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Australian Centre for International Agricultural Research

Lantana: Current Management Status and Future Prospects

Michael D. Day, Chris J. Wiley, Julia Playford & Myron P. Zalucki

Lantana: Current Management Status and Future Prospects

Australian Centre for International Agricultural Research
Canberra 2003

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The information provided in this monograph is correct at the time of print as far as can be ascertained. However, information of lantana's presence or status in particular countries may not reflect what is actually occurring due to difficulties in obtaining that information. Also, some agents may be present in countries where the authors have not listed them, and hence the degree of damage would not be recorded. We have attempted to fill such gaps with personal communications and unpublished data; and the latter may be obtained from the principal author. Even so, some discrepancies may be expected, and we encourage readers who find them to contact the authors so that the information can be updated.

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Foreword

Lantana was the first weed to be targeted for biological control and has been researched longer than any other weed. Yet the program is one of the least successful.

Since 1902, millions of dollars and many years of work have gone into searching for potential biocontrol agents and introducing them to the countries where lantana is a weed. In general, the results have been poor — lantana remains a major weed in most tropical and subtropical countries outside its native home in the Neotropics.

Many reasons have been suggested for this failure, for example the nature of the plant itself, its great diversity and ability to hybridise, and that its origin as a hybrid ornamental plant complicates the search for its centre of origin and thus for potential agents. Searches have been made in Mexico, Central America, the West Indies, and Brazil, and insects have been collected from several different lantana species. These insects have been host-tested and released in Hawaii, South Africa, Australia, several countries in east Africa, south and east Asia, and the Pacific. Over the years, enough papers and reports have been written to fill a library, but many are either unpublished or only published in local journals.

This book brings together the available information about lantana and the insects and diseases that have been studied as its biocontrol agents. The first four chapters deal with the taxonomy and variability of lantana and related plants; it is an indication of the complexity of the weed that these topics occupy four chapters. The next five chapters cover its habitat and ecology, impact as a weed, uses, and non-biological control methods. The following three chapters list the 49 separate agents introduced against lantana or studied for possible use, and discuss possible factors influencing their success or failure. The final two chapters look at potential new research areas and make recommendations for future directions.

As a succinct summary of the mass of information on lantana and its control, this book is intended as a tool for everyone involved in lantana control as well as weed biocontrol scientists in general. We are very grateful to ACIAR for funding the publication of this book and to Paul Ferrar, Crop Science Program Coordinator in ACIAR, for his continued support for lantana biocontrol. It is our hope that this book will mark the completion of a century of biocontrol effort and the beginning of a new and more successful phase of lantana control.

Rachel McFadyen

CEO, CRC Australian Weed Management

Summary & Recommendations

Lantana camara L. is a significant weed of which there are some 650 varieties in over 60 countries or island groups. It has been the focus of biological control attempts for a century, yet still poses major problems in many regions.

Lantana has a significant impact on economic and environmental areas and is difficult to control. The key to good management of lantana is constant vigilance. Repeated control of new regrowth is critical to success. Control of new infestations should be a priority because the species is able to expand its range during good seasons, but does not die out during poor conditions. This book is a resource for land managers and researchers on methods of lantana control, particularly biocontrol.

Twenty-seven countries are deemed climatically suitable to support lantana, yet are reported to not contain the weed. It is recommended that these countries do not allow its importation, even of horticultural varieties.

One of the main reasons for lantana's weediness and for the limited success of biocontrol is the capacity for hybridisation between varieties of *L. camara* and closely related species in the genus. Agents collected from similar lantana species or varieties to those lantana varieties in the target countries, or that have a broad host range, have been more successful at establishing. Also, lantana is found in a wide range of climatic regions, often occurring where biocontrol agents are not adapted. For these reasons it is recommended that the importation of further varieties and species of lantana be restricted in countries where the species is identified as a weed.

Fully effective control techniques are not currently available for this significant pest species. In many areas, the sheer size of the infestations coupled with low land values make conventional control not feasible. However mechanical clearing and hand pulling are suitable for small areas, and fire can be used over large areas. Also there are several control chemicals which are most effective when applied to regrowth following other treatments. The integration of all these control methods, specific to situation and variety, should be implemented to produce more successful results. Given the limited success of biocontrol to date in most areas, it is important for land managers to develop improved control through the integration of multiple techniques.

Biocontrol agents have in many cases, at least seasonally, decreased the volume of individual plants, making other control methods considerably easier. Over 40 agents have been trialled, and although none has resulted in total control, some have been partially successful and so could be released in countries where they are not present. *Teleonemia scrupulosa, Octotoma scabripennis, Uroplata girardi* and *Ophiomyia lantanae* are all widespread and damaging biocontrol agents and have contributed to the partial control of lantana in many regions. These agents should be a high priority for countries initiating biocontrol of lantana.

Calycomyza lantanae, Hypena laceratalis, Epinotia lantana and Lantanophaga pusillidactyla are also widespread and seasonally damaging agents; while not being able to control lantana, may make valuable contributions in regions where few other biocontrol agents are present.

Some biocontrol agents show promise for particular environmental conditions, such as high altitude. Others have only been released in a few areas and would be worthy of further release. There are several recently released agents, such as *Aerenicopsis championi* and the rusts *Prospodium tuberculatum* and *Mycovellosiella lantanae*, that show promise; but their potential has not been determined.

For many countries, some of the more effective and proven biocontrol agents could be introduced to assist in the control of lantana. For other countries where many agents have been released and lantana is still not under adequate control, there are still many potential agents, including a suite of pathogens in the native range, that have yet to be tried.

The more promising areas for future research are the biology, taxonomy and ecology of lantana as well as potential biocontrol agents and techniques for improved integrated control. Throughout the text recommendations for managers of control programs are made. These fall into three major categories: controls on import of lantana; methods for control; and the introduction of biocontrol agents.

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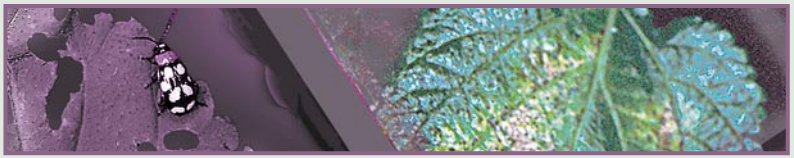
Part I: The Lantana Problem



Part I. The Lantana Problem

Lantana, *Lantana camara* L., is a pantropical weed affecting pastures and native forests in over 60 countries worldwide (Parsons & Cuthbertson 2001). It is a composite species, thought to have originated from two or more lantana species from tropical America. Dutch explorers introduced the plant into the Netherlands in the late 1600s from Brazil (Ghisalberti 2000), and it was then grown in glasshouses in Europe before its importation to other countries as an ornamental. *L. camara* hybridises easily and there are possibly some 650 hybrid varieties worldwide (Howard 1969).

L. camara is considered a problem weed in many of the countries to which it has been introduced. It flowers prolifically and the seeds are dispersed by birds (Swarbrick *et al.* 1998). The plants can grow in individual clumps or as dense thickets, crowding out more desirable species. In disturbed native forests, it can become the dominant understorey species, disrupting succession and decreasing biodiversity. Its allelopathic qualities can reduce vigour of plant species nearby and reduce productivity in orchards (Holm *et al.* 1991). It can affect agriculture by outcompeting native pastures by interfering with the mustering of cattle, and by causing death of stock by poisoning (Swarbrick *et al.* 1998). In plantations in south-east Asia and the Pacific Island communities, it can reduce productivity and interfere with harvesting. However *L. camara* has several uses, mainly as a herbal medicine and, in some areas, as firewood and mulch (Sharma *et al.* 1988; Sharma & Sharma 1989).

L. camara can be controlled through the use of chemicals, mechanical removal, fire, and the subsequent planting of competitive species. However, in many situations these methods are not feasible. Lantana growing on steep hillsides or along creeks is often inaccessible for treatment by chemicals or mechanical removal, and fire is not a recommended option in some native forests or in orchards or plantations. Therefore, in many situations where *L. camara* is a problem, biological control is the only viable long-term solution to its management. Biological control of *L. camara* started in 1902 and since then 41 agents have been released in some 50 countries (Julien & Griffiths 1998). Despite intense efforts in many countries, biological control of lantana is only partially successful and the weed is not adequately controlled anywhere within its introduced range. Several factors have been identified that may influence the success of biocontrol of lantana including taxonomy, climate, and plant biology and ecology (Day & Neser 2000).

1. Taxonomy

The genus *Lantana* L. (Verbenaceae) includes between 40 (Hooker 1973) and 150 (Gujral & Vasudevan 1983; Mabberley 1997) species. Most are native to South America, Central America or southern North America, with a few species occurring naturally in Africa and Asia (Munir 1996). The genus has long been the subject of taxonomic uncertainty (Howard 1969; Stirton 1977), with many species, previously geographically isolated, hybridising freely once co-located (Sanders 1989). Howard (1969) concluded that the genus *Lantana* was not an easy one to consider taxonomically, and that a thorough comprehensive investigation into the group was necessary.

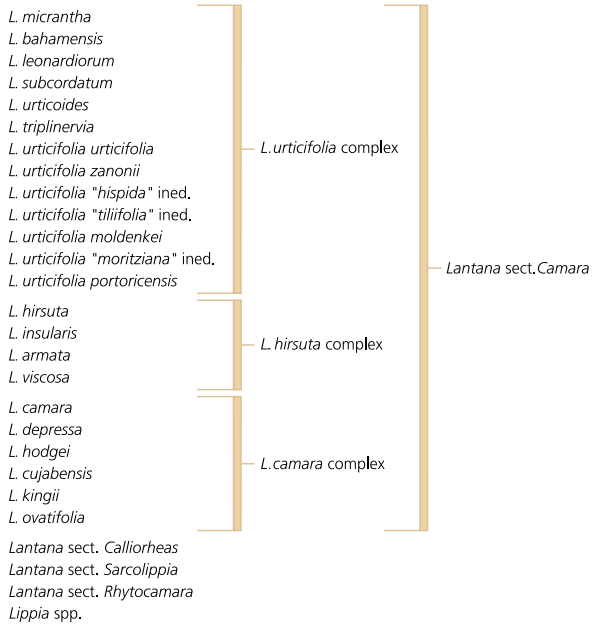


Figure 1.
The four sections within the *Lantana* genus, and the species within the *Lantana* section *Camara*, based on morphological characteristics.

Source: drawn from Sanders 1998, 1989.

Lantana is closely allied to, and difficult to separate from, *Lippia* L. and *Phyla* Loureiro. Munir (1993) suggested that they could all be included in the one genus, while Sanders (1987) states that *Lantana* may be polyphyletic or derived from a number of ancestors. The major difference between *Lantana* and *Lippia* is that the former has fleshy drupes, whereas the latter has a dry two-parted schizocarp (Jansen-Jacobs 1988; Munir 1993). The two genera are especially difficult to distinguish in dried herbarium material, where fruits may not be present. Indeed even if fruits are present, there may be uncertainty over whether they were fleshy or dry when fresh (Jansen-Jacobs 1988; Munir 1993).

Within the genus *Lantana*, four distinct groups are recognised (Figure 1). The Lantana sections *Calliorheas*, *Sarcolippia* and *Rhytocamara* contain the *Lippia*-like species, with the latter two sections containing only a few species each. *Lantana* section *Calliorheas* is more diverse and widespread (Sanders 1987). *Calliorheas* includes *L. montevidensis* (Sprengel) Briquet, a weed in some countries, having been naturalised in Australia, Africa and parts of India, as well as *L. indica* Roxburgh, *L. rugosa* Thunberg and *L. mearnsii* Moldenke (Sanders 1987 and pers. comm.). The fourth section, *Camara* is believed to be monophyletic.

The four sections differ in their haploid chromosome numbers, with x = 12 for *Calliorheas*, while section *Camara* has a base chromosome number of x = 11 (Sanders 1987). *Lippia* is a poorly sampled genus, but appears to have a haploid chromosome number based on x = 9, 15 and 16 (Sanders 1987; Munir 1993). The diversity of *Lantana* and *Lippia* are shown in Figure 2.

Lantana section *Camara* is divided in three complexes based on, *L. urticifolia*, *L. hirsuta* and *L. camara*. The *L. camara*

complex contains the primary weedy lantana commonly referred to as *L. camara* L. *sensu lato* and has a pantropical distribution. *Lantana camara sensu stricto* is known from Mexico, Florida, Trinidad, Jamaica and Brazil and has not been recorded from the Old World (Sanders 1987; Sanders, pers.comm.). It is almost without spines, with flowers opening deep yellow, changing to orange with a red centre, and finally to a more or less red-scarlet (Smith & Smith 1982).

In this book we address only the 'weedy taxa' of *Lantana* section *Camara*, the most widespread and economically and environmentally important taxa within the genus. We reserve the common name 'lantana' specifically for the weedy taxa of the section *Camara* and we will consistently describe different variants of *L. camara* as varieties.

2. Description of *Lantana camara*

There are many texts available with detailed descriptions of lantana (e.g. Everist, 1974; Swarbrick *et al.* 1998). A line drawing displaying the key features of a square stem in cross-section, recurved stems, paired complex flowers arising from axils and clusters of fruit is shown in Figure 3.

3. Variability

Lantana camara is a variable polyploid complex of interbreeding taxa, resulting from hybridisation with species in the other complexes, such as *L. urticifolia* Miller. The resulting taxa have been variously referred to as separate species (White 1929), forms (Everist 1974; Parsons & Cuthbertson 2001), cultivars (Howard 1969), biotypes (Swarbrick 1986), and subspecies or varieties (Anon.1962). These 'taxa' differ in their

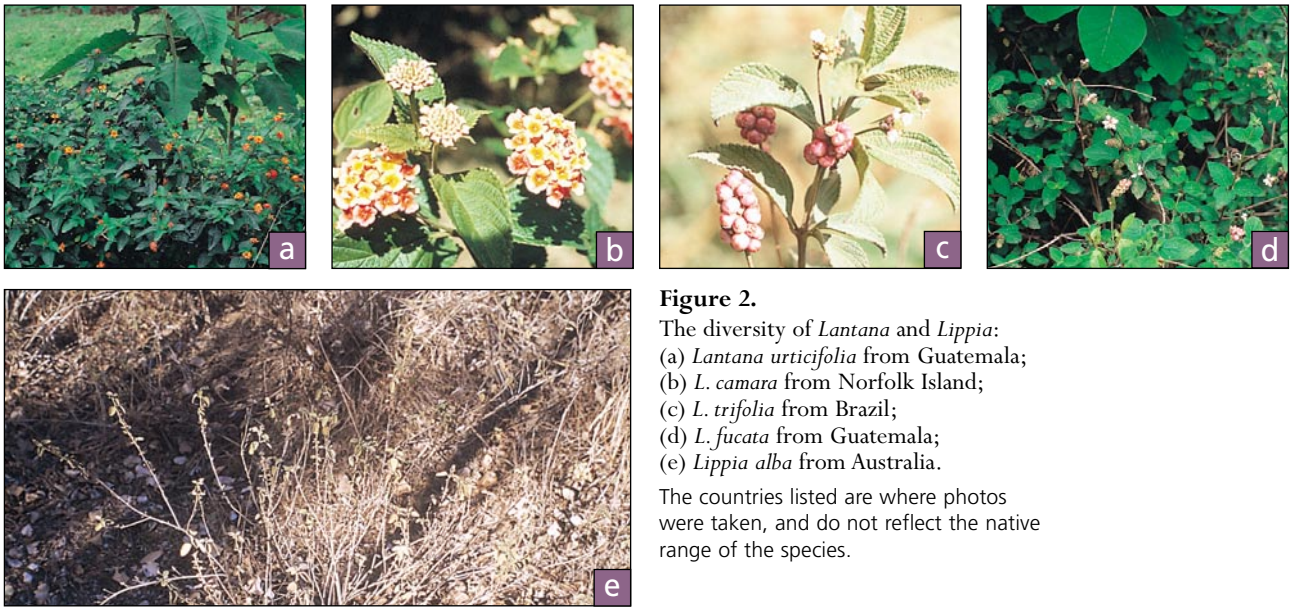


Figure 2.
The diversity of *Lantana* and *Lippia*:
(a) *Lantana urticifolia* from Guatemala;
(b) *L. camara* from Norfolk Island;
(c) *L. trifolia* from Brazil;
(d) *L. fucata* from Guatemala;
(e) *Lippia alba* from Australia.

The countries listed are where photos were taken, and do not reflect the native range of the species.

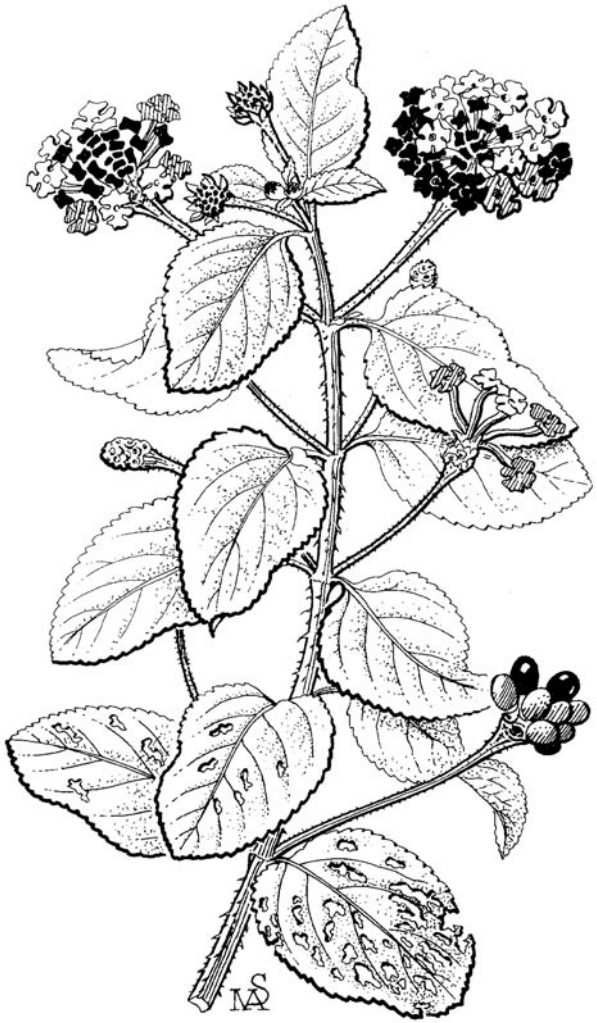


Figure 3.
Lantana camara.
Drawing courtesy of Queensland Department of Natural Resources and Mines (DNRM).

toxicity, flower colour, spininess, leaf shape, susceptibility to herbivore attack, and ecology (Diatloff & Haseler 1965; Haseler 1966; Smith & Smith 1982) (Figure 4).

In Australia, most naturalised varieties are tetraploid (x = 44), but several varieties are triploid (x = 33), one is diploid (x = 22), and one is pentaploid (x = 55) (Everist 1974). The ploidy levels of lantana in India are similar to those in Australia. While no weedy variety has been found to be diploid in India (Sinha & Sharma 1984), fertile diploid varieties are being cultivated there (Ojha & Dayal 1992). Studies on the ploidy levels of *Lantana* spp. in the Americas suggest that polyploid species are more abundant and widespread than diploid species (Sanders 1987). Ploidy level does not appear to have any phylogenetic significance, since polyploidy exists even within varieties (Khoshoo & Mahal 1967) and reproduction between plants of different ploidy levels is not greatly hindered (Sanders 1987). However, apart from correlative evidence to suggest that pentaploid forms are better adapted than other forms to high altitude conditions in India (Ojha & Dayal 1992), there is little evidence to suggest that different ploidy levels have distinguishing traits or are of ecological significance.

The diversity of the weedy lantana was not fully recognised until recently (Willson 1993). Therefore, in early literature, the number of varieties reported as occurring in different countries is generally fewer than in more recent literature. Greathead (1971a) recognised only one variety occurring in South Africa, while over 50 varieties have been recognised in the more recent publication by Wells and Stirton (1988). Similarly, only three lantana varieties were recognised in eastern Australia in earlier accounts (Haseler 1963, 1966; Diatloff & Haseler 1965), but 29 varieties are now recognised (Smith & Smith 1982). In most other countries, especially the

island regions of the South Pacific, there are far fewer lantana varieties present than in the continental countries. However, it is possible that the diversity of lantana present could increase, with hybridisation between existing varieties (Wells & Stirton 1988). Worldwide, there are over 650 variety names but many are probably misspellings and synonyms because detailed botanical descriptions of most varieties are generally unavailable (Howard 1969). Nevertheless, this highlights the diversity within this complex species, and the difficulties associated with any attempts to sort and classify this diversity.

