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A Century of Classical Biological Control of *Lantana camara*: Can Pathogens Make a Significant Difference?

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Abstract

Lantana camara L. (Verbenaceae) is a perennial woody shrub, native to the tropical and sub-tropical zones of the Americas. It is now a major weed in many regions of the Palaeotropics, invading both natural and agricultural ecosystems. It was the first weed ever targeted for classical biological control at the turn of the century, and since then 36 insect species have been released in 33 countries throughout the exotic range. Despite these efforts, control of the weed has generally been disappointing. One of the main reasons for this, is the genetic diversity of the weedy types that have invaded the exotic range following horticultural "improvement", including crossing with other *Lantana* species, resulting in a species complex. Many of these cultivars have proved to be highly invasive; in Australia alone 29 are recorded. In general, the insect agents released have a restricted host range within this complex, and, in addition, the weed is able to tolerate wider climatic and geographical areas.

In the last decade, evidence of a conspicuous and damaging mycobiota on lantana in the Neotropics, has tempted protagonists of biological control to consider fungi as potential agents. In Hawaii, a *Septoria* sp. from Ecuador was released in 1997, whilst in South Africa, neotropical isolates of *Mycovellosiella lantanae* (Chupp) Deighton are currently being screened. In Australia, the Department of Natural Resources, Queensland has commissioned CABI Bioscience to investigate the potential of a sub-tropical rust pathogen, *Prospodium tuberculatum* (Speg.) Arthur (ex Brazil). Glasshouse results show that the agent is highly host specific (50 non-target species tested), and is pathogenic to two of the major Australian biotypes (Pink and Pink-edged red). It is envisaged that this isolate will be released in Queensland in 2000.

Two other pathogens show promise: *Puccinia lantanae* (Farlow) Lindquist and *Ceratobasidium lantanae-camarae* Evans, Barreto and Ellison (web-blight). Preliminary work has started on a Peruvian isolate of the rust, and initial evidence indicates that it is able to infect a wider number of weedy cultivars and it is significantly more damaging to the target plant, causing cankering and stem die-back, than *Prospodium*. Moreover, it would complement the supposed geographic range of *Prospodium* because of its tropical rather than sub-tropical origins.

Keywords: *Lantana camara, Prospodium tuberculatum, Puccinia lantanae*, classical biological control, Australia, pathogens

Lantana camara

Lantana camara (Verbenaceae) is a perennial woody shrub with multicoloured flower clusters and is native to the tropical and sub-tropical zones of the Americas. It can thrive in a very wide range of climatic conditions and flowers may bloom all year round in warm conditions (Holm *et al.* 1977). It is an artificial hybrid species that has been subject to intense horticultural improvement in Europe since the sixteenth century and now exists in many different forms or varieties throughout the world. Flower colour has been the primary feature for distinguishing between different forms. In Australia, these are Red, Pink, White/Pale Pink and Orange (Parsons and Cuthbertson 1992). Scott (1998) has proved with RAPD analysis that there is great genetic diversity within *L. camara* and challenged the assertion that flower colour is the primary determining factor in describing varieties.

Lantana is now a major weed in many regions of the Palaeotropics where it invades natural and agricultural ecosystems. It is regarded as one of the most serious weeds in plantation crops such as coffee, oil palm, coconuts and cotton. It invades pastureland in Australia, East Africa, Fiji, Hawaii, India, the Philippines, South Africa, Zimbabwe and Zambia (Holm *et al.* 1977). In addition to its weed status, lantana is toxic to sheep and cattle. Leaves and seeds contain triterpenoids, which cause death through poisoning and photosensitivity. In East Africa, lantana is known to harbour tsetse fly (*Glossina* spp.), the vector of African sleeping sickness (Leak 1999).

Since *L. camara* is a weed of low value land and natural ecosystems, where other means of control such as mechanical and chemical would be uneconomic or environmentally damaging, biological control is considered to be a viable option.

Biological control programmes with insects

Extensive efforts have been made to find effective biocontrol agents for *L. camara* (Perkins and Swezey 1924, Holloway 1964, Greathead 1968, Harley 1974, Cilliers 1983, Neser and Cilliers 1990). Entomologists have targeted it since the turn of the century with limited success. Koebele conducted the first trial in Hawaii in 1902, releasing a total of 15 insect species (Perkins and Swezey 1924). Since then, biological control programmes have focussed on insect agents and to date, a total of 36 insect species have been released in 33 countries throughout the exotic range (Julien and Griffiths 1998, see Table 1).

