damage (Cilliers, unpublished data).

Of the 30 natural insect enemies used world-wide as biological control agents for *L. camara*, 20 have become established (Julien 1982). In Hawaii 12 of the 23 introduced insects became established and contribute to the biological control of the weed. Of 23 species introduced into Australia up to 1982, 15 species established (Julien 1982, Winder and Harley 1983). In South Africa 19 were introduced and 10 species became established (Cilliers 1983). Of all the insects established on the weedy taxa of *L. camara*, three species are of major importance in Australia and South Africa: *T. scrupulosa*, *O. scabripennis* and *U. girardi* (Harley and Kassulke 1971, Harley *et al.* 1979, Winder and Harley 1983, Cilliers 1983). *T. scrupulosa* became established in 20 countries and the degree of control attributed to this insect varies from good to no significant control (Julien 1982). *O. scabripennis* usually tends to be relatively more abundant than *U. girardi* in sunny situations in inland areas; whereas the latter species apparently thrives better in coastal and also in shady situations (Harley 1971, Cilliers 1982). In Australia, a cold-climate strain of *U. girardi* was introduced at a later stage, and it seems that it is establishing in cooler areas not formerly colonized by the other two hispines (Harley, K.L.S. and Taylor, T., pers. comm., 1983). *U. lantanae* and *Uroplata* sp. near *bilineata* also became established in Australia but their contribution to the overall biological control of *L. camara* is not yet clear (Willson, B.W., pers. comm., 1983; Diatloff 1977). *O. championi* also became established in Australia but is as yet of minor importance (Julien 1982). *C. lantanae* is still expanding its range in both Australia (Julien 1982) and South Africa and is a species that holds promise as a defoliator, but apparently only in coastal areas (Cilliers, unpublished data). In Hawaii the complex of introduced insect natural enemies is reportedly controlling *L. camara* satisfactorily in especially the dry areas (Andres and Goeden 1971, Goeden 1978, Julien 1982).

Evaluation of the effect of *T. scrupulosa*, *O. scabripennis* and *U. girardi* has been done by Harley *et al.* (1979) and Cilliers (1987a,b). Winder and van Emden (1981) tested the effects of four types of leaf-feeding insects on potted *L. tiliaefolia* plants. Winder and Harley (1982) reported on the effect the principal natural enemies in Paraná State, Brazil, had on *L. tiliaefolia* and *L. glutinosa* and the effect of these natural enemies was to reduce growth and vigour of the plants so that interspecific plant competition became a limiting factor. Harley *et al.* (1979) sought information on the seasonal fluctuations in the populations of the insect natural enemies established on *L. camara* and their effect on different taxa of *L. camara*. In their study *T. scrupulosa* was the insect causing the greatest damage. Damage caused by *U. girardi* and *O. scabripennis* during the observation period was not sufficient to produce observable effects. Damage by *T. scrupulosa* to foliage generally increased during summer and peaked during autumn or early winter. Damage then rapidly declined and, in addition, frosting caused rapid defoliation in winter. Variation among lantana taxa as hosts for *T. scrupulosa* was evident in all observations and showed that the "common pink" was the least susceptible, with "common pink-edged red" and "Helidon white" as the most susceptible. Adult *T. scrupulosa* feed extensively on florets as well as the foliage and the damage and consequent suppression of fruiting was similar on all three lantana taxa. Cilliers (1982, 1987b) evaluated the effects of *T. scrupulosa*, *U. girardi* and *O. scabripennis* on two pink-flowering *L. camara* taxa in South Africa. Series of measurements were done on growth, leaf abscission, flowering, fruiting and leaf damage. It was shown that the three insects adversely affected the growth and vigour of the taxa studied. Reductions of leaf-life and of ability of the plant to produce seed were the most important effects on the plant. Characteristically, insect numbers peaked in midsummer, and the resultant stress on *L. camara* led to defoliation and smaller new leaves as well as die-back of twigs and branches during the latter half of summer (Cilliers 1987a,b).

Since 1983, *C. lantanae* has become established in the subtropical coastal belt of South Africa and indications are that populations of this fly build up towards the end of the growing

season. Therefore the stress on *L. camara* is extended over a longer period because previously the plant was only stressed in midsummer (Cilliers, unpubl. data).