The weedy varieties of lantana rarely match morphologically those known from the 'natural' range of the complex in tropical America (Smith & Smith 1982). Perkins and Swezey (1924) remarked that in the original shipment of potential biocontrol insects sent to Hawaii the samples of *Lantana* spp. that hosted insects from Mexico, looked rather different from that found in Hawaii. It is now widely recognised that lantana is morphologically distinct in different regions of its naturalised range compared to *Lantana* in its native range. This has important implications for the collection of potential agents for biological control, as discussed under 'Factors influencing biological control'.

The reason for these morphological differences is that those varieties that have become naturalised are hybrids. It is thought that lantana was first introduced into Europe in 1636 (Stirton 1977), and was especially popular in cultivation during the second half of the 19th Century (Swarbrick 1986). The material grown in Europe included in its parentage a number of American taxa and, through long periods of hybridisation and selection, modern varieties were developed (Stirton 1977). These have subsequently become naturalised and continue to hybridise in the field to make up a very variable complex species (Spies 1984; Cilliers & Neser 1991). However records of the parental material and the crosses performed have not been kept (Stirton 1977), and the origin of these varieties is therefore unknown.

The situation is further complicated by new, so-called sterile, triploid varieties bred and grown in gardens in most countries where weedy varieties are present (Figure 5). Current evidence suggests that these supposedly sterile varieties are capable of hybridising with fertile weedy varieties (Spies & du Plessis 1987; Neal 1999), potentially increasing the genetic variation within naturalised populations. The rates at which these new combinations of genes are being integrated into weedy populations

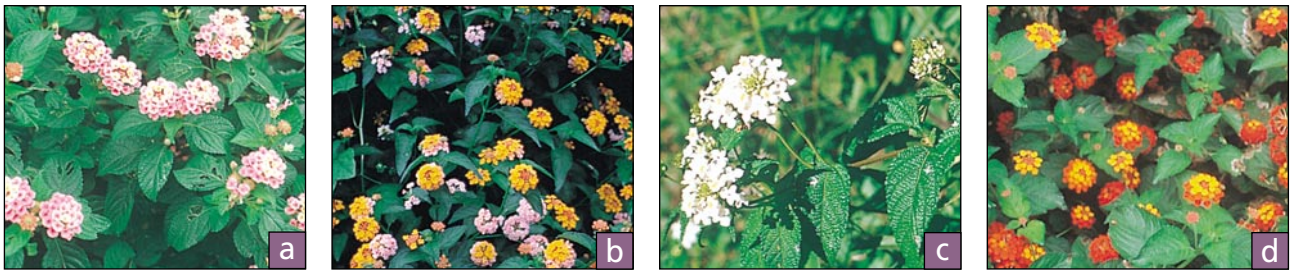


Figure 4.
Varieties of *L. camara* showing the diversity of flower colour: (a) Argentina; (b) Hawaii; (c) Brazil; (d) Australia.

are not known. Moreover, some of these cultivated forms have been re-introduced to the neotropics. This has allowed mixing with the native gene pool, leading to more complex morphological variation (Méndez Santos 2002) which make it even harder to resolve the taxonomy of this group.

4. Distribution

4.1 Native distribution of *Lantana* section *Camara*

The genus *Lantana* is of tropical origin, and reaches its greatest diversity in Central and northern South America and the Caribbean. In addition to the American species, some species are believed to be native to Africa, and at least one to India (Hooker 1973; Stirton 1977). The native African and Asian *Lantana* species all belong to the section *Calliorheas* that is well represented in the neotropics (Sanders 1987).

Lantana section *Camara* is native only to the Americas, with members occurring from Florida and Texas in the north to northern Argentina and Uruguay in the south (Figure 6). *Lantana camara sensu stricto* is found over a wide range in the neotropics (Sanders 1987, 2001), presumably due to naturalisation in regions where it is cultivated.

While it is recognised that the weedy taxa of lantana naturalised in the Old World are of hybrid origin, and so do not

Figure 5.
Lantana is grown in gardens all over the world, for example:
(a) Izucar, Mexico; (b) Parkhurst, Australia; (c) Niagara Falls, US; (d) Montpellier, France.

have a 'native' range *per se*, the hybrids are almost certainly derived from various species within the section *Camara* that originated in the Americas. It is likely that the various weedy varieties are derived from multiple parental species, so that the varieties may have progenitors with different geographic ranges. Our knowledge of the parentage of modern varieties is inadequate, but DNA studies suggest that the common pink variety found in Australia, Fiji and Vanuatu is derived from *L. urticifolia* found in parts of the Caribbean, Mexico and Central America (Scott 1998). Dr R. Sanders (pers. comm.) believes that *L. urticifolia* is a highly variable species, possibly with multiple subspecies being recognised, some of which were previously referred to as species in their own right.

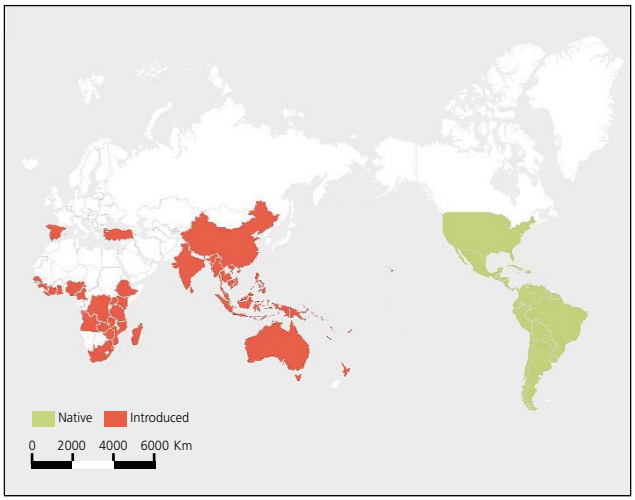


Figure 6.
Areas where the taxa of *Lantana* section *Camara* are native (green) and introduced or naturalised (red).

The map indicates the presence of lantana in a particular country, but not its distribution within that country. Countries and/or island groups that contain lantana are listed in the Appendix.

Lantana had not increased in abundance in Mexico over the first half of the 20th Century (Mann 1954a). However, there was a noticeable increase in the abundance and range of *L. tiliifolia* Chamisso in Brazil following widespread clearing and road construction; yet it is not recognised as a pest in Brazil (Winder & Harley 1982).

4.2 Naturalised distribution of *Lantana camara*

Lantana is now naturalised in approximately 60 countries or island groups between 35°N and 35°S (Figure 6). It is found in many African countries, including some arid regions, and is widespread in Kenya, Uganda and Tanzania. In South Africa, it is common along the east coast and in the tableland area of the north near Tzaneen. Lantana is found throughout India, occurring from the north near Jammu to the south near Trichmur, on the west coast near Bangalore, and in the central region near Jabalpur (Thakur *et al.* 1992). It occurs in the Middle East, and on low-lying coral atolls of the Pacific and Indian Oceans (Waterhouse & Norris 1987). In most of the high volcanic island groups in the Pacific, the distribution of lantana is limited by: its inability to survive under dense, intact canopies of taller native forest species; its susceptibility to frosts and low temperatures; its low tolerance to saline soils; its tendency to rot in boggy or hydromorphic soils; it having never been introduced to some islands; insufficient water, due to low rainfall and/or coralline soils with poor water-holding capacities; and high incidence of tropical hurricanes (Thaman 1974).

In Australia, lantana is mainly found along the east coast from Cape York to southern New South Wales. Small infestations occur in the Northern Territory and northern Western Australia (Parsons & Cuthbertson 2001). The plant is grown as an ornamental shrub in these areas and further south in Victoria and South Australia, but has not become naturalised in the south due to regular frosts (Parsons & Cuthbertson 2001).

The distribution of lantana is still increasing, with many of the countries and islands that were listed in 1974 as not having lantana e.g. Galapagos Islands, Solomon Islands, Palau, Saipan, Tinian, Yap, and Futuna Island. (Thaman 1974), being infested with lantana more recently (Waterhouse & Norris 1987; Denton *et al.* 1991; Harley 1992). Even in areas such as South Africa, India and larger islands such as New Zealand, where lantana has been established for long periods of time, there is evidence that it is still spreading (Stirton 1977; Cilliers 1983; Hill & Seawright 1983; Sharma *et al.* 1988; Wells & Stirton 1988).

A CLIMEX model that predicts the potential range of the naturalised lantana shows that lantana could expand its range even further becoming a weed in countries where it is not already present. Twenty-seven countries have been identified as not having lantana, but have an Environmental Index (EI) greater than 30 (Figure 7). An EI greater than 30 indicates that lantana could establish (R. Sutherst CSIRO, pers. comm.) and has the potential to become weedy if introduced to those countries. Countries and/or islands with locations with EI>30 are listed in the Appendix. Countries with locations with EI>30, but not reported to have lantana, are listed in Table 1.

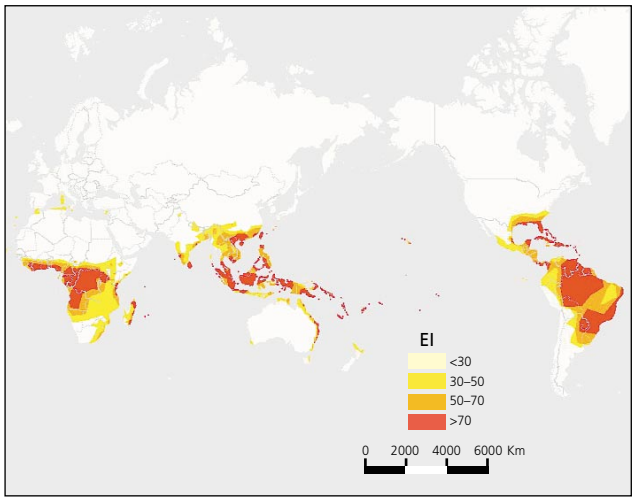


Figure 7.
The predicted range of the naturalised distribution of *Lantana camara* using the computer model CLIMEX.
An Environmental Index (EI)>30 indicates locations suitable for growing lantana.

Not only is the geographic range of lantana still expanding in many areas, but the density of infestations within its range is increasing. This has been recognised as a future threat to ecosystems in Australia (Haseler 1966), the Solomon Islands and Vanuatu (Harley 1992) and is probably occurring in many other countries. Also, there are several regions where lantana is currently limited by the distribution of intact forest, which inhibits its growth (Duggin & Gentle 1998). Increasing logging and habitat disturbance in many regions of the world provides further suitable habitats for the plant (Wells & Stirton 1988). In countries where there are still large areas of native forests, such as in Papua New Guinea, lantana is currently restricted to small, isolated infestations in abandoned settlement sites (W. Orapa SPC, pers. comm.), but it has the potential to spread widely following further clearing of forest for timber or agriculture.

5. Habitat

The diverse and broad geographic distribution of lantana is a reflection of its wide ecological tolerances. It occurs in diverse habitats and on a variety of soil types. It generally grows best in open unshaded situations such as wastelands, rainforest edges, beachfronts, and forests recovering from fire or logging. Disturbed areas such as beside roads, railway tracks and canals are also favourable for the species (Thaman 1974; Winder & Harley 1983; Thakur *et al.* 1992; Munir 1996) (Figure 8).

Country	No. of climatic stations EI = 30–50	EI = 50–70	EI >70	Total no. of stations
Algeria	2	0	0	29
Bangladesh	2	1	0	3
Benin	2	4	1	7
Botswana	1	0	0	8
Burkina Faso	2	0	0	6
Burundi	1	1	0	2
Central African Republic	0	5	4	10
Chad	1	0	0	10
Congo, Republic of	0	0	10	10
Easter Island	0	0	1	1
Equatorial Guinea	0	0	1	1
Gabon	0	1	6	7
Gambia, The	1	0	0	2
Italy	1	0	0	25
Laos	2	4	0	6
Lebanon	1	0	0	1
Lesotho	1	0	0	4
Malawi	4	2	0	6
Mali	3	0	0	19
Monaco	1	0	0	1
Morocco	1	0	0	15
Nepal	1	0	0	1
Sierra Leone	1	2	0	3
Somalia	0	1	0	8
Sudan	5	0	1	21
Taiwan	0	0	2	2
Togo	1	1	3	5

Values taken from Appendix, courtesy P. Mackey DNRM 2002.

Table 1.
Countries not having lantana, but having at least one site with EI>30 suggesting that lantana could establish if introduced.

Lantana benefits from the destructive foraging activities of introduced vertebrates such as pigs, cattle, goats, horses, sheep and deer (Thaman 1974; Denton *et al.* 1991; Fensham *et al.* 1994), and grows well on rich volcanic soils (Humphries & Stanton 1992). It can grow at altitudes from sea-level to 2000m (Matthew 1971). It can tolerate some shade, growing in plantations and open eucalypt forests in Australia (Humphries & Stanton 1992), but it does not flower readily under these conditions (Wells & Stirton 1988). In Brazil, lantana rarely grows in secondary forest and commercial plantations (Winder & Harley 1983). Wapshere (1970) suggested that when there is reduced herbivory by natural enemies, original habitat restrictions, such as climate and soil type, may become less significant and lantana can expand into previously marginal habitats.

Lantana grows under a wide range of climatic conditions. In Australia, the inland limit of its geographical range coincides with the 750mm isohyet in southern Queensland and the 1250mm isohyet in the north (Harley 1973), with infestations being restricted to creek lines in drier areas (Diatloff 1975). It does not appear to have an upper temperature or rainfall limit and is often found in tropical areas receiving 3000mm of rainfall per year, provided that soils are sufficiently well drained. Lantana seldom occurs where temperatures frequently fall below 5°C (Cilliers 1983), and in South Africa it is found in areas with a mean annual surface temperature greater than 12.5°C (Stirton 1977). Some varieties can withstand minor frosts, provided these are infrequent (Graaff 1986). Prolonged freezing temperatures kill aerial woody branches and cause defoliation.

There is some correlation between lantana varieties and climatic tolerances (Matthew 1971; Stirton 1977).

In Australia, the common pink variety is the only variety found at higher altitudes and latitudes, while the common pink-edged red variety is restricted to the warmer regions (Day *et al.* 2003). While lantana varieties are found in cool regions, such as southern Australia and the highlands of Papua New Guinea, they do not necessarily become weeds (W. Orapa, pers. comm.; Parsons & Cuthbertson 2001). Whether varieties will grow as well in climatic conditions different from those in which they occur in their naturalised range has not been examined.

Figure 8.
Lantana can grow in a wide range of habitats:
(a) rainforest (Gibraltar Range National Park, Australia);
(b) open grazing land (Kooralgin, Australia);
(c) drainage ditches (Florida, US);
(d) cleared land (Tzaneen, South Africa);
(e) roadsides (Hawaii, US).

6. Ecology

Lantana flowers in most places all year round if adequate moisture and light are available (Gujral & Vasudevan 1983; Graaff 1986), with flowering peaking during the wet summer months. In cooler or drier regions, flowering occurs only in the warmer or wetter months, due to frost or drought damage (Winder 1980; Swarbrick *et al.* 1998). Plants can flower as early as the second growing season.

Inflorescences are produced in pairs in the axils of opposite leaves (Figure 9a). In almost all colour forms, the flower opens yellow and changes to pink, white or red depending on the variety (Figure 9b). In the forms where this does not occur, a yellow ring is present around the opening to the corollary tube (Sinha & Sharma 1984). The yellow colouration is known to be a visual cue to pollinating insects (Barrows 1976; Mohan Ram & Mathur 1984a), and the act of pollination may stimulate colour change (Mohan Ram & Mathur 1984a).

Initially, lepidopteran species were thought to be the primary pollinators of lantana (Dronamraju 1958; Schemske 1976; Kugler 1980; Hilje 1985). Some butterfly species visit certain lantana taxa more frequently than others due to differences in corolla length, inflorescence diameter and number of flowers per inflorescence. According to this view, different varieties of lantana may have different species of pollinators. Therefore, there may be little cross-pollination between species or varieties of lantana both in the naturalised (Dronamraju 1958) and native (Schemske 1976) ranges of the section *Camara*.

Figure 9.
Lantana morphology:
(a) plant structure;
(b) inflorescences.

More recently, it has been suggested that thrips play a more important role in the pollination of lantana than Lepidoptera (Mohan Ram & Mathur 1984b; Sinha & Sharma 1984). Unlike butterflies, thrips are present all year round, and are more efficient pollinators (Mathur & Mohan Ram 1986). In India, the exclusion of butterflies did not reduce seed-set and Mathur and Mohan Ram (1986) proposed the introduction of bio-control agents to reduce thrips populations in an attempt to decrease pollination and the quantities of seed produced by lantana. In addition to butterflies and thrips, sunbirds (India) and hummingbirds (Brazil) are believed to play a minor role in pollination (Winder 1980).

There are conflicting reports over lantana's ability to selfpollinate. Mohan Ram and Mathur (1984b) considered lantana to be self-compatible, but needed insects for pollination. Neal (1999) also found that individual lantana flowers were capable of self-pollination. However, in laboratory experiments, lantana flowers did not self-pollinate (Barrows 1976). Pollination results in 85% fruit-set (Hilje 1985), with each infructescence (Figure 10) bearing about eight fruits (Barrows 1976).

Seeds are widely dispersed, predominantly by birds, but also by kangaroos, bearded dragons, sheep, goats, cattle, foxes, jackals, monkeys and possibly rodents (Bisht & Bhatnagar 1979; Clifford & Drake 1985; Sharma *et al.* 1988; Wells & Stirton 1988). In continental areas, many indigenous bird

species feed on the lantana fruits, while on some of the island groups, seed dispersal has been mainly facilitated by the introduction of exotic bird species. Birds are very important in exacerbating the weed problem and should not be underrated. By feeding on exotic species such as lantana, birds may increase the density and distribution of the weed at the expense of native vegetation thereby displacing other bird species (Loyn & French 1991).

Introduction of six bird species (including Chinese turtledove, *Streptopelia chinensis*, and the Indian mynah, *Acridotheres tristis)* that feed on lantana berries, has been implicated in the spread of the weed throughout the Hawaiian Islands as no native bird in Hawaii has been observed to eat the fruit (Perkins & Swezey 1924). In Guam, it has been suggested that, as a result of the introduced brown tree-snake preying on native bird populations, there are fewer frugivorous birds to disperse lantana seeds (R. Muniappan UG, pers. comm.). Consequently lantana infestations are increasing more slowly, and this may partially explain why Guam has had better success with biological control of lantana than other nearby islands (Muniappan 1988).

Lantana seeds need high light conditions for germination and early growth (Gentle & Duggin 1997b; Duggin & Gentle 1998), and seedlings are unlikely to survive beneath parent bushes. The germination rate of lantana is low under both laboratory and field conditions (Spies 1983–84; Graaff 1986, 1987; Sahu & Panda 1998), with estimates of 4–20% (Graaff 1987) and 44.5% (Duggin & Gentle 1998). Graaff (1987) suggested that the low germination rate was due to seed dormancy and/or low seed viability, while Spies (1983–84) proposed that the meiotic instability of lantana might produce low germination rates.

Germination rates increased from ten per cent to 46 per cent when the fleshy pulp was manually removed from the seed. This higher germination rate is comparable to that obtained from seeds collected from the faeces of wild birds. Seeds

Figure 10.
Lantana infructescences.

Figure 11.
Lantana can grow in several forms:
(a) low single shrubs, Guatemala;
(b) dense monospecific stands, north Queensland, Australia;
(c) climbing plants up to 15m in height, south-east Queensland, Australia.

germinate at any time of the year given sufficient soil moisture, with most seed germinating after the first summer storms in northern Australia (Parsons & Cuthbertson 2001).

Graaff (1987) suggested that low levels of recruitment may minimise regeneration in lantana eradication programs. However, low germination rates are offset by the extremely low rates of seedling mortality experienced in the field (Sahu & Panda 1998) and lantana's enormous capabilities for vegetative spread (Khoshoo & Mahal 1967) and seed production. Once established, lantana spreads to form large, impenetrable clumps (Anon.1962). The more common means of spread is through layering, where horizontal stems produce roots when in contact with soil (Swarbrick *et al.* 1998) although suckering can occur.

Lantana can also grow from vegetative material. Prostrate stems can root at the nodes if covered by moist soil, fallen leaves or other debris. In Australia, it is particularly well spread by landholders dumping vegetative material in bushland. Neal (1999) found that under glasshouse conditions, lantana stems or leaves could develop roots and grow into plants and eventually flower.

Lantana spp. in tropical America generally occurs in small clumps to about one metre in diameter (Figure 11a), and while it is commonly scattered along roadsides or in open fields, it is not considered a pest (Mann 1954a; Winder & Harley 1982; Palmer & Pullen 1995). In its naturalised range, lantana often forms dense monospecific thickets 1–4m high (Winder & Harley 1983; Swarbrick *et al.* 1998) (Figure 11b), although some varieties may climb trees and reach heights of 8–15m (Smith & Smith 1982; Swarbrick *et al.* 1998) (Figure 11c).