Table 1.
Insect species released worldwide for the control of *Lantana camara* (adapted from Julien and Griffiths 1998).

Insect species	Group	Country released
Aconophora compressa Walker	Hemiptera	Australia
Aerenicopsis championi Bates	Coleoptera	Australia, Hawaii
Alagoasa parana Samuelson	Coleoptera	Australia, South Africa
Apion sp. A	Coleoptera	Hawaii
Apion sp. B	Coleoptera	Hawaii
Autoplusia illustrata Guenée	Lepidoptera	Australia, South Africa
Calycomyza lantanae (Frick)	Diptera	South Africa, Australia, Fiji
Charidotis pygmaea Buzzi	Coleoptera	Australia, Fiji
Cremastobombycia lantanella Busck	Lepidoptera	Hawaii

Insect species	Group	Country released
Diastema tigris Guenée	Lepidoptera	Zambia, Australia, Micronesia, Fiji, Ghana, Hawaii, St. Helena, Tanzania, Uganda
Ectaga garcia Becker	Lepidoptera	Australia
Epinotia lantana (Busck)	Lepidoptera	Micronesia, Hawaii, Marshall Islands, South Africa, Australia
Eutreta xanthochaeta Aldrich	Diptera	Australia, South Africa, Hawaii
Hepialus sp.	Lepidoptera	Hawaii
Hypena laceratalis Walker	Lepidoptera	Micronesia, Hawaii, South Africa, Fiji, Australia, Guam
Lantanophaga pusillidactyla (Walker)	Lepidoptera	Micronesia, Hawaii, Hong Kong, Palau, South Africa
Leptobyrsa decora Drake	Hemiptera	Guam, Zambia, South Africa, Palau, Hawaii, Fiji, Australia, Cook Islands, Ghana
Neogalea sunia (Guenée)	Lepidoptera	Australia, Micronesia, Hawaii, South Africa
Octotoma championi Baly	Coleoptera	Fiji, South Africa, Hawaii, Australia
Octotoma scabripennis Guérin-Méneville	Coleoptera	Guam, South Africa, Niue, New Caledonia, India, Solomon Islands, Hawaii, Ghana, Fiji, Cook Islands, Australia
Ophiomyia lantanae (Froggatt)	Diptera	Cook Islands, South Africa, New Caledonia, Kenya, India, Hong Kong, Hawaii, Guam, Micronesia, Australia, Fiji
Orthezia insignis Browne	Hemiptera	Hawaii
Parevander xanthomelas (Guérin-Méneville)	Coleoptera	Hawaii
Plagiohammus spinipennis (Thomson)	Coleoptera	Palau, Australia, Hawaii, South Africa, Guam
Pseudopyrausta santatalis (Barnes and McDunnough)	Lepidoptera	Micronesia, Fiji, Hawaii
Salbia haemorrhoidalis Guenée	Lepidoptera	Kenya, Zambia, Uganda, Tanzania, South Africa, Palau, Kenya, India, Hawaii, Fiji, Micronesia, Australia, Mauritius
Strymon bazochii (Godart)	Lepidoptera	Australia, Fiji, Hawaii

Insect species	Group	Country released
Teleonemia bifasciata Champion	Hemiptera	Hawaii
Teleonemia elata Drake	Hemiptera	Uganda, Australia, Zambia, Cook Islands, South Africa
Teleonemia harleyi Froeschner	Hemiptera	Australia
Teleonemia prolixa (Stål)	Hemiptera	Australia
Teleonemia scrupulosa Stål	Hemiptera	Tonga, Palau, Papua New Guinea, Zimbabwe, South Africa, Samoa, Solomon Islands, Tanzania, Northern Mariana Islands, Uganda, Vanuata, Zambia, Zanzibar, St. Helena, Hawaii, Niue, Australia, Micronesia, Fiji, Ghana, Guam, Ascension Island, India, Indonesia, Kenya, Madagascar, New Caledonia
Tmolus echion (Druce)	Lepidoptera	Hawaii, Fiji
Uroplata fulvopustulata Baly	Coleoptera	Fiji, Australia, South Africa
Uroplata girardi Pic	Coleoptera	Trinidad, South Africa, Samoa, Solomon Islands, St.Helena, Tanzania, Ghana, Palau, Uganda, Vanuata, Zambia, Tonga, India, Australia, Cook Islands, Micronesia, Hawaii, Guam, Philippines, Mauritius, New Caledonia, Niue, Northern Mariana Islands, Papua New Guinea, Fiji
Uroplata lantanae Buzzi and Winder	Coleoptera	Australia, South Africa