Possible Reasons for Poor or Non-establishment of Candidates

Apart from failures as result of insufficient numbers released, a number of other possibilities for failure also emerged. The main reasons, relevant to the discussion of future prospects, are dealt with below.

Varietal Resistance

Radunz (1971), Harley *et al.* (1979), Cilliers (1987b), among others, all found that *T. scrupulosa* performed very poorly on certain forms of lantana, and there appears to be no doubt that certain forms (e.g., orange-flowered), are not attacked to any extent in South Africa. Harley and Kassulke (1974) also reported possible varietal resistance for *C. lantanae*. This is probably to be expected if one considers that the original parent lantana material from somewhat isolated regions in tropical America would conceivably have developed resistance mechanisms against the most destructive natural enemies in their areas of origin.

Climatic Regions (Including Altitude)

Reports on establishment of different species repeatedly indicated that colonies thrived only under certain climatic conditions, or in certain climatic regions. One example among many is *C. lantanae* which has been cultured for several years and released in very large numbers in different climatic regions of South Africa, but has never established more than temporarily in any area other than along the east coast. Here it established rapidly and spread very widely within a few years (Cilliers, unpublished data). This phenomenon is also to be expected considering the diversity in climatic conditions where the plants and insects originally occurred.

The reasons for failure to establish could be a combination of various factors in operation simultaneously, with resultant population decreases, sufficient to prevent successful establishment. Some of these factors such as reduced vigour of the insect on marginally unsuitable strains of the host may be quantifiable, but others (such as host plant selection by dispersing adults once released) may be more subtle and difficult to explain. A quick survey of the species cultured and released in large numbers (e.g., *Alagoasa* sp., *Leptobyrsa decora* Drake, *Plagiohammus spinipennis* [Thomson], additional species of *Teleonemia* and *Uroplata*, and many others) but which failed to become established, clearly demonstrates that insects that are easily cultured and released in large numbers are not necessarily the ones that will establish successfully. The tingid *L. decora*, for instance was kept in culture for some six years and released in very large numbers in different parts of South Africa on a variety of host forms, but, although it survived locally, and had even become abundant temporarily, did not appear to have survived beyond the first summer season (Nieman, E., pers. comm., 1987). *U. lantanae* Buzzi and Winder collected from *L. tiliifolia* in Brazil showed promise as a biological control agent of *L. camara* in Australia, but failed to establish although it accepted varieties of *L. camara* in the insectary (Winder *et al.* 1984).

The matter is complicated by the fact that many cultures over the years survived in captivity on potted plants of given "cultivars", but failed to survive when released on these plants in the field.

Discussion

Since the "cultivars" in the *L. camara* complex of species, hybrids, varieties, forms or whatever status is afforded to the entities, are apparently not stable and are part of a very plastic continuum in which hybridization is still occurring continuously, "lantana" is a very difficult target for biological control. In most other biological control programmes the

targets, which usually start from small introductions, can be expected to be of fairly homogeneous genetic make-up. Wherever a few different reproductively isolated strains are involved (for example in *Chondrilla juncea* L., Compositae, in Australia) biological control by host-specific organisms is much more complicated, and injudicious releases may soon lead to survival of host forms resistant to the control agents, unless the latter were selected to cope with the entire target populations.

Unfortunately the exact form(s) of the host used for culturing and on which the cultures were released, and the exact form(s) of the plant on which the cultures originated, are not always reported in the literature. Even if these particulars were available, the plastic state of the *L. camara* complex of entities would make it difficult to pin these down reliably. The characteristics so far used in attempts to classify the forms of lantana, such as flower colour, shape, leaf texture, growth form, prickliness, etc., are not necessarily linked to chemical or physiological characteristics of the plant; i.e., to at least some of the factors at play in the insect-host relationships determining suitability.