The temporal growth patterns of lantana vary depending on local climatic conditions. In tropical sites, growth is continuous throughout the year, while in cooler climates such as southern Brazil plants cease growth and defoliate to varying degrees during dry winter months (Winder 1980). This defoliation is often caused by frost and/or drought. Rapid growth occurs over spring and early summer following early rains (Figure 12).

Lantana infestations are very persistent and may block the natural succession of plant communities (Lamb 1991). While lantana infestations usually increase in wetter years, they do not recede during dry years (Waterhouse 1970). Mature lantana is fire tolerant; moreover, removal of other biomass and increase in soil nutrients through burning may increase germination (Gentle & Duggin 1997b; Duggin & Gentle 1998). The mortality rate among mature lantana plants in their naturalised range is very low (Sahu & Panda 1998). In many regions, lantana is defoliated annually by the complex of introduced biological control agents or during times of drought. Plants recover once the insect numbers have waned over the winter months and early season rains commence (Greathead 1971b; Gupta & Pawar 1984; Muniappan & Viraktamath 1986; Baars & Neser 1999; Day & Hannan-Jones 1999).

There is little information available regarding lantana's capacity for recovering from, and compensating for, different levels of natural foliage removal. In Brazil, there is a lag effect of herbivory, where attack by phytophagous insects during the previous season reduces growth to a far greater extent than attack in the current season (Winder & Harley 1982). In artificial defoliation experiments where whole leaves have been removed at various levels and frequencies, plants are able to recover (Winder & van Emden 1980; Broughton 2000b). However, these procedures do not accurately reflect the actions of leaf-feeding insects, so it is not surprising that lantana was able to tolerate these 'pruning' sessions. A more realistic defoliation experiment would involve a prolonged process rather than acute 'prunings'.

7. Impact

7.1 Impact on the natural environment

Lantana in forest communities has the potential to block succession and displace native species, resulting in a reduction in biodiversity (Lamb 1991; Loyn & French 1991). Under conditions of high light, soil moisture and soil nutrients, lantana is a very effective competitor against native colonisers (Gentle & Duggin 1998). Lantana infestations result in marked changes in the structure and floristics of natural communities.

One of the obvious changes that occur with the replacement of forest understorey by lantana is a decrease in community biomass and a proportional increase in the foliage component in the vegetation (Bhatt *et al.* 1994) (Figure 13).

As the density of lantana in forest increases, species richness decreases (Fensham *et al.* 1994). One possible explanation is that allelopathic effects of lantana result in severe reductions in seedling recruitment of almost all species under lantana and a reduction in the girth growth of mature trees and

Figure 12.
Lantana infestations are very persistent and can tolerate prolonged dry periods as shown by:
(a) plants suffering from drought and water stress;
(b) plants in the same area recovering to form dense thickets (Cangai, NSW).

Figure 13.
The effect of lantana on forest communities:
(a) as a dominant understorey species in open woodland (Queensland, Australia);
(b) totally blocking succession and regeneration in disturbed rainforests (NSW, Australia).

shrubs (Lamb 1982; Gentle & Duggin 1997a). Allelopathy may explain why invasive weeds such as lantana can survive secondary succession and become monospecific thickets (Hardin 1960). Allelopathic effects, resulting in either no growth or reduced growth close to lantana, have been demonstrated in the fern *Christella dentata* (Forsskaol) Brownsey & Jermy (Pteridophyta), milkweed vine *Morrenia odorata* (Hooker & Arnott) Lindley (Asclepiadaceae), rye *Lolium multiflorum* Lamarck (Poaceae) and many crops such as wheat, corn and soybean (Achhireddy & Singh 1984; Achhireddy *et al.* 1985; Mersie & Singh 1987; Sharma *et al.* 1988; Jain *et al.* 1989). Singh and Achhireddy (1987) found reductions in the growth of citrus growing in the same pot as lantana under nonlimiting conditions and attributed this to chemical factors excreted by the lantana. Jain *et al.* (1989) found 14 phenolic compounds present in lantana that in combination can reduce seed germination and growth of young plants.

Lantana does not invade intact rainforests, but is found on its margins (Diatloff 1975; Humphries & Stanton 1992). Where wet sclerophyll forests and rainforests have been disturbed through logging, gaps are created; this allows lantana to encroach on the forests. Further logging aggravates the condition and allows the lantana to spread or become thicker (Waterhouse 1970). At some sites, lantana infestations have been so persistent that they have completely stalled the regeneration of rainforest for three decades (Lamb 1991). Such is its impact that, for example, in south-east Queensland lantana was ranked as the most significant weed of non-agricultural areas (Batianoff & Butler 2002). Lantana competition may have caused the extinction of the shrub *Linum cratericola* Eliasson (Linaceae), and is a major threat to other endangered plants in the Galapagos Archipelago (Mauchamp *et al.* 1998). The replacement of native pastures by lantana is threatening the habitat of the sable antelope in Kenya (Greathead 1971b).

Lantana can greatly alter fire regimes in natural systems (Humphries & Stanton 1992). Grassy woodlands rarely have sufficient fuel load to produce fires intense enough to penetrate into the surrounding rainforest, but the fuel load provided by lantana has been implicated in a destructive wildfire in northern Queensland (Fensham *et al.* 1994). The fire hazard provided by lantana in rainforest situations is paralleled in deciduous forests of the northern hemisphere (Anon. 1962). Lantana burns readily during hot, dry conditions, even when green (Gujral & Vasudevan 1983). Lantana occurring on rainforest margins is seen as a major threat to this community as a result of increased inroads of fire into the rainforest. This is particularly so when lantana occurs on the edges of forest tracks and creeks in natural forests such as in national parks.

Some countries, such as India, USA and South Africa that are infested with *L. camara* contain some native species in the genus (Hooker 1973; Sanders 1985; Wells & Stirton 1988). For example, in Florida USA *L. camara* may compete and hybridise with the endangered, indigenous *L. depressa* Small (section *Camara*), thus contaminating the gene pool of this rare plant (Sanders 1985; Anon. 1999). The threat posed to other species in the genus growing in regions that have been colonised by exotic *L. camara* has not been assessed. Elsewhere in India and Africa, the native species of *Lantana* belong to the section *Calliorheas* (Sanders 1987, 2001) so the major threat is competition rather than hybridisation.

In Australia, lantana is sometimes seen as beneficial by rejuvenating and enriching soil (Willson 1968, and there is some evidence that soil nutrient pools and nutrient mobility in Australian eucalypt forests are increased by lantana presence (Lamb 1982). While increased soil nutrients may be desirable in agricultural systems, this is likely to disrupt natural succession

patterns in native communities. As lantana is a strong competitor, under conditions of increased soil fertility (Gentle & Duggin 1998) its re-establishment following mechanical or chemical removal may be encouraged.

Lantana has many secondary impacts, especially in many tropical countries where it can harbour several serious pests. Malarial mosquitoes in India (Gujral & Vasudevan 1983) and tsetse flies in Rwanda, Tanzania, Uganda and Kenya shelter in bushes and are the cause of serious health problems (Greathead 1968; Katabazi 1983; Okoth & Kapaata 1987; Mbulamberi 1990). The problem in Rawanda was pointed up by the Africa News Service on 26 October 2001: 'A total of 25 people in Bulongo and Butansi, Luuka county, Iganga district, have been confirmed to be suffering from sleeping sickness, reports Moses Nampala. A medical clinical officer, James Zironda, said several cases handled by his unit had sleeping sickness, a disease caused by the bite of a tsetse fly. "The biggest percentage of the patients we are handling have fresh irritations that developed as a result of recent bites from tsetse flies," Zironda said.' These pests were previously brought under reasonable control through the clearing of the vegetation that harboured them. Subsequently, lantana has colonised cleared ground with the result that these disease-carrying pests have reinvaded some cleared areas inhabited by humans and domestic stock (Greathead 1968).

7.2 Impact on agricultural areas

Lantana is a major problem in agricultural areas in most countries in which it occurs. It is especially a problem in regions where agriculture is a major industry, such as Australia, East Africa, Fiji, Hawaii, India, the Philippines, South Africa and Zambia (Holm *et al.* 1991). Once established in pastures, lantana forms large, impenetrable thickets, outcompeting valuable pasture species, blocking the movement of domestic stock to waterholes, poisoning stock and interfering with mustering (Figure 14).

Culvenor (1985) suggests that, in Queensland, loss of pasture is the greatest single cost of lantana invasion in grazing areas (A$3m per year at 1985 values). In dense stands of lantana, the capacity of the soil to absorb rain is lower than under good grass cover (Cilliers 1983). This could potentially increase the amount of run-off and the subsequent risk of soil erosion in areas infested with lantana. This contrasts with popular opinion that lantana is a useful cover crop for preventing erosion in fallow plantations (Greathead 1968; Willson 1968; Waterhouse 1970). While lantana may protect bare soil, other cover crops are likely to be more effective and productive.

Lantana has been implicated in the poisoning of cattle, buffalo, sheep, goats (Sharma *et al.* 1988), horses and dogs (Morton 1994), guinea pigs and captive red kangaroos (Johnson & Jensen 1998). The field cases occur mainly in young animals that have either been newly introduced into an area where lantana grows (Everist 1974), or are without access to other fodder (Yadava & Verma 1978; Sharma 1994).

Figure 14.
Lantana can overrun pastures (Kooralgin, Australia).

In Queensland, lantana accounts for the deaths of 1000–1500 cattle per annum, and is regarded as one of the most important poisonous plants in agricultural areas (Harley 1973; Culvenor 1985). In South Africa, lantana poisoning accounts for about a quarter of reported livestock poisonings by plants (Wells & Stirton 1988). Livestock deaths due to lantana have been reported from Brazil (Tokarnia *et al.* 1984), Cuba (Alfonso *et al.* 1982), Fiji (Willson, 1995), Kenya (Ide & Tutt 1998), India (Sharma 1988), Mexico (de Aluja 1970) and Florida, US. (Morton 1994). Poisoning results in cholestasis, hepatotoxicity and photosensitisation, with the early clinical signs being anorexia and severe constipation (Sharma 1994) (Figure 15). Children and adults in many countries often consume ripe fruits, without any ill effect. However, the consumption of green fruit has caused the deaths of humans in Australia and the US (Morton 1994), as well as in India (Sharma 1994). Apart from causing death of livestock, sublethal doses of lantana toxin cause a reduction in potential production due to abortion, loss of milk production in dairy cows, and chronic wasting in beef cattle (Seawright 1963).

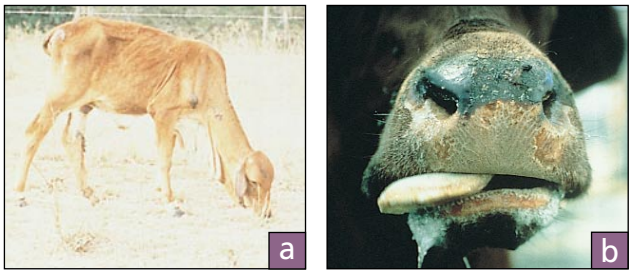


Figure 15.
Effect of lantana on animals:
(a) a cow suffering from lantana poisoning;
(b) typical symptoms of photosensitisation (Queensland, Australia).

Lantana varieties vary in their level of toxicity (Diatloff & Haseler 1965). The predominant variety in Australia, New Zealand and Vanuatu, common pink, is not toxic (Smith & Smith 1982; Hill & Seawright 1983; Harley 1992) while the pink-edged red variety in Australia is highly toxic. However, because varieties of lantana are known to hybridise freely, the variants now considered safe may not remain so (Gujral & Vasudevan 1983) and efforts to prevent the introduction of toxic varieties should be made by countries containing only non-toxic varieties.

The triterpenoid ester, lantadene A, is believed to be the major hepatotoxin in lantana foliage (Hart *et al.* 1976; Sharma & Sharma 1989). Two other triterpenoid esters, lantadene B and icterogenin have been known for some time and others have been more recently isolated (Wollenweber *et al.* 1997). Not all lantana varieties contain all of the hepatotoxins found within the *L. camara* complex (Sharma & Sharma 1989) and this may partially explain why some varieties are more toxic to cattle than others. Toxicity cannot be reduced through the making of silage and the plant cannot be processed into cattle feed (Yadava & Verma 1978).

In addition to its impact on grazing lands, lantana often causes a reduction in yield or impedes harvesting in plantations and perennial crops (Figure 16). It is a problem in coconut plantations in the Philippines (Cock & Godfray 1985), Fiji (Kamath 1979), the Solomon Islands and Vanuatu (Figure 16a) (Harley 1992); oil palms and rubber in Malaysia (A. A. Ismail MARDI, pers. comm.); bananas in Australia and Samoa; copra in Vanuatu (Harley 1992); citrus in Florida (Habeck 1976) (Figure 16b); tea in India and Indonesia (Holm *et al.* 1991); and timber plantations in Australia (Diatloff 1975), South Africa (Graaff 1986), Fiji (S.N. Lal MAFF, pers. comm.), Indonesia (Anon. 1962) and India (Holm *et al.* 1991).

Lantana affects timber plantations by competeing with young trees for light, moisture and nutrients, adversely affecting their growth rates, adds to the fire hazard and impedes access for thinning and felling operations (Anon. 1962; Graaff 1986). Unlike most grazing situations, it is difficult to control with fire or mechanical means due to possible damage to the plantation. In Queensland hoop pine plantations, lantana is one of the most important weeds and costs of control in 1970 exceeded A$200,000 per year (Waterhouse 1970), while costs of harvesting are greatly increased if lantana is present.

In India's sandalwood forests, lantana has been implicated in the spread of sandal spike disease, as it is believed to be an alternate but unaffected host for the pathogen (Gujral & Vasudevan 1983). Lantana is recognised as an alternate host for several insect pests of agricultural importance such as *Thrips tabaci* Lindeman and *Hoplothrips flaviceps* Jones (Holm *et al.* 1991).

8. Uses of lantana

Lantana was originally introduced to most countries as a garden ornamental, and it is still popularly grown. In some countries, it is planted as a hedge to contain or keep out livestock (Bradley 1988; Ghisalberti 2000). Today, lantana is seen as a pest in most countries in which it has naturalised. However, it has several minor uses, mainly in herbal medicine. There has been much work conducted, especially in India, on the chemical constituents of lantana and their potential for exploitation. Extracts from the leaves exhibit antimicrobial, fungicidal, insecticidal and nematicidal activity, but not antiviral activity (Chavan & Nikam 1982; Sharma & Sharma 1989; Begum *et al.* 2000).

The use of lantana extracts as potential biocides has been suggested. For example, aqueous leachate at 1–3% can kill water hyacinth, a troublesome weed in many tropical countries (Saxena 2000). Its application as a weedicide would depend on the size of the waterbodies being treated and

Figure 16.
The effect of lantana on horticulture: (a) growing among coconut trees (Vanuatu); (b) in citrus orchards (Florida, US).

the cost of extraction of the leachate. The active constituents have not yet been characterised (Achhireddy *et al.* 1985; Sharma & Sharma 1989). However, verbascoside, which possesses antimicrobial, immunosuppressive and antitumor activities, has been isolated (Mahato *et al.* 1994) while lantanoside, linaroside and camarinic acid have been isolated and are being investigated as potential nematocides (Begum *et al.* 2000).

The essential oils contained in lantana have been investigated for use as a perfumery ingredient. Yields vary significantly among plants from different regions (Sharma & Sharma 1989; da Silva *et al.* 1999) and commercialisation may be difficult because the raw material cannot be dried or stored without losing much of its oil (Morton 1994). Lantana oil is sometimes used for the treatment of skin itches, as an antiseptic for wounds (Anon. 1962), and externally for leprosy and scabies (Ghisalberti 2000). Plant extracts are used in folk medicine for the treatment of cancers, chicken pox, measles, asthma, ulcers, swellings, eczema, tumors, high blood pressure, bilious fevers, catarrhal infections, tetanus, rheumatism, malaria and atoxy of abdominal viscera (Anon. 1962; Kirtikar & Basu 1981; Ghisalberti 2000).

The stems of lantana, if treated by the sulphate process, can be used to produce pulp for paper suitable for writing and printing (Gujral & Vasudevan 1983). However it is hard to harvest, so is likely to be uneconomical. The roots of lantana contain a substance that may possibly be used for rubber manufacture (Gujral & Vasudevan 1983) although the economic viability of production has not been examined. Lantana twigs and stems serve as useful fuel for cooking and heating in many developing countries (Sharma *et al.* 1988), although it is less important than other fuel sources such as windrows, woodlots or natural bush (Bradley 1988). Mixed with cattle dung, lantana has been used for biogas production, while the seeds have supplementary nutritive value when fed with wheat straw to sheep (Sharma *et al.* 1988).

Lantana has been used as a cover crop in deforested areas, helping to enrich the soil and protect against erosion (Anon. 1962; Greathead 1968; Willson 1968; Munir 1996; Ghisalberti 2000). Lantana is never actively planted for the purpose of a cover crop, although it is often retained in areas, especially those sensitive to erosion, as a cover crop where it has incidentally established on disturbed sites. It has already been noted that lantana does not necessarily control erosion, and there has been limited research conducted on its true value as a cover crop.

Lantana has been implicated in increased nitrogen uptake and yield of rice and wheat in India when added to rice or wheat fields prior to transplanting (Sharma & Verma 2000), while long-term additions of lantana residues can improve the structural composition of the soil by decreasing surface cracking (Bhushan & Sharma 2002). However, while lantana may increase the concentrations and mobility of nitrogen compounds beneath infestations (Lamb 1982), there is little evidence to suggest that other minerals are affected.

The germination or growth rate of crops planted in sites previously infested with lantana may be inhibited due to allelopathic effects, even after four weeks of decomposition (Achhireddy & Singh 1984). The leaves and twigs of lantana are occasionally used as green manure, being rich in potassium salts and manganese (Anon. 1962) but caution needs to be taken to ensure allelopathic chemicals found in lantana are sufficiently leached prior to use. The majority of these uses are of academic interest only, with fuel being one of the only routine practical uses (Sharma *et al.* 1988). There are numerous other plants that grow quickly and can be used

as fuel or to check soil erosion, and lantana is not indispensable for these purposes.

In many regions, lantana has become a dominant component of natural and agricultural ecosystems. The rapid removal of natural forests without replacement by structurally similar native vegetation may be partially replaced with thickets of lantana. Consequently, the amount of available habitat for native animals may decrease. However, in some areas, weeds such as lantana may provide shelter and vital winter food for many native birds. While native birds prefer native fruit-bearing plant species, exotic weeds may be the only food source available following the clearing of lowland rainforest for agriculture (Crome *et al.* 1994; Date *et al.* 1996).

Lantana can be a useful replacement habitat for birds in general (Figure 17). A number of endangered bird species utilise lantana thickets when their natural habitat is unavailable. In Australia, the vulnerable black-breasted buttonquail, *Turnix melanogaster*, feeds and roosts in lantana thickets adjacent to its more favoured habitat, vine forest (Smith *et al.* 1998). While buttonquails prefer intact vine forest, lantana provides an important temporary refuge for them between forest remnants (Smith *et al.* 1998). In central Kenya, where natural riverine thickets have been almost completely cleared, the endangered Hinde's babbler, *Turdoides hindei*, has become dependent on lantana thickets, and unless sufficient suitable natural habitat can be restored the survival of this species depends on the retention of lantana infestations (Njoroge *et al.* 1998).

Apart from benefiting some bird species, lantana is a major nectar source for many species of butterflies and moths. As lantana often grows in highly disturbed landscapes where native vegetation has been cleared, it provides an important replacement habitat until native vegetation can be restored.

Figure 17.
Some bird species such as silvereyes have benefited from the presence of lantana (Queensland, Australia).

Part II: Control of Lantana

Part II. Control of Lantana

9. Conventional control

Biocontrol of lantana, despite its limited success to date, would appear to be the only likely technique for long-term control in pasturelands and native forests. On the other hand, more conventional techniques of control can be used in high-value areas, and much work has been done in this area.

9.1 Chemical control

Herbicide treatments are considered most effective when the target weeds are actively growing. This has been shown in Australia, Zimbabwe and Hawaii (Killilea 1983; Motooka *et al*. 1991; Hannan-Jones 1998). Three application methods are most effective on lantana: foliar spray, basal bark, and cut stump. Of these, basal bark and cut stump are effective with least impact on native or desirable species. Foliar spray is highly effective, particularly on regrowth (Diatloff & Haseler 1965; Cilliers 1983; Graaff 1986; Erasmus & Clayton 1992), but some collateral damage to other species may occur due to drift.

Detailed studies show that suitable conditions for growth can improve the success of chemical applications. Fluroxypyr and glyphosate were both more effective when rain had fallen in the six weeks before application and the minimum temperature was greater than 15°C (Hannan-Jones 1998). Most chemicals should be applied late in the growing season (Hannan-Jones 1998), but the application of some chemicals is best carried out when lantana is actively growing in spring and summer (Cilliers 1983).

Figure 18.
Spraying lantana (south-east Queensland, Australia).