In Australia, 26 insect species were released between 1914 and 1995 in an attempt to control the weed. The vast majority of these programmes have been unsuccessful mainly because insect populations are limited by unfavourable climatic conditions. Lantana is highly invasive and is able to colonise a diverse range of habitats. Some insect species are not effective in low rainfall areas or are subject to predation and parasitism. The most successful programmes have been those with *Octotoma scabripennis* Guérin-Méneville, *Uroplata girardi* Pic, *Salbia haemorrhodalis* Guenée and *Teleonemia scrupulosa* Stål. *U. girardi,* a hispine beetle released in 1966 and 1972 (Harley 1974), was able to have a significant impact on lantana in some areas of Queensland, but its effects were limited at high altitudes and in cool conditions.

Nineteen insect species were released in South Africa during the period 1961 and 1995 (Julien and Griffiths 1998). *O. scabripennis* and *U. girardi* have exerted some degree of control in association with *T. scrupulosa*. *Hypena laceratalis* (Fabicious) has had very little effect despite its success in Hawaii (Cilliers and Neser 1991).

The general lack of success of these insect agents is also due to the broad genetic base and the uncertainty of the taxonomy of *L. camara*. Different cultivars behave as distinct weed "species" which vary in their susceptibility to insects (Taylor 1989). Twenty-nine biotypes exist in Australia alone (Smith and Smith 1982) and some of the agents released there have shown preference for only a few of these. No insect agent released to date has caused significant damage to the very important Common Pink biotype.

Biological control programmes with pathogens

Fungi have been used for many years for the control of arthropod pests but have been underexploited against invasive weeds. This is certainly so in the case of lantana. Evans (1987) considered fungal pathogens to have great potential as agents for classical biological control of weeds. The rust fungi have received the most attention because of their high level of host specificity. The first deliberate introduction of a pathogen was of *Puccinia chondrillina* Bubak and Sydenham into Australia from Italy in 1971 to control skeleton weed (*Chondrilla juncea* L.). Several other rusts have recently been released against *Mimosa pigra* L., *Cryptostegia grandiflora* (Roxburgh) R. Brown and *Parthenium hysterophorus* L. in Australia. Barreto *et al.* (1995) examined the mycobiota of *L. camara* in Brazil and selected several fungal pathogens as potential biological control agents, including *Prospodium tuberculatum*, *Puccinia lantanae* and *Ceratobasidium lantanae-camarae.* Only one fungal agent, a *Septoria* sp., has so far been released for the control of lantana, compared to 36 insect agents. However, a number of projects to assess fungal pathogens as classical biocontrol agents are currently in progress.

Septoria sp.

A *Septoria* sp. isolated from *L. camara* in Ecuador was screened and found to be pathogenic to four *L. camara* selections from Hawaii. The fungus was released in 1997 and is considered to be a promising biological control agent for the weed in Hawaiian forests (Trujillo 1995, 1997).

Prospodium tuberculatum

Prospodium tuberculatum is an autoecious rust, limited to the tropical and subtropical regions of North and South America. Pycnia and aecia are unknown and attempts to induce teliospore formation in the glasshouse have been unsuccessful (unpublished report). Urediniospores are ellipsoid or globoid and cinnamon-brown in colour. It is predominantly a leaf pathogen, only occasionally infecting petiole and stem tissue in the glasshouse. Maximum infection occurs at 20°C and after a 13-hour dew period. Chlorosis in the area of subsequent pustule eruption is visible between 14 and 18 days, depending on the concentration of inoculum. Pustule formation begins on day 21 and pustules are fully erumpent, with mature spores by day 25. Pustules continue to produce new, viable spores until at least day 48. The fungus causes rapid senescence of infected leaves, even at low inoculum densities, leading to premature leaf fall.