In the light of the foregoing, we believe that there are still various potentially productive options left that could be exploited to achieve more satisfactory levels of biological control of lantana. These are:

1. Renewed attempts could be made to introduce some of the organisms regarded as potentially very useful by Koebele, but which he did not ship to Hawaii, or which failed to survive in sufficient numbers to allow establishment (Sweezy and Perkins 1924) because of logistic restrictions of the time. These include cecidomyiids which cause galling of flowers and other parts of the plant, leaf-feeding chrysomelids, a twig-boring cerambycid, and apionids which develop in flower stalks or seeds. He also recorded a large variety of lepidopterans which feed on flowers, of which only a few were successfully established in Hawaii.
2. Re-importation of species of which cultures were released but not established should be considered. It is known that Hawaii only had two forms of lantana, and if varietal resistance proves to be as important as present indications suggest, failures with establishment may easily have been a result of unsuitable host-plant material.
3. Attempts should be made to import as many "strains" as possible of the species already established in an attempt to increase the range of susceptible forms of the weed, like Harley (1974) did with *T. scrupulosa*. With varietal resistance as an accepted phenomenon, continuous selection for resistance within the known variable lantana populations to the most damaging species, such as *T. scrupulosa*, is very likely to be occurring. This may easily lead to a shift in the resistance levels of the populations which may soon mask the effect of the insects on the plant. The candidates need not necessarily be closely matched with the targets; for instance, the attacked varieties of *L. camara* in Australia do not occur within the native range of the genus (Sands and Harley 1981). On the other hand, *O. scabripennis* and *U. girardi*, successful biological control agents for *L. camara*, were collected from *L. glandulosissima* in Mexico, and possibly from *L. tiliaefolia* in Brazil (Winder *et al.* 1984).
4. As so many of the candidates become established only in specific climatic regions, further attempts should be made to obtain populations of already introduced insect species (or of additional species) from climatic regions that match the areas where lantana continues to create severe problems. Sands and Harley (1981) and Wapshere (1985) stressed this point.
5. Groups of organisms, such as eriophyid mites (e.g. *Eriophyes lantanae* Keifer) are known to affect members of the *L. camara* complex almost throughout the distribution range of the plant (Keifer and Denmark 1976, Flechtmann and Harley 1974), and pathogenic fungi (Sweezy and Perkins 1924) deserve further attention. Obviously a range of organisms, rather than a few key species, would be required to allow natural enemies to induce the maximum level of stress over as much as possible of the growing period of the plant, over as much as possible of the genetic material, and over as wide as possible a climatic range.

Most of these ideas are not new, and have already been attempted. As early as 1902 Koebele attempted to collect on lantanas that resembled the Hawaiian plants as closely as possible

from sites that matched lantana-infested Hawaiian sites. However, if further work is to be done, it is imperative to be more purposeful in obtaining the correct material, rather than on a trial-and-error basis. One way in which this could be done would be to expose, in the country of origin, plant material from areas of introduction, where they are troublesome. This could attract populations of species able to exploit particular strains of the plants. If such plants are also exposed in areas climatically-similar to the areas where they cause problems, insect populations which are better "pre-adapted" climatically may be obtained. This approach need not cause insurmountable quarantine problems.

With re-introduction of new forms of previously imported species into large populations of the original form(s), interpretation of results will be difficult, or even impossible unless the incorporation of new genetic material into the populations can be monitored. At this stage it is not known to what extent the genetic contributions of different sources of the established insects have persisted. Even though the introduced material was of mixed origin, there could have been rapid elimination of certain traits during the initial culturing periods. To this end, sophisticated iso-enzyme studies on the established populations and on all new introductions should be made to allow more confident interpretations of any progress that may be observed. Similarly, with the likelihood of strong selection in the presence of damaging insects acting on heterogeneous host populations, attempts should be made to monitor the genetic make-up of the weed populations, and here again suitable techniques will have to be employed.

If we accept that lantana is not one weed, but a complex of quite different entities from a large, but often insular original distribution, now pooled, and not sexually isolated, we should realize that we have the makings of a very difficult biological control subject. In that light, the apparent lack of spectacular progress over the last 86 years should not discourage further work. Further work will just have to be more purposeful, and miracles should not be expected overnight by funding organizations.

Acknowledgements

We thank: Drs. V.D. Wassermann and H.G. Zimmermann for reading and useful criticisms of the manuscript; Miss C. Craemer for typing of the manuscript; Miss H. de Beer for technical assistance.

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