The addition of a surfactant may provide some improvement in the success of many chemicals such as fluroxypyr (Love 1989), although there was no significant difference when a surfactant was added to metsulfuron methyl (Motooka *et al*. 1991).

Plant size may affect control success. Smaller plants are better controlled in most cases with 2,4-D and Torfon (picloram +2,4-D) (Master 1985) or fosamine (Killilea1983), while results with glyphosate show improved control on larger plants (Wells 1984). The differences between these results may be explained by the use of the terms 'small' and 'large' plants. For example, a small plant could be either a young plant with a small root system or regrowth of an old plant with a large root system.

Follow-up treatment is essential. It is reported that control of regrowth is easier than control of mature plants. This is probably due to more efficient penetration of young leaves by the herbicide and low plant resources after previous stress (Hannan-Jones 1998). Chemical control is therefore often more effective after fire or mechanical control. Indeed these techniques are usually ineffective without follow-up chemical control.

Several herbicide groups are used with effective results on lantana and most can be used either as a foliar spray (Figure 18) or as a basal bark application. It is important to follow the directions on the chemical container. Trade names are not used in this book as they may differ between countries (Table 2).

Active ingredient*	Rate**	Treatment	Remarks***
Fluroxypyr	1L/100L water	foliar	Thorough coverage is required
Glyphosate	1L/100L water	foliar	Thorough coverage is required
Glyphosate trimesium	2L/100L water	foliar	Thorough coverage is required
Dichloprop	0.5L/100L water	foliar	Thorough coverage is required
Picloram + 2,4-D	0.65L/100L water	foliar	Thorough coverage is required
Picloram + Triclopyr	0.5L/100L water 1L/60L diesel	foliar basal bark cut stump	Thorough coverage is required Complete coverage around stem Cut stem close to ground; apply immediately
2,4-D amine	0.4L/100L water	foliar	Some red-flowering varieties are resistant
2,4-D ester	2.5L/100L diesel	basal bark cut stump	Complete coverage around stem Cut stem close to ground; apply immediately
Metsulfuron methyl	10g/100L water	foliar	Less effective in the tropics
Metsulfuron methyl + glyphosate	95g/100L water	foliar	Thorough coverage is required
Imazapyr	0.2L/100L water	foliar cut stump	Apply to seedlings and coppice 10ml/100 mm of stump diameter
Triclopyr	1L/60L diesel	basal bark cut stump	Complete coverage around stem Cut stem close to ground, apply immediately
Tebuthiuron	1.5L/3.5L water	foliar	Thorough coverage is required

* Chemicals are not necessarily available in all countries.

** These are rates recommended by the manufacturer and may vary for different countries.

*** Foliar sprays should be applied during the active growing season.

Sources:

Anon. 1998. Pest Facts: *Lantana camara*. Department of Natural Resources and Mines, Brisbane, Australia.

Ensbey, R. 2001. Noxious and Environmental Weed Control Handbook 2001/2002: A guide to weeed control in non-crop, aquatic and bushland situations. NSW Agriculture, Orange, Australia.

Grobler *et al*. 2000. A guide to the use of herbicides. National Department of Agriculture, Pretoria, South Africa

Sharma, O. P. 1988.

Table 2.

Registered herbicides used in Australia, India and South Africa in the control of *L. camara*.

Several chemical groups are involved: benzoic acid-based chemicals (dicamba); phenoxy acid-based chemicals (2,4-D, 2,4,5-T, dichloroprop); pyridine-based chemicals (fluroxypyr, picloram, clopyralid, triclopyr); inhibitors of acetolactate synthase (metsulfuron-methyl, Imazapyr); and inhibitors of EPSP synthetase in the shikimic acid pathway (glyphosate). Inhibitors of photosynthesis have very little impact on lantana, possibly due to its ability to drop leaves and re-foliate quickly (Swarbrick *et al*. 1998).

Glyphosate is effective and widely used on lantana in Australia (Toth & Smith 1984; Hannan-Jones 1998), while 2,4-D produces highly variable results in Africa (Graff 1986). This may be due to varietal differences among the plants. In Australia, the red-flowering varieties are more difficult to kill and the pink-flowering ones the easiest (Diatloff & Haseler 1965). Variable control of different flowering varieties is also reported in Mauritius (Birch 1961 in Swarbrick *et al*. 1998).

In New South Wales National Parks, glyphosate is used to spray large stands of lantana, particularly where soil stability is important. The roots and stems of the dead plants shelter native plant regrowth, protect native seedlings from grazing marsupials, and reduce erosion. Where preservation of native grasses is important or grass species are important for preventing surface erosion, metsulfuron-methyl is used to kill the lantana but not the grasses (R. Joseph NSW NPWS, pers. comm.).

Herbicides are expensive and the costs of chemicals sometimes cannot be justified for use against lantana. In many areas the cost of chemical control of lantana may equal or exceed the value of the land (Erasmus & Clayton 1992; Thakur *et al*. 1992; Willson 1995). Costs of six herbicide treatments registered in South Africa for control of lantana were compared. All treatments produced more than 75% mortality of treated plants, however imazapyr in water was cheaper than picloram/triclopyr in diesel, owing to the cost of the mixers. Glyphosate was also more expensive than imazapyr (Erasmus & Clayton 1992). A large unpublished study in D'Aguilar National Park in Queensland, Australia included a cost-per-hectare comparison. The study found that the cost of 2,4-D ester was much lower than the slightly more effective fluroxypyr, and was therefore promoted for further use (Anon. 1999a).

It has been noted that the requirement for follow up control is rarely considered and yet success requires at least one follow-up treatment in most cases (Erasmus & Clayton, 1992). In some cases, chemical control costs were found to be similar to the value of the land, particularly when follow-up is considered. However, the continuous loss of productive land to lantana must be considered when valuing the land.

9.2 Mechanical control

Mechanical removal, using either modified bulldozers (Figure 19) or ploughing, removes standing plants. Clearing by tractor or stick-raking is considered superior to burning when dealing with mature lantana plants (Bartholomew & Armstrong 1978). This technique, however, is restricted to flat country or gentle accessible slopes. In inaccessible areas such as steep rocky country or along creeklines, manual removal may be seen as a preferred option. Manual removal of plants minimises disturbance to nearby vegetation and is effective in killing the plants, especially those in small, isolated clumps growing along fencelines or in public parks. Manual uprooting of lantana plants is labour intensive and costly but is often the only method available to farmers in developing countries (A.A. Ismail MAFF, pers. comm.). Mechanical and manual control can be expensive and control costs should be considered where land is of low value. Regrowth following mechanical or manual removal requires follow-up treatment that may be in the form of spot spraying with chemicals or additional mechanical removal.

9.3 Control by fire

Fire is one of the cheapest methods for controlling lantana and is often used in grazing areas. Regular burning will reduce the number of plants. Mature lantana is fire tolerant and regrowth from seeds and basal shoots is common. However, in these situations, regrowth of individual plants can be treated with chemicals more efficiently than large stands; so fire is often used as a pre-treatment to herbicides (Department of Natural Resources & Mines 2001) (Figure 20). Indeed, the Queensland Department of Natural Resources and Mines recommends the use of fire as part of a management program for the control of dense lantana infestations. The Department recommends; exclusion of stock to establish a fuel load, burning when a permit is available, sowing improved pastures, and excluding stock until the pasture has established. Finally, it recommends burning again in the hot dry months before rain, and spot spraying regrowth when it is vigorously growing between 50cm and a metre tall.

In dry forests, controlled burning can be utilised to keep lantana under control; however, in wet sclerophyll forests, such as the Blackbutt forests of south-east Queensland, burning damages the trunks of valuable timber trees (Waterhouse 1970).

Figure 19.
Mechanical clearing of lantana using a modified bulldozer (Queensland, Australia).

Figure 20.
Fire is often used to manage large infestations of lantana prior to herbicide application (Queensland, Australia).

Fire should not be used in plantation situations when lantana is growing among valuable plant species.Therefore in many tropical countries, where lantana grows under coconut plantations, fire is not an option. It is also inappropriate in areas of high conservation value, particularly where, in areas such as rainforest, lantana provides a fuel load that changes the intensity of fires experienced by the ecosystem.

9.4 Post-removal management

Follow-up control has been stressed as significant in all conventional control methods. Mechanical or fire removal of large plants is often followed by chemical control of regrowth and seeding plants. Many years of work can be wasted if follow-up does not occur for at least two years following the last seeding.

The mass removal of lantana infestations may result in the exposure of bare soil, which becomes vulnerable both to erosion and re-invasion of lantana and other weeds. To avoid reinfestation, control programs should involve the establishment of competitive plant species, which can grow quickly to shade out developing lantana seedlings (Figure 21). In Australia, exotic grasses and leguminous vines have been utilised in pasture situations (Goodchild 1951; Bartholomew & Armstrong 1978). Establishment of native species is used in many parts of Australia, particularly in areas of high conservation value (B. Noble Qld EPA, pers. comm).

In India, trees such as *Ricinus communis* L. (Euphorbiaceae) and *Ficus elastica* Roxburgh & Hornemann (Moraceae) have been used to shade out regenerating lantana (Gujral & Vasudevan 1983), while *Leucaena glauca* (L.) Bentham (Fabaceae) has been used in Indonesia and *Tithonia diversifolia* (Hemsley) A. Gray (Asteraceae) has been tried in Sri Lanka (Anon. 1962).

10. Biological control

In many areas the control of lantana using conventional techniques is either impossible or not feasible, due to: size of the infestations; inaccessibility of these areas; the costs involved; the ability of lantana to invade from nearby infested areas; the need for ongoing treatments; or the fact that most infestations are on degraded land of little economic value. So conventional methods are impractical (Khan 1945; Haseler 1963; Willson 1968; Stirton 1977; Scheibelreiter 1980; Thakur *et al*. 1992). For these reasons, biological control would seem to be the only practical method that may reduce the areas infested.

The advantages of biological control over other control methods include: a high benefit to cost ratio for successful programs, no build-up of resistance of the weed to the agent, and sustainable management of the target plant, as agents are self-perpetuating and self-disseminating. After initial introduction, agents can spread throughout the weed population and respond to fluctuations in host numbers.

Figure 21.
Several leguminous plants such as glycine (soybeans) can grow over and shade lantana (Queensland, Australia). Cattle grazing on glycine can subsequently trample lantana.

Biological control is non-polluting, and attack by agents is usually limited to a specific target weed (Table 3). There have been isolated instances where agents have attacked non-target species, but such damage is usually minimal e.g. *Teleonemia scrupulosa* Stål has fed on *Sesamum indicum* L. (Pedaliaceae) (Greathead 1971b).

The first attempt at the biological control of lantana began in 1902, when 23 insect species were imported into Hawaii from Mexico. Eight of these species established. This was the first time that entomologists had gone to the native range of a weed to find biocontrol agents (Perkins & Swezey 1924). By 2003, 41 agents had been deliberately or accidentally released on lantana throughout the world (Table 3).

Many other species attack lantana in its native range, but have not yet been used as biocontrol agents (Koebele 1903; Krauss 1953a, 1962; Mann 1954a,b; Winder & Harley 1983; Barreto *et al*. 1995; Palmer & Pullen 1995). In addition to these potential agents, there are many other insect species occurring in countries where lantana is a weed that occasionally feed on the plant (Perkins & Swezey 1924; Beeson & Chatterjee 1939; Perkins 1966; Moore 1972; M. Day & E. Snow NR&M, unpublished data). Many of these species are flower-feeding moths that have a broad host range, but these appear to play a negligible role in checking lantana growth and reproduction (Beeson & Chatterjee 1939; Greathead 1971a; Denton *et al*. 1991) and are not suitable for introduction elsewhere. Other species such as *Olethreutes* sp. (Tortricidae), *Plusia acuta* Walker (Noctuidae) and *Aristea onychota* Meyrick (Gracillariidae) from Africa (Scheibelreiter 1980; Löyttyniemi 1982) and *Asphondylia lantanae* Felt (Cecidomyiidae) from India (Felt 1920) have limited host preferences and have been identified as potential lantana biocontrol agents.

Species	Family	Origin	Guild	Climatic Requirements	Established	Varietal Preference	Parasitism	Host-specificity[a]	Agent Potential[b]
Aconophora compressa	Membracidae	Mexico	stem sucker	Temperate, dry	yes	lab only	None known	5	**
Aerenicopsis championi	Cerambycidae	Mexico	stem borer	Tropical, coastal	no	–	Minor	3	u
Alagoasa parana	Chrysomelidae	Brazil	leaf feeder	Subtropical, coastal	no	lab only	None known	1	*
Apion sp. A	Apionidae	Mexico	flower feeder	Not known	no	–	None known	1	*
Apion sp. B	Apionidae	Mexico	seed feeder	Not known	no	–	None known	1	*
Autoplusia illustrata	Noctuidae	Colombia	leaf feeder	Not known	no	–	Moderate	2	*
Calycomyza lantanae	Agromyzidae	Trinidad	leaf miner	All except temperate	yes	no	Minor	3	***
Charidotis pygmaea	Chrysomelidae	Brazil	leaf feeder	Subtropical, coastal	no	lab only	None known	2	*
Cremastobombycia lantanella	Gracillariidae	Mexico	leaf miner	Not known	yes	–	Minor	1	*
Diastema tigris	Noctuidae	Panama	leaf feeder	Not known	no	–	Moderate	1	*
Ectaga garcia	Depressariidae	Brazil	leaf feeder	Subtropical, coastal	no	lab only	Heavy	2	*
Epinotia lantana	Tortricidae	Mexico	flower feeder	All except temperate	yes	no	Minor	1	**
Eutreta xanthochaeta	Tephritidae	Mexico	stem galler	Temperate, dry	yes	–	Minor	1	***
Falconia intermedia	Miridae	Jamaica	sap sucker	All except temperate	yes	yes	None known	3	***
Hypena laceratalis	Noctuidae	Kenya	leaf feeder	All except temperate	yes	no	Minor	2	**
Lantanophaga pusillidactyla	Pterophoridae	Mexico	flower feeder	All except temperate	yes	no	Minor	3	**
Leptobyrsa decora	Tingidae	Colombia, Peru	sap sucker	Tropical, tablelands	yes	no	None known	5	***
Mycovellosiella lantanae	Mycosphaerellaceae	Brazil	pathogen	Subtropical, coastal	yes	no	Minor	1	**
Neogalea sunia	Noctuidae	US	leaf feeder	Subtropical, coastal	yes	no	Minor	1	**
Octotoma championi	Chrysomelidae	Costa Rica	leaf miner	Tropical, tablelands	yes	no	None known	2	*
Octotoma scabripennis	Chrysomelidae	Mexico	leaf miner	All except temperate	yes	no	Minor	1	****
Ophiomyia camarae	Agromyzidae	Florida	leaf miner	Tropical, coastal	yes	no	None known	3	**
Ophiomyia lantanae	Agromyzidae	Mexico	seed feeder	All except temperate	yes	no	Minor	1	****
Orthezia insignis	Ortheziidae	Mexico	sap sucker	Not known	yes	no	Moderate	5	*
Parevander xanthomelas	Cerambycidae	Mexico	root feeder	Not known	no	–	None known	1	*
Phenacoccus parvus	Pseudococcidae	unknown	sap sucker	Subtropical, inland	yes	no	None known	5	*
Plagiohammus spinipennis	Cerambycidae	Mexico	stem borer	Tropical, dry	yes	–	None known	1	**
Prospodium tuberculatum	Pucciniaceae	Brazil	pathogen	All except temperate	yes	yes	Minor	1	**
Pseudopyrausta santatalis	Pyralidae	Mexico	leaf feeder	Not known	no	–	None known	1	*
Salbia haemorrhoidalis	Pyralidae	Cuba, US	leaf feeder	Tropical, coastal	yes	no	Moderate	1	**
Septoria sp.	Sphaeropsidaceae	Ecuador	leaf pathogen	Not known	yes	–	None known	1	**
Strymon bazochii	Lycaenidae	Mexico	flower feeder	Tropical	yes	–	Moderate	5	*
Teleonemia bifasciata	Tingidae	Trinidad	flower feeder	Not known	no	–	None known	1	*
Teleonemia elata	Tingidae	Brazil	leaf/flower feeder	Not known	no	lab only	None known	1	*
Teleonemia harleyi	Tingidae	Trinidad	flower feeder	Not known	no	no	None known	1	*
Teleonemia prolixa	Tingidae	Brazil	flower feeder	Not known	no	lab only	None known	1	*
Teleonemia scrupulosa	Tingidae	Mexico	sap sucker	Subtropical, dry	yes	yes	None known	5	****
Tmolus echion	Lycaenidae	Mexico	flower feeder	Not known	yes	–	Heavy	5	*
Uroplata fulvopustulata	Chrysomelidae	Costa Rica	leaf miner	Tropical, tablelands	yes	no	None known	1	*
Uroplata girardi	Chrysomelidae	Argentina, Brazil	leaf miner	All except temperate	yes	no	Minor	1	****
Uroplata lantanae	Chrysomelidae	Brazil	leaf miner	Not known	no	lab only	None known	1	*

Notes:

[a] Some agents have been observed feeding on non-target plant species. Additional host-specificity testing should be conducted prior to further introductions if agents rate >2.
1 Specific to *Lantana* section *Camara*
2 Specific to *Lantana* spp.
3 Confined to *Lantana* and *Lippia* genera
4 Confined to Verbenaceae
5 Not specific

[b] Based on release, establishment and performance of agents.
* agent has not established anywhere or has established with minor damage and/or is localised in its distribution.
** agent has established causing moderate damage, localised or widespread.
*** agent has established causing substantial damage, localised or widespread.
**** agent has established causing severe damage and is widespread.
u *Aerenicopsis championi* has only been released at a few sites and failed to established. Its potential is unknown.

Table 3: Guild, parasitism, host-specificity, and other features of introduced agents.

Following the moderate success experienced in Hawaii, other regions imported insects that had proven safe and effective in Hawaii. To date, most countries infested with lantana have released, or have experienced the incidental establishment of, at least one of the 41 species of insects that have been utilised in lantana biocontrol programs around the world. About a third of the countries where lantana is a problem have five or more agents established, with Australia, South Africa and Hawaii each releasing in excess of 20 species (Julien & Griffiths 1998; Day & Neser 2000) (Table 4).

The most widespread and successful agent, in terms of the number of countries in which it has been introduced and established, is the sap-sucking bug *Teleonemia scrupulosa*. This species has been introduced to 31 countries and has established in 29 (Julien & Griffiths 1998). The leaf-mining beetle *Uroplata girardi* has been introduced to 26 countries and has established in 24 while the seed fly *Ophiomyia lantanae* has established in 24 countries out of 28 introductions. The leaf-mining fly *Calycomyza lantanae* and the leaf-feeding moth *Hypena laceratalis* have both established in all 15 countries in which they have been introduced (Julien & Griffiths 1998) (Table 4). The actual number of agents intentionally or accidentally introduced and their status in each country may vary from that presented in Table 4, because accurate and recent surveys have not been conducted for many countries.

The relative success of biocontrol varies considerably among countries. In all but a few places (namely Hawaii, Guam and some Micronesian islands), the level of control attained is negligible or at best seasonal. Although control has often been better on islands than in continental countries, not all islands have experienced satisfactory levels of control (e.g. Vanuatu, Fiji) and even on islands such as Hawaii, control is only successful in drier areas (Julien & Griffiths 1998).

In tropical America, lantana is not considered a pest and the large number of natural enemies present assist in keeping populations down. Winder and Harley (1982) believed that the main effect of organisms on lantana was to reduce its competitiveness, so that interspecific plant competition becomes a limiting factor. While biocontrol agents will possibly never actually kill lantana directly, they may cause plants to become stunted, produce less seed and allow more valuable native or pasture species to out-compete lantana.

This has been evident in Guam and Hawaii where native vegetation has been increasing in areas previously infested with lantana (Muniappan 1988).

Several countries/islands have implemented biological control of lantana, with Hawaii, Australia and South Africa being the main participants. Hawaii is no longer involved in the release of new biocontrol agents, but active programs continue in Australia and South Africa. Collaboration has always been a major feature in the biocontrol of lantana with many of the earlier agents being sent to Australia and other countries from Hawaii. In the 1960s, Australia supplied several agents to South Africa and parts of the Pacific; new agents recently tested and released in South Africa are currently being tried in Australia.

Details of the agents that have been released, either deliberately or unintentionally, as biocontrol agents for lantana are given below. Lantana species belong to the section *Camara* unless stated otherwise.

10.1 *Aconophora compressa* Walker (Hemiptera: Membracidae)

Natural distribution

Aconophora compressa was found at altitudes of over 1000 m from Mexico to Colombia on *L. camara, L. hirsuta* and *L. urticifolia* (Palmer *et al*. 1996). Laboratory cultures originated from populations occurring on *L. urticifolia* in Mexico and Guatemala.