Screening of a Brazilian isolate (CABI ref: W1241) is complete and glasshouse inoculations indicate that the agent is pathogenic to two of the major weed biotypes in Australia. These are the Common Pink, a highly invasive biotype, and the "Pink-edged-red" biotype, which is extremely toxic to cattle. Fifty non-target species, belonging to, or very closely related to the family Verbenaceae were selected (based on the centrifugal phylogenetic system of Wapshere (1974)) and inoculated with the rust. No macroscopic symptoms were observed and microscopic symptoms were studied using the Bruzzese and

Hasan (1983) staining technique. A range of incompatible symptoms was observed. In general, spore germination did not occur but occasional distorted germ tubes were observed. Penetration of the host was attempted on some very closely related species but no haustoria were formed.

It is envisaged that this isolate will be released in Queensland in 2000.

Puccinia lantanae

Puccinia lantanae is a microcyclic rust of tropical origin. Aecia and uredinia are unknown. Telia are sub-epidermal and teliospores are of two kinds: unicellular and bicellular.

Inoculations were undertaken at CABI Bioscience by suspending infected plant pieces bearing telia of *P. lantanae* over healthy lantana plants. Plants were incubated at 20°C for 48 hours in a dew chamber to induce teliospore germination and basidiospore liberation. Chlorosis begins 9 days after inoculation with pustule formation occurring on approximately day 14. *P. lantanae* can cause significant damage to *L. camara*, infecting leaf, petiole and stem tissues, resulting in cankering and stem die-back as well as premature leaf drop.

Initial screening of a Peruvian isolate (CABI ref: W1914) of this rust from the Amazon river has begun and results show that it is pathogenic to a wider range of weedy cultivars of lantana than *P. tuberculatum.* In addition, it would complement the supposed geographic range of *P. tuberculatum* because of its tropical rather than sub-tropical origins.

Successful infection has been obtained with ten biotypes to date: two from Australia, three from South Africa, two from Madagascar and one from each of Thailand, India and Hawaii.

Mycovellosiella lantanae

The hyphomycete *Mycovellosiella lantanae* var. *lantanae* is currently being screened at Plant Protection Research Institute (PPRI), Stellenbosch, South Africa (A. Den Breeÿen, personal communication). Several isolates from Florida and Brazil are being screened for their pathogenicity to South African biotypes of *L. camara.* The pathogen causes chlorosis, necrosis and defoliation. The isolate from Florida is pathogenic to an orange coloured biotype and other isolates are being screened for their pathogenicity to other coloured biotypes.

It is hoped that the pathogen will be released in South Africa in late 2000.

Ceratobasidium lantanae-camarae

Ceratobasidium lantanae-camarae or web blight produces external white mycelial webs on the stems and petioles of lantana and can cause severe leaf fall and shoot die-back. It appears to be restricted to tropical, humid areas but attempts to assess its specificity and pathogenicity have not been successful due to difficulties in manipulating the fungus in the glasshouse situation. Field evidence suggests that it is specific to *L. camara* since no symptoms were observed on adjacent plants of *L. lilacina* in Amazonian Ecuador (Ellison and Evans 1996). Leaf symptoms can be confused with those caused by a herbicide suggesting that extracellular toxins are released by the fungus.

Conclusions

From the evidence presented in this paper, fungal pathogens clearly have the potential to play a significant role in the classical biological control of *L. camara*. The interaction of insects and pathogens has not been investigated in any detail on this weed. However, from field observations in the native range, the debilitating effect of pathogens should complement the action of the insect agents currently established on susceptible weedy varieties in the exotic range. In addition, the range of lantana varieties attacked by pathogens is proving to be different from that of the insect agents. For example, the common Pink biotype appears to be more resistant than other weedy varieties to the insect agents that have been released in Australia. This biotype is one of the three most important weedy types in Queensland and the major biotype invading New South Wales from the north of the continent. *Prospodium tuberculatum* and *Puccinia lantanae* are both highly damaging to this biotype.

The genetic diversity of the *L. camara* complex is a limiting factor in the control of the weed using classical biological control agents. Genetic analysis of populations has begun to clarify the situation, but further work is essential if biocontrol programmes (whether with insects or fungi) are to succeed.

Prospodium tuberculatum has been assessed and screened for release in Australia. Once the pathogen is successfully established, and visibly causing damage to susceptible populations of the weed, it is hoped that there will be a renewal in governmental and private sector interest in the sustainable control of lantana. Funding may then be forthcoming to investigate other, perhaps even more promising, agents for release in future years.

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