	A. compressa	A. championi	A. parana	Apion sp. A	Apion sp. B	A. illustrata	C. lantanae	C. pygmaea	C. lantanella	D. tigris	E. garcia	E. lantana	E. xanthochaeta	F. intermedia	H. laceratalis	L. pusillidactyla	L. decora	M. lantanae	N. sunia	O. championi	O. scabripennis	O. camarae
Ascension Is. (UK)																						
Australia	IET	IN	IN			IN	IEP	IN		IN	IN	IEP	IN	IT	IEM	IEM	IEP		IEM	IEM	IEP	
Cape Verde Is.															IEU							
Cook Is.																	IU				IN	
Federated States of Micronesia										IN		IEP			IEM	IEP			IN			
Fiji							IEM	IN		IN					IEM		IN			IN	IN	
Ghana										IN					IEM		IN				IEM	
Guam (US)							IEU					IEC			IEM	IEC	IN				IN	
Hawaii		IN		IN	IN				IEP	IN		IEC	IEP		IEC	IEM	IEP		IEC	IN	IEC	
Hong Kong																IEU						
India										IN		IEM				IEM					IEM	
Indonesia							IEU															
Kenya																						
Madagascar																						
Malaysia							IEP															
Marshall Is. (US)												IEU										
Mauritius										IEU					IEP							
Myanmar																IEU						
New Caledonia															IEM				IEM		IEM	
New Zealand																IEU						
Niue																					IU	
Northern Mariana Is. (US)												IEC			IEM	IEP						
Palau (US)												IEC				IEM	IN					
Papua New Guinea							IEM								IEM	IEM						
Philippines							IEU								IEM							
Republic of South Africa			IN			IN	IEM		IEM			IEU	IN	IET	IEM	IEM	IN	IET	IN	IU	IEP	IET
St Helena Is. (UK)										IN					IEU							
Samoa																					IU	
Singapore							IEU															
Solomon Is.							IEU														IU	
Sri Lanka																						
Swaziland							IEM								IEM							
Tanzania							IEU			IN												
Thailand							IEM															
Tonga																	IU					
Trinidad																						
Uganda							IEU			IN												
Vanuatu																						
Vietnam							IEM															
Zambia										IN							IN					
Zanzibar																						
Zimbabwe																						
Total Introduced	1	2	2	1	1	2	15	2	2	11	1	9	3	2	15	12	10	1	5	4	12	1
Total Established	1	0	0	0	0	0	15	0	2	1	0	9	1	1	15	12	2	1	3	1	6	1

I = INTRODUCED; E = ESTABLISHED; N = NOT ESTABLISHED; C = CONTROL; P = PARTIAL/SEASONAL CONTROL; M = MINOR DAMAGE ONLY; T = TOO EARLY TO ASSESS; U = DEGREE OF CONTROL IS UNKNOWN.

Table 4:
Biocontrol attempts of lantana in various countries (based on Julien & Griffiths 1998).

	O. lantanae	O. insignis	P. xanthomelas	P. parvus	P. spinipennis	P. tuberculatum	P. santatalis	S. haemorrhoidalis	Septoria sp.	S. bazochii	T. bifasciata	T. elata	T. harleyi	T. prolixa	T. scrupulosa	T. echion	U. fulvopustulata	U. girardi	U. lantanae	Total Introduced	Total Established
Ascension Is. (UK)		IEC													IEC			IEP		3	3
Australia	IEP			IEP	IN	IET		IEM		IN		IN	IN	IN	IEP		IEM	IEP	IN	30	16
Cape Verde Is.		IEU																		2	2
Cook Is.	IU			IEP								IN						IEC		6	2
Federated States of Micronesia	IU						IN	IEM							IEM			IEC		10	6
Fiji	IEP						IN	IEM		IEM					IEC	IN	IN	IEC		15	7
Ghana	IEM														IEM			IEC		7	5
Guam (US)	IEC				IN			IN							IEC			IEC		11	7
Hawaii	IEM	IEM	IN		IEP		IN	IEC	IEM	IEM	IN				IEC	IEM		IEC		25	17
Hong Kong	IU																			2	1
India	IEM	IEM						IN							IEP			IEM		9	7
Indonesia	IEU														IEM					3	3
Kenya	IEM							IN							IEM					3	2
Madagascar	IEM														IEP					2	2
Malaysia	IEM														IEU					3	3
Marshall Is. (US)																				1	1
Mauritius								IEC							IEP			IEM		5	5
Myanmar	IEU																			2	2
New Caledonia	IEC														IEC			IEC		6	6
New Zealand																				1	1
Niue															IU			IEC		3	1
Northern Mariana Is. (US)	IEP														IEC			IEC		6	6
Palau (US)	IEP				IN			IN							IEM			IEC		8	5
Papua New Guinea	IEU														IEM			IEM		6	6
Philippines	IEM														IEU			IEU		5	5
Republic of South Africa	IEM	IEU			IN			IEM				IN			IEP		IN	IEP	IN	24	14
St Helena Is. (UK)		IEP													IEC			IU		5	3
Samoa															IEC			IEC		3	2
Singapore	IEU																			3	3
Solomon Is.															IEC			IEC		4	3
Sri Lanka	IU	IU																		2	0
Swaziland	IEU														IEM					4	4
Tanzania								IN							IEM			IN		5	2
Thailand																				1	1
Tonga															IEM			IEP		3	2
Trinidad																		IEU		1	1
Uganda	IEM							IEM				IN			IEU			IEM		7	5
Vanuatu	IEU														IEM			IEM		3	3
Vietnam	IEM																			2	2
Zambia								IU				IN			IEP			IEM		6	2
Zanzibar	IEM														IEM					2	2
Zimbabwe	IEM														IN					2	1
	28	7	1	2	5	1	3	13	1	3	1	5	1	1	31	2	3	26	2		
	24	6	0	2	1	1	0	7	1	2	0	0	0	0	29	1	1	24	0		

Biology

Adults and nymphs suck the sap of woody stems. It is a gregarious species, with females guarding their egg batches and developing nymphs until maturity. Females lay eggs in batches of up to 65 and the development of nymphs takes 28 to 42 days under laboratory conditions in Australia (Palmer *et al*. 1996) and 28 to 108 days under South African laboratory conditions (Baars & Neser 1999). *Aconophora compressa* occurs throughout the year in its native range, with populations increasing during the growing season (June to December) and damaging numbers occurring from November to February (Palmer *et al*. 1996).

Potential as a biocontrol agent

A. compressa was identified as a potentially useful biocontrol agent during surveys conducted between 1988 and 1995 (Palmer & Pullen 1995), although it may be the same species identified by Mann in 1953 as *A. marginata* Walker (Willson 1993). A. *compressa* has been released only in Australia; the rearing of laboratory populations has been unsuccessful in Hawaii (Willson 1993).

A. compressa was selected for controlling lantana because its feeding habits are independent of the leaf status of the host plant, so populations should not be affected by the extensive leaf drop which tends to occur in lantana in response to stress (Palmer *et al*. 1996). Successful establishment has been confirmed at about ten release sites in Queensland and New South Wales. The insect has caused leaf-drop, reduced flowering, and dieback in branches on affected plants. The insect has spread along coastal south-east Queensland; but further south, populations have been slow to build up and spread, moving only several hundred metres over a few years.

It is too soon to know how useful *A. compressa* will be in controlling lantana in Australia. CLIMEX modelling suggests that both coastal areas and the dry, cool and high-altitude areas of Queensland and New South Wales should be climatically suited to the insect (Palmer *et al*. 1996). Heatwaves in south-east Queensland in 1997, 1998 and 2000 severely affected populations at several sites. The agent shows minor preference for some varieties over others under laboratory conditions, but it has established on most varieties in Australia (Day *et al*. 2003).

Figure 22.
Aconophora compressa:
(a) adults; (b) nymphs.

Figure 23.
Damage to plants by *Aconophora compressa* (Cangai, NSW, Australia).

A. compressa has potential to be an effective agent in the dry, cool, high-altitude areas of Fiji, Hawaii, India, Indonesia and parts of Vanuatu. It can also develop on several species in the family Verbenaceae such as *Citharexylum spinosum* L. and *Stachytarpheta cayennensis* (Richard) Vahl both of which are introduced species in Australia. *A. compressa* can also complete development on *Jacaranda mimosifolia* D.Don (Bignoniaceae) and the weed *Baccharis halimifolia* L. (Asteraceae), albeit in low numbers. In South Africa, *A. compressa* can develop on native *Lantana* and *Lippia* and *Aloysia citriodora* (Paulau) (Verbenaceae) (Heystek & Baars 2001) and was not approved for release. Therefore, additional host-specificity testing on desirable plant species should be conducted before the release of this agent.

10.2 *Aerenicopsis championi* Bates (Coleoptera: Cerambycidae)

Natural distribution

Aerenicopsis championi was found at low altitudes with well-drained soils along the east coast of Mexico to Panama on *L. camara*, *L. hirsuta* and *L. urticifolia* (Callan 1964; Palmer *et al*. 2000). Laboratory cultures originated from populations occurring on *L. urticifolia* in Mexico.

Biology

The beetle is univoltine, completing one generation per year. Adults emerge in spring and live for up to two months feeding on the young leaves of lantana (Chock & Chong 1955; Callan 1964). Eggs are inserted into the midrib of young leaves or tender stems. The larvae hatch after six days and gradually bore down the stem, which withers and the branch dies back. Larvae can feed for up to nine months and pupation occurs in the stem (Chock & Chong 1955; Callan 1964; Palmer *et al*. 2000).

Potential as a biocontrol agent

A. championi was sent to Hawaii in 1902. The survival rate on these shipments was poor, resulting in very few individuals being released (Perkins & Swezey 1924). In 1953, it was re-introduced into Hawaii (Callan 1964) but once again failed to persist (Willson 1993), possibly due to the clearing of the release site (Callan 1964). Rearing proved extremely difficult with the mortality of young larvae being over 90% (Chock & Chong 1955). Under glasshouse conditions, lantana is generally healthier and it can respond to larval attack by forming callus tissue that kills the larvae. Mortality can be decreased by rearing the larvae in cut stems placed in a sand-peat mix (Palmer *et al*. 2000), or by using artificial diet.

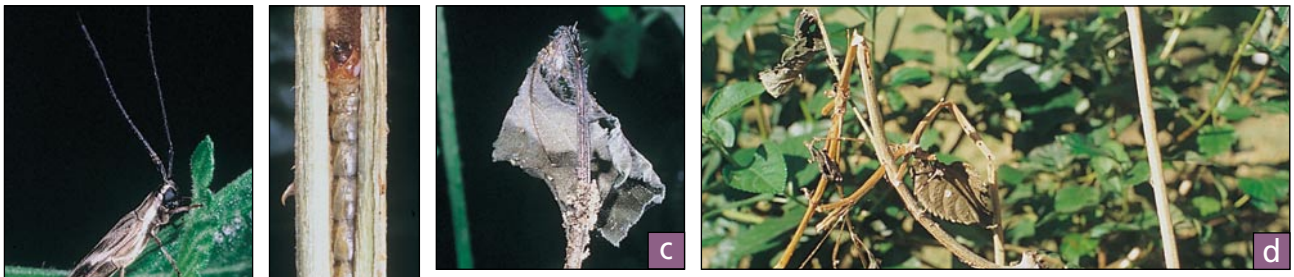


Figure 24.
Aerenicopsis championi:
(a) adult; (b) larva in stem; (c) & (d) damage to potted lantana (AFRS, Sherwood, Queensland).

A. championi was imported in low numbers into Fiji in 1956, but these were not released (Rao *et al*. 1971). The insect was first released in Australia in 1995. Releases were conducted by releasing adults into cages placed over plants or by placing larvae in holes drilled into lantana stems. Because limited numbers were available for release, a total of only seven release sites were used, with approximately 20 adults being released at each site. Within three years, populations at all sites (in south-east Queensland) appeared to have died out (Palmer *et al*. 2000). The insect was released again in 1999 (in northern New South Wales) and in 2001 in southeast Queensland. It was still persisting in early 2002. It is too early to determine whether the insect has established at these later sites.

If the rearing difficulties can be overcome, *A. championi* would be a useful addition to the suite of agents established in most other countries. It has the potential to be a very damaging agent because the insect can kill branches and stunt plant growth. However, the long generation time means that it is unlikely to expand rapidly. The insect is ideally suited to regions where the lantana undergoes regular defoliation. Larvae feed in the stems during winter when the plant is stressed and has lost many of its leaves.

There have been mixed reports as to the likely importance of parasitism in limiting populations of *A. championi* in the naturalised range of lantana. Parasitism of immatures by the ichneumonid *Agonocrytus chichimecus* (Cresson) was observed in Mexico (Palmer *et al*. 2000), and some parasitism of late instar larvae imported from Mexico into Australia was observed. An unidentified parasitoid has been found attacking late instar larvae in the field in Australia, but it is too early to determine what impact the parasitoid will have on the agent.

10.3 *Alagoasa parana* Samuelson (Coleoptera: Chrysomelidae)

Natural distribution

Alagoasa parana was found in shady areas of southern Brazil on *L. tiliifolia* and *L. glutinosa* Poeppig (Winder *et al*. 1988). Laboratory cultures originated from populations occurring on *L. tiliifolia*.

Biology

A. parana adults and larvae feed on the foliage and flowers. Eggs are laid in the leaf litter and newly emerged larvae move up the plant to feed. Development to adult takes 80–90 days. Larvae pupate in moist, loose soil and emerging adults over-winter in the litter at the base of the host plant and begin feeding and oviposition in spring (Winder *et al*. 1988). There is only one generation a year. Insect abundance varies seasonally, between about 4 and 8 adults per 100 branches (Winder *et al*. 1988).

Potential as a biocontrol agent

A. parana was first released in Australia in 1981 at various sites in south-east Queensland and northern New South Wales. The NSW populations failed to establish (Taylor 1989) but one population, at Mt Glorious in south-east Queensland, persisted for several years before the site was damaged by fire (Day & Holtkamp 1999). The initial breeding and release program was prematurely terminated due to lack of funding, and the lack of establishment was probably due to limited numbers being released. This species was released in South Africa in 1985, from material obtained from Australia, but failed to establish (Cilliers & Neser 1991).

A. parana was re-imported into Australia in 1998, and releases of at least 500 insects were conducted at each of four sites in northern NSW and southern Queensland.

Insects have not been recovered so it is unlikely that the agent has established.

The ability to diapause is an important trait for biocontrol agents intended for dry areas where lantana drops its leaves in winter (Day & Hannan-Jones 1999; Day & Holtkamp 1999). However, as *A. parana* has a long and vulnerable larval stage and has only one generation per year, it cannot increase to large numbers quickly. Also it appears to prefer the moist and cool habitats associated with shady rainforest fringes, so its potential as a biocontrol agent for lantana is limited (Taylor 1989). For these reasons, it is unlikely that further releases of this insect will be made in Australia, and it is considered a low priority for release in other countries.

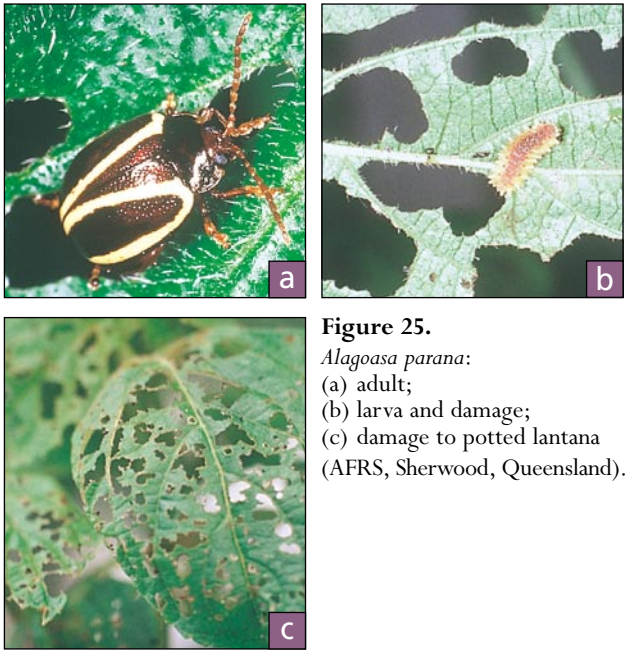


Figure 25.
Alagoasa parana:
(a) adult;
(b) larva and damage;
(c) damage to potted lantana (AFRS, Sherwood, Queensland).

10.4 *Apion* spp. (Coleoptera: Apionidae)

Natural distribution

Originally, it was thought that only one species of apionid beetle was present in the material sent to Hawaii, although two species were later recognised (Koebele 1903). These species were found in Mexico on *L. camara* and *L. urticifolia* (Koebele 1903). Laboratory cultures of both species originated from populations occurring on *L. urticifolia*.

Biology

Little information is available on these agents. One of the two unidentified species bores into the flower petioles, while the other is a seed-feeder. Infested petioles became unusually large and spongy, and the seeds fall off before ripening (Koebele 1903).

Potential as biocontrol agents

Both species were released in low numbers in Hawaii in 1902 but neither became established (Perkins and Swezey 1924). In Mexico, these species were common during the whole season and were recognised by Koebele (1903) as potentially valuable biocontrol agents. Other apionid species have been found in subsequent surveys (Palmer and Pullen 1995) but only now have these been given serious attention.

10.5 *Autoplusia illustrata* Guenée (Lepidoptera: Noctuidae)

Natural distribution

Autoplusia illustrata has been found from Costa Rica in Central America to Colombia in South America on *L. camara* and *L. hispida* H.B.K. (section *Camara*) and *L. trifolia* L. and *L. montevidensis* (section *Calliorheas*) (Diatloff 1976). It is not known from which lantana species it was collected to start laboratory cultures.

Biology

A. illustrata adults lay eggs on the underside of leaves. Eggs hatch in about seven days and larvae feed on leaves for four weeks. Pupation occurs in the leaf litter and adults emerge after about 12 days. Adults live for two weeks and lay about 80 eggs (Diatloff 1976).

Potential as a biocontrol agent

A. illustrata was released in Australia in 1976 and in South Africa in 1984. It proved easy to rear and was released widely as larvae (Taylor 1989) yet failed to establish in either country. It is not known why the agent failed to establish. In Colombia, *A. illustrata* was attacked by parasites and predators but the rates were not determined (Diatloff 1976). While parasitism may limit population size, it is unlikely to account for the failure of a species to establish in either Australia or South Africa.

The wide natural host range of *A. illustrata* suggests that it should be able to withstand a wide range of climatic conditions from cool subtropical mountainous areas to hot, humid lowlands (Diatloff 1976) and develop on a number of lantana varieties. However it failed to establish and is unlikely to be re-released in Australia. There has been limited success with other leaf-feeding Lepidoptera on lantana, as they tend to be restricted to areas where lantana is in foliage year round or only have a seasonal impact in drier areas. Moreover the potential for parasitism or predation may prevent populations ever reaching sufficient numbers to cause significant damage.

10.6 *Calycomyza lantanae* (Frick) (Diptera: Agromyzidae)

Natural distribution

Calycomyza lantanae was found from Florida, Texas, Trinidad, Mexico, Puerto Rico and Peru (Harley & Kassulke 1974a) and Brazil (Winder & Harley 1983) on *L. camara*, *L. tiliifolia*, *L. glutinosa* and *L. urticoides* Hayek (Winder & Harley 1983; Palmer & Pullen 1995). It is not known from which lantana species it was collected in order to start laboratory cultures.

Biology

C. lantanae adults feed on flowers and larvae form blotch mines in the leaves. Larvae feed for about 6–8 days and pupation occurs in the soil or leaf litter. Development from

Figure 26.
Autoplusia illustrata adult.

Figure 27.
Calycomyza lantanae:
(a) adult; (b) larval mines.

Figure 28.
Damage to lantana by *Calycomyza lantanae* (Gatton, Queensland, Australia).

egg to adult takes about 25 days. In the insectary, adult mortality is high unless drinking water is provided as a fine spray (Harley & Kassulke 1974a).

Potential as a biocontrol agent

C. lantanae was introduced and established in Australia in 1974 (Taylor 1989), in Guam in 1992 (Muniappan *et al*. 1992), Fiji in 1996 (Willson 1995; S.N. Lal MAFF, pers. comm.) and South Africa in 1982 (Baars & Neser 1999). It has subsequently spread from South Africa to Tanzania and Uganda pre 1997 (Julien & Griffiths 1998). It was also recorded throughout Papua New Guinea (post-1977), the Solomon Islands (pre-1997), Indonesia (post-1977), Singapore (post-1977), Malaysia (post-1977), the Philippines (1983), Thailand (mid-1980s) (Cock & Godfray 1985; Ooi 1987; Harley 1992; Muniappan *et al*. 1992; Julien & Griffiths 1998), and Vietnam (pre-2002). Most of these countries have not actively released lantana biocontrol agents, and in some, *C. lantanae* is the only leaf-feeding insect established (Julien & Griffiths 1998).

The fly prefers warm, moist areas, with most damage occurring on actively growing shoots. In Australia *C. lantanae* is found throughout the lantana infestations of Queensland and northern New South Wales. It is rarely found in the temperate regions of NSW (Taylor 1989; Day *et al*. 2003) and the temperate inland regions of South Africa (Cilliers & Neser 1991). However, in both Australia and South Africa, range expansion to more temperate regions has been reported and adaptation to cooler regions has been suggested (Taylor 1989; Cilliers & Neser 1991) although the reasons for this expansion are unknown.

In Australia, *C. lantanae* is found on all varieties of *L. camara*, *L. montevidensis* (section *Calliorheas*) and *Lippia alba* (Miller) N.E. Brown, which is also a weed in Australia. Harley & Kassulke (1974a) observed that *C. lantanae* tends to be found in larger numbers on the common pink-edged red variety compared with the common pink variety. However, this apparent 'preference' may be an artefact. In temperate areas, only the common pink lantana is present; absence of *C. lantanae* due to environmental conditions may falsely suggest that the insect does not prefer this variety. In warm areas where both common pink lantana and common pink-edged red lantana are found, *C. lantanae* is present on both. Laboratory trials to assess any preferences have not been conducted.

C. lantanae would be a useful addition to the complex of biocontrol agents occurring on lantana in tropical regions. Its high reproductive potential enabling rapid population expansion and efficient dispersal makes it an ideal agent. However, it is not as damaging as other agents released on lantana. Parasitism has been recorded in Peru and Trinidad (Harley & Kassulke 1974a), Fiji (S.N. Lal MAFF, pers. comm.) and South Africa (Baars & Neser 1999). While it has been suggested that the fly may be parasitised in Australia (Harley & Kassulke 1974a), this has not yet been confirmed.

It seems likely that *C. lantanae* will continue to spread to additional countries, such as India and West Africa, from nearby infested areas of south-east Asia and South Africa respectively. Therefore, before any future introductions are carried out, surveys to determine whether the fly has already established in the target country should be conducted.

10.7 *Charidotis pygmaea* Klug (Coleoptera: Chrysomelidae)

Natural distribution

Charidotis pygmaea was found on *L. fucata* Lindley (section *Calliorheas*) in cool shaded environments (Day *et al*. 1999) in southern Brazil and northern Uruguay. An unidentified *Charidotis* was also found on *L. tiliifolia* (section *Camara*) (Winder & Harley 1983). Laboratory cultures of *C. pygmaea* originated from populations occurring on *L. fucata*.

Biology

C. pygmaea adults and larvae feed on the underside of leaves. Adults can live for about six months and lay eggs on the underside of leaves. Oviposition is generally lower in the dry winter months when the adults enter a reproductive diapause as lantana plants yellow and drop leaves (Day *et al*. 1999). Larvae feed for about 35 days with pupation occurring on the leaves or stems.

Potential as a biocontrol agent

C. pygmaea was introduced into Australia in 1995, as it was thought to be suited to the cool temperate areas in which few agents had been performing well. Small numbers were released on *L. camara* until laboratory trials showed that the insect performed better on *L. montevidensis* (Day *et al*.1999). Subsequently, releases were conducted on only this species. However, *L. montevidensis* is only a problem in hot dry areas and the insect failed to establish, with heat stress likely to be a major factor (Day & McAndrew 2002). The beetle also failed to establish when released in Fiji in 1995 (S.N. Lal MAFF, pers. comm.). It is no longer being considered as a biocontrol agent for *L. camara* in Australia or South Africa (Baars & Neser 1999; Day & McAndrew 2002).

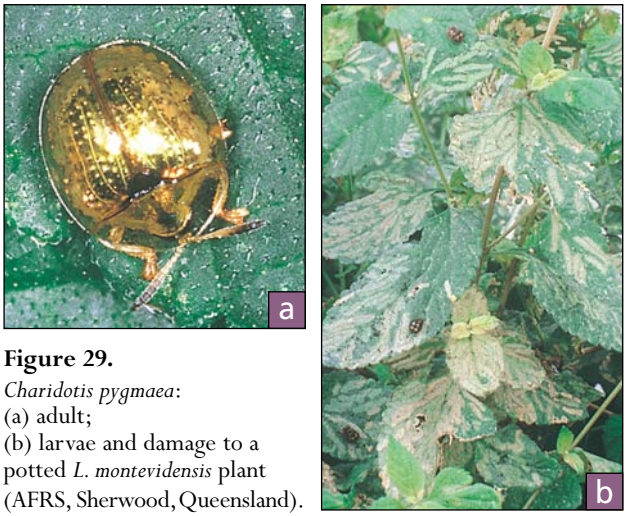


Figure 29.
Charidotis pygmaea:
(a) adult;
(b) larvae and damage to a potted *L. montevidensis* plant (AFRS, Sherwood, Queensland).

10.8 *Cremastobombycia lantanella* Busck (Lepidoptera: Gracillariidae)

Natural distribution

Cremastobombycia lantanella was found in Texas and Mexico on *L. camara*, *L. hirsuta*, *L. urticifolia* and *L. urticoides* (Palmer & Pullen 1995). It is not known from which lantana species it was collected in order to start laboratory cultures.

Biology

C. lantanella adults feed on the flowers and lay their eggs on the leaves. The larvae burrow beneath the epidermis of the leaves, causing the formation of blotch mines (Harley 1971; Palmer & Pullen 1995). The early instars are sap feeders, while the last instars are tissue feeders. The life cycle takes about five weeks and there are several generations per year (Willson & Palmer 1992).

Figure 30.
Cremastobombycia lantanella mines on lantana in Mexico.

Potential as a biocontrol agent

C. lantanella was one of the first insects introduced into Hawaii by Koebele in 1902 (Swezey 1923). Since its introduction, *C. lantanella* has spread throughout the Hawaiian Islands (Swezey 1924; Gardener & Davis 1982). Swezey reported about six mines per leaf soon after it established, but these numbers are rarely seen today (Perkins 1966) and it is now of minor importance in controlling lantana (Harley 1971; Gardener & Davis 1982). Although it was never deliberately introduced, *C. lantanella* is widely established in South Africa; but, as in Hawaii, it causes negligible damage, possibly due to parasitism (Baars & Neser 1999). Consequently, it is considered a low priority and is unlikely to be released in Australia.

10.9 *Diastema tigris* Guenée (Lepidoptera: Noctuidae)

Natural distribution

Diastema tigris was found in both North and Central America and some of the islands of the West Indies (Bennett 1963) on *L. camara* and *L. urticifolia* (Palmer & Pullen 1995). Laboratory cultures originated from populations in Panama but it is not known from which species of lantana.

Biology

D. tigris adults lay their eggs on the underside of leaves. Larvae feed on the leaves and pupate in the soil after feeding for about 30 days (Bennett 1963). There is no other information on the biology of this agent.

Potential as a biocontrol agent

D. tigris has been one of the least successful biocontrol agents utilised against lantana. It was first released as a biocontrol agent in Hawaii and Fiji in 1954 (Kamath 1979) and Micronesia in 1955 (Schreiner 1989), but failed to establish in all three island groups. There was renewed interest in the moth during the 1960s and 70s, when it was propagated in several insectaries and widely released throughout the world. It was re-released in Hawaii in 1962 (Julien & Griffiths 1998) and introduced into Uganda in 1963 (Greathead 1971a), Australia in 1965 (Julien & Griffiths 1998), Mauritius in 1967 (Greathead 1971a), Tanzania in 1967 (Greathead 1971b), Zambia in 1970 (Löyttyniemi 1982), India in 1971 (Muniappan & Viraktamath 1986; Rao *et al*. 1971; Sankaran 1971), Ghana in 1971 (Scheibelreiter 1980) and St Helena in 1971 (Julien & Griffiths 1998). It failed to establish in all countries

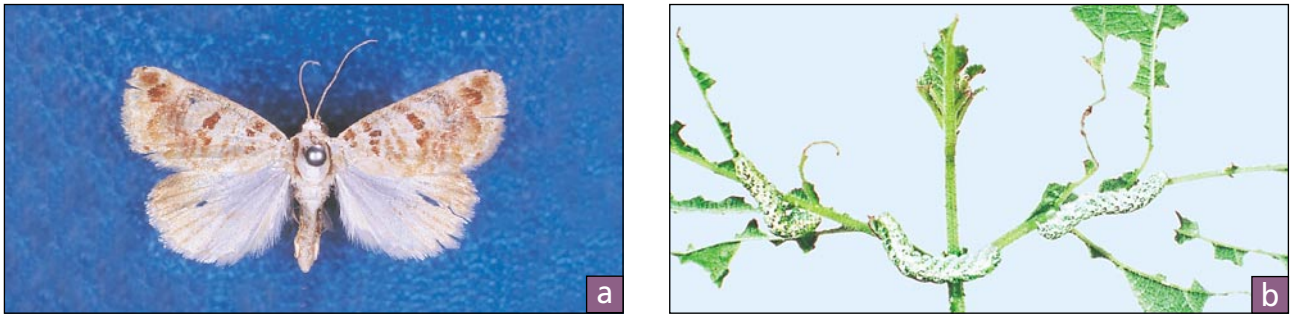


Figure 31.
Diastema tigris:
(a) a pinned adult; (b) larvae and damage on potted lantana (AFRS, Sherwood, Queensland).

except Mauritius (Greathead 1971a), although there have been no recent surveys to confirm its presence in Mauritius.

The reasons for its failure to establish are not clear. In the 1960s CSIRO in Australia, experienced difficulties in rearing laboratory populations, with high mortality and low hatching rates among eggs. Uganda and Fiji encountered fungal disease, which wiped out laboratory stocks (Parham *et al*. 1956). The difficulties associated with rearing meant that only small numbers were released. A total of 1482 moths were released across 18 sites in Australia (an average of 82 individuals per site) (CSIRO unpublished records). In Uganda, two releases, totalling 800 larvae, failed to result in establishment (Greathead 1971b). Low numbers were released in Fiji (Rao *et al*. 1971). Release data are not available for other countries.

Although limited numbers released could partially explain its failure to establish, it is unlikely that *D. tigris* will be trialed as a biocontrol agent again. Other lepidopterous leaf-feeding agents have failed to make an impact on lantana and parasitism is likely to be high.

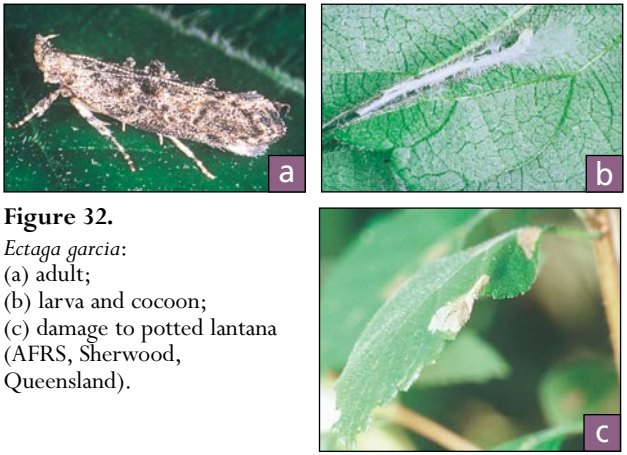


Figure 32.
Ectaga garcia:
(a) adult;
(b) larva and cocoon;
(c) damage to potted lantana (AFRS, Sherwood, Queensland).

10.10 *Ectaga garcia* Becker (Lepidoptera: Depressariidae)

Natural distribution

Ectaga garcia was found in southern Brazil and Argentina on *L. tiliifolia* (section *Camara*) and *L. fucata* (section *Calliorheas*) (Day *et al*. 1998), while larvae have been reared from *L. montevidensis* and *L. griesebachiana* Moldenke (both in section *Calliorheas*) in Argentina and Brazil (Becker 1994). Laboratory cultures originated from populations occurring on *L. fucata* in Brazil.

Biology

E. garcia adults feed on the flowers and lay their eggs on the underside of leaves. Larvae feed on the leaves forming protective cocoons and causing the leaves to roll. Development from egg to adult takes about 45 days. Substantial feeding by larvae may cause stunted growth and a reduction in flowering on a seasonal basis (Day *et al*. 1998).

Potential as a biocontrol agent

Australia is the only country to release *E. garcia*. One reason is that *E. garcia* also attacks *L. montevidensis* whose control was also being sought. The insect was imported in 1993, but the colony died out after only a few small releases. The insect was imported again in 1997 (Day *et al*. 1998). Several release methods were tried including the release of pupae and adults in cages and mated adults in open releases at many sites in Queensland and New South Wales. So far, there is no evidence that the moth has established at any site (Day *et al*. 2003). Laboratory and field studies showed that there was low survival on *L. camara*, even in field cages. In Brazil, *E. garcia* is heavily parasitised by tachinid flies and braconid wasps and it may become parasitised in its introduced range if it establishes (Willson & Garcia 1992). The insect is not considered a high priority for other countries.

10.11 *Epinotia lantana* (Busck) (Lepidoptera: Tortricidae)

Natural distribution

Epinotia lantana was found in Mexico on *L. camara* and *L. urticifolia* (Palmer & Pullen 1995), but it is not known whether it occurs in other countries. Laboratory cultures originated from populations occurring on *L. urticifolia*.

Biology

E. lantana adults oviposit in shoot tips and inflorescences. The larvae tunnel into the new shoots or feed on the flowers, hollowing out the receptacles of the flower heads. Pupation occurs in the hollowed-out receptacles or among the webbed remains of flowers (Harley 1971).

Potential as a biocontrol agent

E. lantana was introduced to Hawaii in 1902 and has spread throughout the island group. It was introduced to Australia in 1914 where it spread along the east coast (Common 1957). In 1948, it was introduced to the island of Pohnpei in Micronesia (Denton *et al*. 1991). It was introduced to South Africa in 1984, although it may have been present before being deliberately released (Baars & Neser 1999). The moth has been reported from Guam, India, and Northern Mariana Islands, Palau, some of which are some distance from the nearest points of deliberate introduction (Muniappan & Viraktamath 1986; Denton *et al*. 1991). In Vanuatu, the larvae of a superficially similar species, *Crocidosema plebejana* Zeller, attacks the receptacles of lantana and feeds on some Malvaceae, including cotton (Harley 1992).

The usefulness of *E. lantana* as a biocontrol agent is equivocal. In Australia, several reports suggest that *E. lantana* has little impact on the fruit production of lantana, in spite of its being seasonally abundant (Harley 1971; Waterhouse & Norris 1987; Taylor 1989). However, on some Micronesian islands, *E. lantana*, in conjunction with another flower-feeding moth, *Lantanophaga pusillidactyla* Walker, is reported to be responsible for an 80 per cent decline in fruit production (Denton *et al*. 1991), while 73 per cent of inflorescences in Hawaii were infested with *E. lantana*, greatly reducing seed formation (Swezey 1924). Muniappan *et al*. (1996) found that, collectively, foliage-feeders had a greater impact on seed production than did flower or fruit feeders. Field studies have not been conducted on the impact of *E. lantana* alone, because it always occurs with other biocontrol agents.

In India, *E. lantana* is parasitised, albeit at low levels, by several species (Muniappan & Viraktamath 1986). However,

Figure 33.
Epinotia lantana:
(a) adult; (b) larva in a bud.

Figure 34.
Damage to lantana buds by *Epinotia lantana* (Hawaii, US).

there is nothing published regarding the parasitism experienced by this moth in other countries.

Epinotia lantana tolerates a wide variety of climatic conditions and it should be considered for countries where it does not occur. However, it appears to be more effective on islands, rather than mainland areas such as South Africa, Australia and India. Surveys of insects attacking lantana in the target country should be conducted before it is imported to determine whether the moth is already present. Some host testing should be conducted prior to release in any country because *E. lantana* has been reported to feed on the ornamental *Tecoma stans* L. (Bignoniaceae) in Hawaii (Swezey 1924).

10.12 *Eutreta xanthochaeta* Aldrich (Diptera: Tephritidae)

Natural distribution

Eutreta xanthochaeta was found in the western parts of Mexico, feeding on *L. camara* and *L. urticifolia* (Koebele 1903; Palmer & Pullen 1995). Laboratory cultures originated from populations occurring on *L. urticifolia*.

Biology

E. xanthochaeta females oviposit in the growing tips of new shoots. The larvae bore into the stem and induce solitary, spheroid galls at the apical region of growing shoots. Each gall contains one larva. The length of the larval and pupal stages depends on climatic conditions, but usually the larval stage lasts 4–5 weeks and the pupal stage lasts 2–3 weeks. The fly shows a preference for new shoots, especially re-growth shoots, and high proportions of those shoots attacked are killed.

Potential as a biocontrol agent

E. xanthochaeta was one of the original insects introduced into Hawaii in 1902, where it has established on all islands (Swezey 1924) and occurs throughout the year (Duan *et al*. 1998). Harley & Kunimoto (1969) observed it attacking many of the shoots produced beneath the girdles made by *Plagiohammus spinipennis* Thomson.

The fly was released in Australia, unsuccessfully, in 1914 and the 1970s (Julien & Griffiths 1998). Its failure to establish was in part due to the low numbers released (CSIRO unpublished records). *Eutreta xanthochaeta* was also released in low numbers in South Africa in 1983 and failed to establish. It is being considered for re-introduction in both South Africa (Baars & Neser 1999) and Australia (Day & Holtkamp 1999).

Figure 35.
Eutreta xanthochaeta:
(a) adult;
(b) galls on lantana (Hawaii, US).

Figure 36.
Eutreta xanthochaeta: damage to lantana (Hawaii, US).

In Hawaii, much effort has been devoted to the study of parasites affecting *E. xanthochaeta*. This is because many exotic parasitoids have been introduced into Hawaii to control fruit fly populations and it was thought that these parasites might also be attacking *E. xanthochaeta* (Duan *et al*. 1997b). Exposed larvae are heavily attacked by fruit-fly parasitoids, but those contained within galls experienced low rates of parasitism (Duan & Messing 1996; Duan *et al*. 1997a). In addition, Duan *et al*. (1998) suggested that fruit fly parasitoids may not play a role in regulating gall fly populations because they do not show a spatial density-related response to *E. xanthochaeta* populations. However, *E. xanthochaeta* suffers high mortality from other factors such as vertebrate predators that open immature galls and feed on the larvae while *Epinotia lantana* tunnels into galls and destroys the gall fly's habitat (Duan *et al*. 1998).

The results of the Hawaiian studies have implications for the potential success of *E. xanthochaeta* in Australia, because the primary fruitfly parasitoid, *Diachasmimorpha tryoni* (Cameron) attacking *E. xanthochaeta* was originally obtained from Australia (Duan *et al*. 1998). Although it is likely to suffer some parasitism, *E. xanthochaeta* may be valuable in damaging the new growth that follows fire, slashing, or damage by other insects. Little is known of the climatic range tolerated by the fly; and Harley (1971) reports that it may show preference for some lantana varieties. *E. xanthochaeta* would be a useful agent for other countries, but more information about its biology, response to parasitism, climate, and lantana varieties should be obtained first.

Figure 37.
Falconia intermedia:
(a) adult; (b) nymphs.

10.13 *Falconia intermedia* Distant (Hemiptera: Miridae)

Natural distribution

Falconia intermedia was found in Mexico, Guatemala and Honduras on *L. camara*, *L. urticifolia* and *L. hirsuta* (Palmer & Pullen 1998). Laboratory cultures originated from populations occurring on *L. urticifolia* in Jamaica.

Biology

F. intermedia adults and nymphs feed on the intercellular tissues on the under surface of leaves, causing severe chlorosis, defoliation and a reduction in flowering. Adults live for about three weeks and lay 2–3 eggs per day. Eggs are laid on the underside of leaves and nymph development is completed in 20–25 days (Baars & Neser 1999; Day & McAndrew 2003). Consequently, populations have the potential to build up very quickly in the field.

Potential as a biocontrol agent

F. intermedia was released in South Africa in 1999, where it established and is causing significant damage to lantana infestations at several release sites. The insect has been released in Australia in NSW and Queensland. Due to severe drought in 2002, the insect has not been recovered at any site in NSW. However, populations persist in far north Queensland.

In both South Africa and Australia, *F. intermedia* displayed some preference for certain lantana varieties (Urban & Simelane 1999; Day & McAndrew 2003). In Australia, the red-flowering and orange-flowering lantana are preferred to the common pink variety. *F. intermedia* is able to complete development on *L. alba* in Australia; this applies also to several *Lippia* spp. native to South Africa, although in all such cases, performance is poorer than on lantana (Baars & Neser 1999; Day & McAndrew 2003).

F. intermedia shows considerable promise as a biocontrol agent due to its high reproductive and dispersal potential and its ability to cause substantial damage to lantana in its native range. The climatic tolerances of *F. intermedia* are not known, but it appears to prefer areas that are warm and moist all year round. It is unlikely that *F. intermedia* will perform well in areas that are subject to seasonal drought where defoliation of lantana occurs.

Figure 38.
Damage to lantana by *Falconia intermedia*:
(a) a few weeks after release; (b) about one year after release (Tzaneen, South Africa).

10.14 *Hypena laceratalis* Walker (Lepidoptera: Noctuidae)

Potential as a biocontrol agent

Hypena laceratalis was found in Kenya and Zimbabwe and is the only lantana biocontrol agent not originating in the Americas. It is believed to be native or naturalised over a wide geographic range encompassing Africa, Asia and Australia (Greathead 1971a; Scheibelreiter 1980; Cock & Godfray 1985; Muniappan & Viraktamath 1986; Cilliers & Neser 1991). Little information has been published on the host range of *H. laceratalis*, but it appears to be specific to *Lantana* spp. (Callan 1964). In addition to *L. camara*, it has been recorded on *L. trifolia* in Kenya (Krauss 1962) and *L. montevidensis* in Australia (Day *et al*. 2003). Laboratory cultures of *H. laceratalis* originated from populations occurring on *L. camara* in Kenya.

Biology

H. laceratalis adults feed on flowers and oviposit on the underside of leaves. The larvae feed on the underside of leaves, eating the lower epidermis and underlying mesophyll and leaving the upper epidermis intact. The larvae feed for about 12 days and development to adult takes about 28 days (Callan 1964). The short generation time means that populations are able to undergo rapid expansion when conditions are suitable, and a seasonal abundance of the moth, mostly in summer, has been reported in many countries (Beeson & Chatterjee 1939; Harley & Kunimoto 1969; Baars & Neser 1999; Day *et al*. 2003).

Potential as a biocontrol agent

H. laceratalis was first utilised for biocontrol in Hawaii in 1957 (Callan 1964). Soon after its introduction, it was observed to be in very large numbers and exerting significant control on lantana (Davis & Krauss 1962; Krauss 1962) although the level of control has declined since, possibly due to parasitism (Gardner & Davis 1982). Following the initial success in Hawaii, populations of the moth were sent to several countries, namely Micronesia in 1958, Fiji in 1960, South Africa in 1961, Australia in 1965 and Guam in 1967 (Julien & Griffiths 1998). Around the time of release, the moth was found to exist already in Australia and South Africa, having been previously misidentified during pre-release surveys (Greathead 1971a).

H. laceratalis causes severe seasonal damage to lantana especially in Queensland, Australia and has at times with other agents, defoliated plants. In spite of this, the African/Hawaiian strain was still introduced in the hope that it would provide even better control than the strain already existing (Haseler 1966; Harley 1971). It is not known whether the new strain established in Australia, but damage caused by the moth failed to increase (Harley 1971). It is possible that, due to the low numbers of the African strain released by CSIRO and the large population already present in the field, the African genetic material was not incorporated into existing Australian populations.

Other countries where *H. laceratalis* has been introduced have not experienced the same levels of success as in Hawaii. A combination of parasitism and poor performance on some lantana varieties has been proposed as likely influencing factors. In many Micronesian islands, as well as Fiji, *H. laceratalis* has either failed to establish or exists in low densities (Muniappan 1989; Denton *et al*. 1991; Harley 1992). It is thought that because these islands are close to Australia, Indonesia and the Philippines, where *H. laceratalis* and its parasites are naturalised (Harley 1971; Cock & Godfray 1985), the moths may suffer from higher rates of parasitism than in the more geographically isolated Hawaiian Islands. In Africa, native parasites are reported to keep *H. laceratalis* at such low numbers that it exerts little control on lantana (Greathead 1971a; Cilliers & Neser 1991).

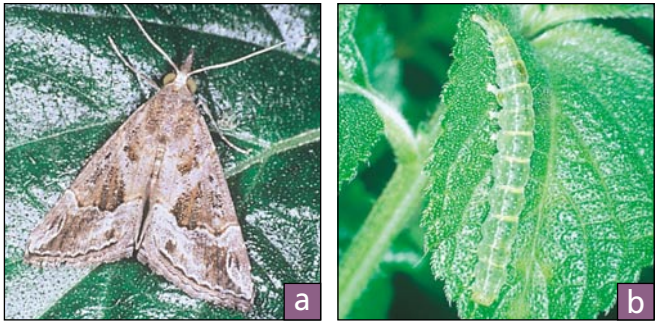


Figure 39.
Hypena laceratalis: (a) adult; (b) larva.

Figure 40.
Hypena laceratalis: damage to lantana (Brisbane, Queensland, Australia).

Another possible explanation for the difference in performance of *H. laceratalis* is that different countries/islands have different lantana varieties. The Hawaiian lantana varieties may be more susceptible to attack than those found on other islands. Diatloff & Haseler (1965) reported that *H. laceratalis* in Australia prefers all the red-flowering lantana to the common pink variety. However, recent observations by Day *et al*. (2003) show that *H. laceratalis* can heavily damage all lantana varieties in Australia on a seasonal basis. In Fiji, the pink-edged red is only moderately attacked by *H. laceratalis*, while an orange-flowering variety dominant on Yap (an island in Micronesia where both *Teleonemia scrupulosa* and *H. laceratalis* failed to establish), appears to be resistant to attack (Muniappan 1989; Schreiner 1989).

H. laceratalis appears to prefer warmer lowland areas to higher altitudes and may be a useful biocontrol agent of lantana on islands where parasitism rates are generally low (Perkins 1966).

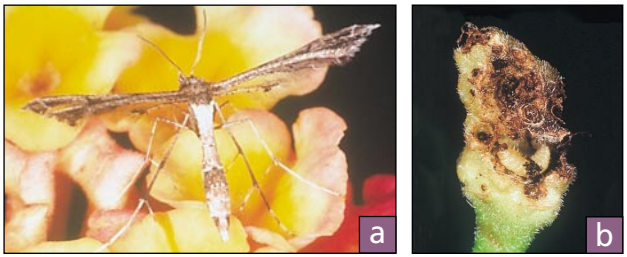


Figure 41.
Lantanophaga pusillidactyla: (a) adult; (b) larva.

Figure 42.
Lantanophaga pusillidactyla: Damage to lantana flowers (Brisbane, Australia).

10.15 *Lantanophaga pusillidactyla* (Walker) (Lepidoptera: Pterophoridae)

Natural distribution

Lantanophaga pusillidactyla was found throughout Mexico and the Caribbean on *L. camara*, *L. urticifolia* and *L. hirsuta* (Palmer & Pullen 1995). Its native range is not clear because it now has a global distribution, probably as a result of being spread on imported plants.

Biology

L. pusillidactyla adults oviposit in flower heads and the larvae feed within the flowers or tunnel around the receptacle. The larvae feed for about 7–10 days and pupate in the inflorescences. Flowers within an inflorescence that are not eaten produce fruit (Swezey 1924). Although very common, it does not significantly reduce the reproductive capacity of lantana (Beeson & Chatterjee 1939; Gardner & Davis 1982; Muniappan & Viraktamath 1986). However, Muniappan (1989) reported that, in combination with *E. lantana*, the moth reduces seed production on Yap by 80 per cent.

Potential as a biocontrol agent

L. pusillidactyla was one of the original insects released in Hawaii in 1902; it was released throughout the islands of Micronesia in 1948 (Denton *et al*. 1991). It has been released in small numbers in several other countries, although it was later revealed that the moth had occurred there before being deliberately introduced. This species is recorded in most entomological surveys conducted in countries where lantana is naturalised (Fletcher 1920; Löyttyniemi 1982; Muniappan & Viraktamath 1986; Sen-Sarma & Mishra 1986; Muniappan 1988; Denton *et al*. 1991). *L. pusillidactyla* has been reported on several closely related species throughout its distribution. In India, it feeds in the flowers of *L. indica* and *Lippia geminata* H.B.K. (Fletcher 1920), while in Australia it has been found

on *L. montevidensis* and *Lippia alba*. It is not known how *L. pusillidactyla* came to have such a wide distribution, but it is thought that it was introduced in shipments of ornamental lantana.

The moth is one of the few lantana agents that can tolerate wide climatic conditions, occurring throughout much of the range of lantana in Australia (Day & Holtkamp 1999; Day *et al*. 2003). It is likely to have reached its potential geographic range throughout the world, and before any attempts are made to introduce it to 'new' areas, surveys should be conducted to ensure that it is not already present. *L. pusillidactyla* is unlikely to be important in reducing the spread of lantana, because many flowers containing the insect can still set seed. Parasitism has been suggested as a reason for its low population density in some countries (Beeson & Chatterjee 1939).

10.16 *Leptobyrsa decora* Drake (Hemiptera: Tingidae)

Natural distribution

Leptobyrsa decora was collected near Lima, Peru, where it causes severe defoliation of lantana (Harley 1971). It has also been found in Columbia and Ecuador. It is not known from which lantana species it was collected in order to start laboratory cultures.

Biology

L. decora adults and nymphs form colonies on the undersides of leaves, where they suck the sap causing light-coloured spots on the upper leaf surface. The total life cycle takes 31 days in summer and 44 days in winter (Harley & Kassulke 1971), adults surviving for 60–90 days (Misra 1985; Mishra & Sen-Sarma 1986). In heavy infestations, the affected plants

Figure 43.
Leptobyrsa decora:
(a) adult;
(b) nymphs;
(c) feeding damage by adults and nymphs.

Figure 44
Leptobyrsa decora: damage to lantana (near Malanda, Queensland, Australia).

become leafless (Harley & Kassulke 1971; Misra 1985; Mishra & Sen-Sarma 1986).

Potential as a biocontrol agent

Tingids possess several useful attributes as biocontrol agents. They have a high reproductive potential, are easy to rear in large numbers, and are relatively free of parasites (Harley & Kassulke 1971). *L. decora* was released in Australia in 1969; but despite its being widely released in very large numbers throughout Queensland and New South Wales, establishment has been confirmed in only limited areas of northern Queensland (Day & Hannan-Jones 1999; Day *et al*. 2003). It was released in Hawaii in 1970 and by 1972 was firmly established; its spread, however, has been slow (Gardner & Davis 1982). Attempts to establish this species in Fiji, Zambia, South Africa, Palau and Ghana have failed (Kamath 1979; Scheibelreiter 1980; Löyttyniemi 1982; Julien & Griffiths 1998).

The reasons for its failure to establish elsewhere are unclear. Judging by its Australian distribution, the potential range of this species seems to be limited by climatic conditions and it is unlikely to establish in subtropical or temperate regions. Its failure to establish in New South Wales is believed to be due to extended non-reproductive periods over winter (Taylor 1989). Rainfall is important, as heavy storms are likely to increase mortality by dislodging leaves or individuals while lack of rain may make the stressed lantana unsuitable for attack (Mishra & Sen-Sarma 1986).

L. decora is likely to be a useful agent in tropical regions with high altitudes. Little is known about its preference for lantana varieties due to its limited distribution but it is found in large numbers on both common pink and common pink-edged red lantana in northern Queensland (Day *et al*. 2003). Host testing revealed that *L. decora* is able to complete an entire life cycle on *Tectona grandis* L.f. (teak), although survival and performance was much lower than on lantana. Consequently, *L. decora* was not released in India, where teak is a valuable timber crop (Misra 1985; Mishra & Sen-Sarma 1986; Muniappan & Viraktamath 1986).

10.17 *Mycovellosiella lantanae* (Chupp) Deighton (Mycosphaerellaceae)

Natural distribution

Mycovellosiella lantanae is widespread throughout the neotropics and is tolerant of a range of subtropical climatic zones. It was found in Brazil (Barreto *et al*. 1995) and Florida (Den Breeÿen *et al*. 2000). It has been recorded on only *L. camara* (Tomley & Evans 1992; Barreto *et al*. 1995) and laboratory cultures were collected from this species in Florida (Den Breeÿen *et al*. 2000).

Biology

M. lantanae is a leaf-spot fungus, causing chlorotic, grey lesions of leaves and necrosis of flower buds and stalks. Damaged plants can become defoliated, reducing vigour and reproductive potential (Den Breeÿen *et al*. 2000).

Figure 45.
Mycovellosiella lantanae infection on the underside on leaves.

Figure 46.
Damage to lantana plants by *Mycovellosiella lantanae* in Brazil.

Potential as a biocontrol agent

M. lantanae is one of three pathogens to be utilised against lantana and follows the growing interest in the use of fungal pathogens for the biological control of weeds (Julien 1989; Neser & Cilliers 1989). Two varieties of *M. lantanae* are recognised in the Neotropics, with *M. lantanae* var. *lantanae* being the variety showing the most potential as a biocontrol agent (Barreto *et al*. 1995). A third variety of the species has been reported on *L. camara* naturalised in India (Bhalla *et al*. 1999), although the level of damage it causes to the weed is not recorded.

Isolates of *M. lantanae* var. *lantanae* from Florida have been screened in South Africa and the agent was approved for release in 2002 (A. Den Breeÿen PPRI, pers. comm.). It is too early to determine if the agent has established in the field or to assess its impact on *L. camara* (A. Den Breeÿen PPRI pers. comm.). In laboratory tests, the fungus attacked several lantana varieties grown under glasshouse conditions (A. Den Breeÿen PPRI, pers. comm.) and it is hoped that it will be useful for other countries wishing to utilise pathogens against lantana. However, Trujillo & Norman (1995) found that the pathogen does not affect lantana varieties occurring in Hawaii.

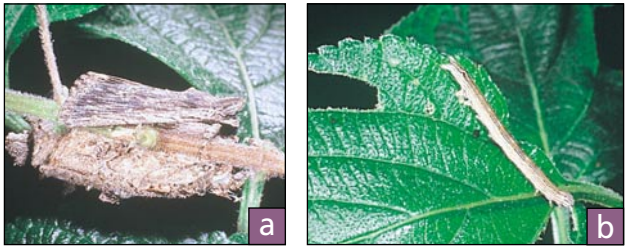


Figure 47.
Neogalea sunia:
(a) adult and characteristic pupal case;
(b) larva and damage to lantana (Brisbane, Queensland, Australia).

10.18 *Neogalea sunia* (Guenée) (Lepidoptera: Noctuidae)

Natural distribution

Neogalea sunia was found from southern USA to Argentina (Waterhouse & Norris 1987). It is common in California but less so in Mexico (Krauss 1962). It has been recorded on *L. camara*, *L. urticifolia* and *L. urticoides* in Mexico (Palmer & Pullen 1995) and from *L. tiliifolia* in Brazil (Winder & Harley 1983). Laboratory cultures of *N. sunia* originated from populations occurring in US but it is not known from which lantana species.

Biology

N. sunia adults feed on nectar and lay eggs on the underside of leaves. The larvae feed on foliage and flowers for about three weeks. Pupation occurs on the stems of lantana. The development time from egg to adult is about seven weeks (Harley 1956a).

Potential as a biocontrol agent

N. sunia was introduced to Australia and Hawaii in the 1950s, and it established in both places. In Australia, mostly larvae were released. However, higher success rates of establishment were reported when the adults were released instead (Haseler 1963). The moth was not seen in the field for many years following its release, before being observed in the 1960s (Krauss 1962). In Hawaii, the moth is occasionally locally abundant. However, usually populations remain at low levels and have little control on lantana (Haseler 1963; Harley 1971; Taylor 1989). *N. sunia* failed to establish in Micronesia and in South Africa, despite repeated attempts to release it (Baars & Neser 1999). The incidental establishment of this moth in New Caledonia has been reported, although only one specimen was located (Gutierrez & Forno 1989).

N. sunia larvae and pupae are parasitised by several species which can restrict populations in Australia, Hawaii and its native range (Haseler 1963; Callan 1964; Waterhouse 1970; Waterhouse & Norris 1987; Taylor 1989). Laboratory colonies frequently suffered from disease, which wiped out whole cultures in Trinidad, Uganda, South Africa and Australia (Oosthuizen 1964; Greathead 1971b; CSIRO unpublished records).

Diatloff & Haseler (1965) reported that *N. sunia* in Australia is found more often on white-flowering and red-flowering varieties than on the common pink lantana. However, laboratory trials to determine preferences have not been conducted and recent surveys in Australia have shown that this insect will readily attack all varieties (Day *et al*. 2003). Because *N. sunia* causes little impact on lantana overall and populations can suffer parasitism, it is not considered a high priority agent for other countries contemplating importing lantana biocontrol agents.

10.19 *Octotoma championi* Baly (Coleoptera: Chrysomelidae)

Natural distribution

Octotoma championi was found in Mexico, Costa Rica and Guatemala and more recently, Texas, US, following the widespread naturalisation of lantana in that region (Riley & Balsbaugh 1988). It has been recorded on *L. camara*, *L. urticifolia*, *L. hispida* and *L. hirsuta* (section *Camara*) and *L. trifolia* (section *Calliorheas*) (Diatloff 1977; Palmer & Pullen 1995). Laboratory cultures originated from populations occurring on *L. camara* in Costa Rica.

Biology

O. championi adults feed on the upper surface of leaves and oviposit singly through the upper leaf epidermis. The larvae form mines between the upper and lower epidermis and are incapable of transferring to another leaf. Up to four larvae can develop fully in one large leaf (Diatloff 1977); more than four immature larvae per leaf may result in premature shedding of the leaf. During host testing, larval survival was lower in *L. trifolia* and *L. montevidensis* (both section *Calliorheas*), which have small leaves and are more susceptible to dropping leaves (Diatloff 1977). The development from egg to adult takes about 40 days. Adults are long-lived, so adults from two successive generations may be found together in the field. Adults emerging in late autumn can survive the dry winter period by entering a facultative diapause (Diatloff 1977). In Costa Rica, there are usually three generations per year.

Potential as a biocontrol agent

O. championi was first utilised as a biocontrol agent in Hawaii in 1954 under the name of *O. plicatula* (Krauss 1962). It failed to establish following the release of only

Figure 48.
Octotoma championi:
(a) adult;
(b) larval mines.

three adults (Krauss 1964). During the mid-1970s there was renewed interest in the beetle, and it was introduced to Australia, South Africa and Fiji. The South African and Fijian attempts failed (Julien & Griffiths 1998; Baars & Neser 1999), while *O. championi* established around Sydney and southern New South Wales, following releases throughout Queensland and NSW (Taylor 1989). Surveys conducted from 1995 to 1997 failed to find the beetle in Queensland (Broughton 1998). However, small populations were subsequently found at several sites on the Atherton Tableland of northern Queensland (Day *et al*. 2003). Further attempts were made to introduce the beetle into South Africa during the late 1990s, although establishment has not been confirmed.

O. championi shows a preference for shaded conditions (Taylor 1989) and may require cool climates. Its potential range in Australia may not have been reached, and there may be several regions between the tablelands of north Queensland and southern NSW that are climatically suitable. It does not cause significant damage to lantana in any of the regions in which it has established and therefore is not recommended as a priority agent for any country. Parasites and predators appear to play a minor role in regulating field populations of *O. championi* in Costa Rica, where maximum parasitism rates were under 20 per cent (Diatloff 1977).

10.20 *Octotoma scabripennis* Guérin-Méneville (Coleoptera: Chrysomelidae)

Natural distribution

Octotoma scabripennis was found from Mexico through to Nicaragua (Callan 1964) on *L. camara*, *L. urticifolia* and *L. glandulossima* Hayek (Palmer & Pullen 1995). Laboratory cultures originated from populations occurring in Mexico on *L. urticifolia*.

Biology

O. scabripennis adults feed and oviposit on the upper surface of leaves. Larvae mine the leaves and cause blotches to occur. Development of egg through to adult takes 34–45 days, with a pre-oviposition period of 3–4 weeks. There are normally three generations per year (Harley 1969). Adults avoid seasonally unfavourable conditions by entering a facultative diapause (Harley 1969).

Potential as a biocontrol agent

O. scabripennis is one of the most damaging lantana insects (Taylor 1989; Cilliers & Neser 1991; Broughton 1998; Day *et al.* 2003). It was first released, in small numbers, in Hawaii in 1902, but failed to establish (Callan 1964). It was then re-introduced in 1953, but was not observed for a decade. It has since spread throughout the wetter regions of the Hawaiian Islands (Callan 1964).

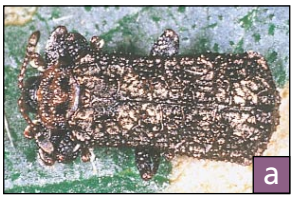


Figure 49.
Octotoma scabripennis:
(a) adult;
(b) larval mines.

O. scabripennis was released in Australia in 1966 and spread rapidly (Harley 1969). It has a mainly subtropical distribution, preferring shady, wetter coastal areas (Day *et al*. 2003). The insect may still be spreading and adapting to some local climatic conditions (Taylor 1989), as it is found in isolated populations in the cooler, tableland areas of tropical northern Queensland and has been recorded in areas where previously it hadn't been found (Day *et al*. 2003). It is thought that the fleshier leaves of Australian lantana varieties may be more suited to leaf-mining insects than those in Hawaii (Harley 1969). *O. scabripennis* has reportedly established in Ghana (Scheibelreiter 1980).

Establishment has occurred in moist, coastal regions in South Africa, in the northern region of India, and in New Caledonia (Muniappan & Viraktamath 1986; Julien & Griffiths 1998; Baars & Neser 1999) although it is not as damaging in India and New Caledonia as in Australia and South Africa (Sen-Sarma & Mishra 1986; Julien & Griffiths 1998). The reasons for this are unclear. It is possible that the species may be still increasing in India, as it was only introduced there in 1972. The insect has failed to establish in Fiji, Cook Islands, Zambia and Guam (Kamath 1979; Löyttyniemi 1982; Julien & Griffiths 1998). Beetles have been released in the Solomon Islands and Niue, but establishment has not been confirmed (Julien & Griffiths 1998). A proposal by the Florida citrus industry to introduce *O. scabripennis*, among other species, to assist in the control of lantana in south-eastern US was rejected as lantana is considered 'native' to the region and because it is a popular garden plant (Habeck 1976).

Damage is most prominent in late spring and summer when plants can become defoliated, reducing flowering and seed-set (Cilliers 1987; Baars & Neser 1999; Day *et al*. 2003). Populations decrease over winter, when temperatures are low and the plants are dry (Day & Holtkamp 1999). Although the beetles may seasonally defoliate plants, reducing flowering and vigour, the plants do not die (Baars & Neser 1999; Day & Hannan-Jones 1999).

O. scabripennis is one of the most valuable biocontrol agents available for the control of lantana and is recommended for introduction into countries where it is not already present. Like other chrysomelids, it is easy to rear and transport and it is able to build up to large populations in the field. The effect of parasites and predators on *O. scabripennis* has been debated. Harley (1969) and Taylor (1989) reported that *O. scabripennis* is relatively free from attack by parasites and predators while Broughton (2001) recorded some 30 per cent of larvae killed by parasites. *O. scabripennis* are also eaten by birds, ants and spiders (Sen-Sarma & Mishra 1986; Taylor

Figure 50.
Damage to lantana by *Octotoma scabripennis* in: (a) Kauai, Hawaii, US; (b) Cangai, NSW, Australia.

1989) but this feeding pressure and the effect of parasites are together insufficient to inhibit population expansion. Consequently large and damaging populations of *O. scabripennis* are frequently achieved on a seasonal basis. *Octotoma scabripennis* does not show preferences for particular lantana varieties and is equally damaging to all taxa (Day *et al*. 2003).

10.21 *Ophiomyia camarae* Spencer (Diptera: Agromyzidae)

Natural distribution

Ophiomyia camarae was found in Mexico, the Caribbean Islands, Florida, Venezuela and Brazil (Stegmaier 1966; Winder & Harley 1983; Palmer & Pullen 1995; Baars & Neser 1999). It has been recorded on *L. camara* in Mexico, Trinidad and Florida (Steg- maier 1966; Palmer & Pullen 1995), *L. tiliifolia* in Brazil (both section *Camara*) (Winder & Harley 1983) and *L. trifolia* (section *Calliorheas*) in Venezuela (Baars & Neser 1999).

Biology

O. camarae adults drink water or feed on nectar in lantana flowers and lay their eggs on the underside of leaves (Simelane 2002). Larvae tunnel along veins and enter the midrib. Late instar larvae form herringbone-shaped mines in the leaves, disrupting translocation and causing leaves to abscise prematurely. There is usually only one mine per leaf but larger leaves can support 2–3 mines (Stegmaier 1966; Simelane 2002). Pupation occurs in the leaves and larvae in leaves that abscise prematurely can still complete development. The development time from egg to adult is about four weeks and adults live for about three weeks (Simelane 2002).

Potential as a biocontrol agent

O. camarae is similar in appearance to two other agromyzid biocontrol agents released on lantana, *Ophiomyia lantanae* and *Calycomyza lantanae*. *Ophiomyia camarae* was released in South Africa in 2001 and has established at several sites. However, it is too early to determine its impact on lantana. The larvae tunnel along the midrib, blocking the transport system and promoting early abscission of leaves (Simelane 2002). *O. camarae* appears to prefer shady areas in the field where lantana is growing under canopy.

The fly has a short life cycle and a high capacity for rapid population growth. It has performed well on several South African lantana varieties during preliminary host-specificity testing and as such, would make a valuable contribution to other biocontrol of lantana programs. There was however,

Figure 51.
Ophiomyia camarae mines on a leaf of a potted lantana plant (PPRI, South Africa).

Figure 52.
Ophiomyia lantanae: (a) adult; (b) mines in seeds (Brisbane Forest Park, Queensland, Australia).

minor oviposition and larvae completed development on several indigenous South African *Lippia* species (Baars & Neser 1999). Consequently, some host-specificity testing would be recommended before its importation to other countries.

10.22 *Ophiomyia lantanae* (Froggatt) (Diptera: Agromyzidae)

Natural distribution

Ophiomyia lantanae is found from southern Brazil to southern US on *L. camara*, *L. urticifolia* and *L. tiliifolia* (Winder & Harley 1983; Palmer & Pullen 1995). Laboratory cultures originated from populations occurring on *L. urticifolia* in Mexico.

Biology

O. lantanae adults feed on nectar from flowers and oviposit in immature fruits (usually one egg per fruit). The larvae feed mainly on the endosperm and in the pericarp of the fruit (Swezey 1924; Harley 1971) but do not damage the embryo. Thus the seed may be weakened, but not killed (Waterhouse & Norris 1987). It has a life cycle of about 21 days.

Potential as a biocontrol agent

O. lantanae was one of the original insects introduced into Hawaii in 1902 (Swezey 1923) and has since been introduced to many other countries (Julien & Griffiths 1998). In many of those countries however, the fly was found to be already present prior to its deliberate introduction (Froggatt 1919; Greathead 1971a; Rao *et al*. 1971; Sen-Sarma & Mishra 1986; Baars & Neser 1999). Also, *O. lantanae* occurs in many countries to which it was never introduced intentionally (Greathead 1971a; Scheibelreiter 1980; Löyttyniemi 1982; Cock & Godfray 1985; Ooi 1987; Denton *et al*. 1991; Harley 1992). Beeson and Chatterjee (1939) suggested that the high biotic potential of the fly and the upper air currents were sufficient to account for its rapid dispersal. However, it is possible that it was accidentally introduced in the shipments of lantana plants sent to the countries where lantana has become a weed (Scheibelreiter 1980; Sen-Sarma & Mishra 1986).

In the naturalised range of lantana, *O. lantanae* is often reported to infest high proportions (50–95%) of fruit (Swezey 1924; Haseler 1966; Winder 1982; Muniappan & Viraktamath 1986; Denton *et al*. 1991). In Brazil, however, the fly's populations are much smaller (only 2.5% of fruit infested), possibly due to natural enemies (Winder 1982). The parasitism rates observed in the fly's native range varied from low (host: parasite ratio of 14–18:1) to high (1:1) (Winder 1982). In contrast, parasitism rates in the fly's naturalised distribution are generally considered to be low (Rao *et al*. 1971; Muniappan & Viraktamath 1986).

Early reports suggested that *O. lantanae* was responsible for the large-scale destruction of lantana seed (Perkins & Swezey 1924). However, such effects on seed viability remained unsubstantiated (Harley 1971). There is still dispute over the ability of the fly to reduce seed viability. Experimental studies examining the germination rates of infested versus uninfested fruit have revealed mixed results, with one study demonstrating lower germination rates among infested fruit (Graaff 1986).

Swezey's (1924) reported that 51 per cent of infested berries had the embryo damaged while Broughton (1999) examined dissected fruit and found that no embryos were damaged by the fly. While embryos may not be killed by *O. lantanae*, both studies failed to examine whether seeds from damaged fruits have poorer survival due to reduced energy stores available to the growing embryo. Irrespective of whether the fly may or may not reduce seed viability, there is strong

evidence to suggest that infested fruit are less likely to be eaten by seed-dispersing birds (Denton *et al*. 1991). Therefore fruit damaged by *O. lantanae* are less likely to be dispersed and the long-distance spread of the weed can be slowed (Taylor 1989). Seed germination is generally poor unless the fleshy pericarp is removed (a process usually performed in the gut of birds) (Beeson & Chatterjee 1939; Swarbrick *et al*. 1998).

O. lantanae is one of the few biocontrol agents that is able to tolerate wide environmental gradients under which lantana occurs (Day & Holtkamp 1999). It develops on all *L. camara* varieties equally well (Harley 1971; Graaff 1986). Each of these factors has allowed the insect to spread widely throughout the naturalised range of lantana. Although *O. lantanae* can damage up to 95 per cent of fruit, there is acceptance that it has limited effectiveness at controlling the spread of lantana as, in many countries, lantana continues to spread (Froggatt 1919; Greathead 1968; Cock & Godfray 1985). Nevertheless, *O. lantanae* would be a useful agent in countries where it is not already present.

10.23 *Orthezia insignis* Browne (Hemiptera: Ortheziidae)

Natural distribution

Orthezia insignis was found in Mexico (Koebele 1903), Brazil (Winder & Harley 1983), Cuba (Krauss 1953a), Guatemala and Honduras (Krauss 1953b) on *L. urticifolia*, *L. tiliifolia* (section *Camara*) and *L. undulata* Shrank (section *Calliorheas*). Laboratory cultures originated from populations occurring on *L. urticifolia* in Mexico.

Biology

O. insignis adults and nymphs suck the sap from stems and leaves. Eggs are wrapped in a silken pouch attached to the stems of the host plant. Eggs hatch in about 10 days and nymphs take 44 days to complete development; however, these periods may vary depending on the particular species and variety of host plant involved. There are three nymphal instars. Adults lay about 55 eggs (Epila 1986). On lantana, *O. insignis* has a lifecycle of about three months (Beeson & Chatterjee 1939). When present in large numbers it kills branches and stems.

Figure 53.
Orthezia insignis adults and nymphs.

Figure 54.
Orthezia insignis damage to lantana (Tzaneen, South Africa).

Potential as a biocontrol agent

It is believed that *O. insignis* was accidentally imported into Hawaii before 1902. In some locations, it severely injured lantana and was spread around the islands by ranchmen (Perkins & Swezey 1924). Koebele condemned their actions (Muniappan & Viraktamath 1986), because *O. insignis* was reported to attack a range of plants, including some economically important species.

O. insignis was first observed in Sri Lanka in 1893 (Beeson & Chatterjee 1939) and may have been the source of the Hawaiian insects (Julien & Griffiths 1998). It was subsequently introduced into India in 1915 and was encouraged to spread until its polyphagous nature was appreciated (Beeson & Chatterjee 1939). Subsequent attempts to exterminate it failed and the scale remains patchy in occurrence (Muniappan & Viraktamath 1986). Before the deliberate release of other insects, *O. insignis* was the only agent capable of decreasing the extent of lantana in India (Beeson & Chatter- jee 1939).

O. insignis is common throughout South Africa and its accidental introduction has been reported from Ascension Island and St Helena, off the west coast of Africa, in the early 1980s (Julien & Griffiths 1998). In both islands, it causes severe damage to lantana and several native species. On St Helena, biocontrol of *O. insignis* was initiated to protect the native flora. It was successful and the scale population has declined such that *O. insignis* is unlikely to have any impact on lantana in the future (Julien & Griffiths 1998). Since *O. insignis* is polyphagous, it is not recommended for the control of lantana.

10.24 *Parevander xanthomelas* (Guérin-Méneville) (Coleoptera: Cerambycidae)

Natural distribution

Parevander xanthomelas was found from Mexico north to southern USA (Palmer & Pullen 1995) and was collected from *L. camara* and *L. urticifolia* (Koebele 1903).

Biology

Little is known regarding the biology of *P. xanthomelas* (Willson & Palmer 1993). The adults feed and mate on flowers of various Asteraceae during sunny mornings in autumn. Adults have never been observed on lantana flowers. Eggs are laid singly or in small batches in cracks in the bark at the base of lantana plants. They may take some months to hatch and larvae burrow directly into the base of plants (Willson & Palmer 1993). Over the dry season, the larvae progressively burrow deeper into the roots, completely hollowing out the roots by the time the rainy season arrives (Koebele 1903). Pupation occurs near the base of the plant (Willson & Palmer 1993). There is only one generation per year.

Potential as a biocontrol agent

Only a very few *P. xanthomelas* were sent to Hawaii, with only one of these being a female (Koebele 1903). Not surprisingly,

Figure 55.
Pinned *Parevander xanthomelas* adult.

the species failed to establish. It has not been introduced into any other country. More recently, preliminary research has been conducted to examine the potential of this insect for inclusion in lantana biocontrol programs (Palmer & Pullen 1995). As there are no other root-feeding insects being used against lantana, *P. xanthomelas* has the potential to utilise a vacant niche. However, as with other cerambycid borers, the rearing of sufficient numbers for release may prove difficult. This is due to the slow growth rates of larvae, the specialised ovipositing and feeding behaviour of the adult beetles and the low reproductive potential of females.

10.25 *Phenacoccus parvus* Morrison (Hemiptera: Pseudococcidae)

Natural distribution

Phenacoccus parvus was found in Central America where its principal host is *L. camara* (Marohasy 1997). While it prefers to settle on lantana, host tests have revealed that it performs equally well on eggplant, tomato and other plants belonging to Solanaceae (Marohasy 1997) and has been reported from plant species in many other families (Williams & Hamon 1994; Marohasy 1997). There is no information on where it originated or on which species it is found.

Biology

P. parvus is facultatively parthenogenic, with three instars. Development from hatched crawler to the commencement of oviposition takes about 26 days (Marohasy 1997). Females live for an average of 20 days and can produce over 400 eggs. Oviposition occurs on the underside of fully expanded mature leaves. Crawlers show a preference for the under surface of mature leaves and cluster along leaf veins. All feeding stages are mobile, although their mechanism for dispersal between bushes is unknown (Marohasy 1997).

Potential as a biocontrol agent

P. parvus has been accidentally or self-introduced into several countries and has spread rapidly throughout the Old World (Williams & Hamon 1994). It is widespread throughout the Pacific Islands (Julien & Griffiths 1998), and is such a problem of crops in the Cook Islands that biological control of the mealy bug has been proposed (Williams & Hamon 1994). It first appeared in Australia in 1988 (Swarbrick & Donaldson 1991) and outbreaks occurred on lantana in south-east Queensland in the 1990s. The populations were so large that the mealybug was responsible for the large-scale die-

Figure 56. *Phenacoccus parvus* adults and nymphs.

Figure 57. *Phenacoccus parvus* damage to lantana (Kilcoy, Queensland, Australia).

back of lantana infestations (Williams & Hamon 1994; Marohasy 1997) and the mealybug was deliberately redistributed to new areas by graziers (Julien & Griffiths 1998).

There was concern that the bug would become a pest of horticulture, however, *P. parvus* was never found on tomato crops growing alongside lantana during the outbreak. While other plant species were occasionally attacked by the mealybug, these were restricted to those growing alongside heavy infested lantana and outbreaks never occurred on plants other than lantana (Marohasy 1997). It is possible that crops were rarely attacked because of the widespread use of insecticides in crops such as tomatoes. Since the outbreak in the 1990s, populations of *P. parvus* have remained fairly low, with population outbreaks appearing to be restricted to when droughts occur.

As *P. parvus* is polyphagous, its use as a biocontrol agent is not recommended. Another polyphagous mealybug species identified as *P. madeirensis* Green has been observed to be locally common in Ghana, even killing lantana in some regions (Scheibelreiter 1980). Whether or not this species is conspecific with *P. parvus* requires further assessment.

10.26 *Plagiohammus spinipennis* Thomson (Coleoptera: Cerambycidae)

Natural distribution

Plagiohammus spinipennis was found in wet, mountain areas from Mexico to Peru (Callan 1964) on *L. hirsuta* (section *Camara*) (Palmer & Pullen 1995). There is no information on whether it occurs on other lantana species. Laboratory cultures originated from populations occurring in Mexico.

Biology

P. spinipennis adults feed mainly on the midrib and main veins of lantana leaves, although young shoots and stems are also eaten (Callan 1964). Eggs are laid in an incision into the bark of lantana stems. The young larvae girdle the stems, before burrowing into the cambium layer (Krauss 1962). They then burrow into the xylem tissue and may extend into the roots (Callan 1964). *P. spinipennis* is univoltine, with the larval stages lasting 8–9 months (Waterhouse & Norris 1987). Infested shoots begin to wither when the larvae are two weeks old (Chock & Chong 1955) and branches are severely weakened or killed by the actions of older larvae (Callan 1964; Waterhouse & Norris 1987).

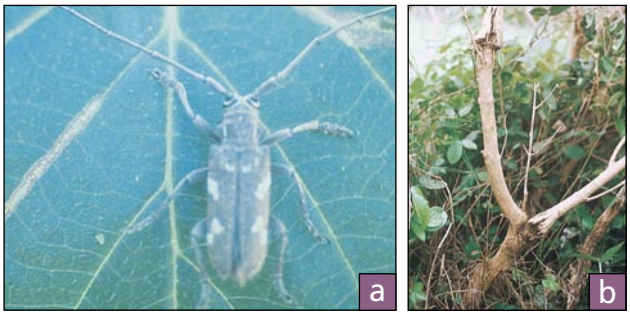


Figure 58.
Plagiohammus spinipennis: (a) adult; (b) larval damage (Hawaii, US).

Figure 59.
Plagiohammus spinipennis: damage to lantana plants (Hawaii, US).

Potential as a biocontrol agent

P. spinipennis was introduced to Hawaii in 1960 (Krauss 1962) and established at several localities where the larvae girdled 97 per cent of plants and 78 per cent of stems. All attacked plants were severely damaged (Harley & Kunimoto 1969). There were initial problems associated with rearing (Chock & Chong 1955; Willson 1974), but these were overcome by using a synthetic diet (Harley & Willson 1968; Hadlington & Johnston 1973; Willson 1974). The development of this diet enabled the production of sufficient numbers of the beetles for release.

P. spinipennis was introduced into Australia in 1967. Despite large numbers of larvae and adults being released over many sites, it was believed to have established at only one site near Kempsey, New South Wales (Taylor 1989), although its persistence at this site is now doubtful (Day *et al*. 2003). Until the mid-1980s, Taylor (1989) observed one or two stems per bush being killed by the borer each year. However, recent surveys have failed to find any trace of the insect and the site was severely burnt in the late 1990s (Day *et al*. 2003).

Attempts to rear *P. spinipennis* in Fiji failed (Kamath 1979) and it failed to become established in Guam, Palau and South Africa (Julien & Griffiths 1998). In South Africa, a colony persisted for 17 years in a garden at the Plant Protection Research Institute laboratories, Pretoria, without spreading elsewhere (Cilliers & Neser 1991).

In Hawaii, wetter sites are more favourable for the borers, with a minimum annual rainfall of 1350 mm required for population expansion. The distribution of rainfall relative to the lifecycle of the insect is critical. Rain shortly before the oviposition period encourages vigorous growth suitable for larvae while under dry conditions in Hawaii, the larvae suffer higher mortality (Harley & Kunimoto 1969).

P. spinipennis has only properly established in Hawaii. One possible reason for this is that the lantana varieties in Australia are very different to those in Hawaii and *P. spinipennis* may not perform well on the Australian varieties. The insect would be a useful addition to the suite of insects attacking lantana in regions with high rainfall (Callan 1964) if a cost-effective mass-rearing method could be developed.

P. spinipennis can be confused with similar taxa and host range studies have only been conduced on insects collected at Jalapa, Mexico (Harley 1971).

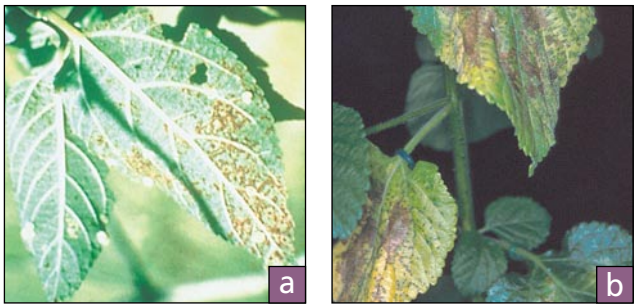


Figure 60.
Prospodium tuberculatum:
(a) spores on leaves;
(b) necrosis of leaves.

Figure 61.
Prospodium tuberculatum damage to lantana (Brazil).

10.27 *Prospodium tuberculatum* (Spegazzini) Arthur (Uredinales: Puccinaceae)

Natural distribution

Prospodium tuberculatum was found in Brazil, Ecuador and Mexico (Tomley 2000). It was recorded on several species of lantana in Brazil (Barreto *et al*. 1995). Isolates were collected in Brazil from *L. camara*.

Biology

P. tuberculatum is an autoecious rust, with a reduced life-cycle that is completed on only one plant species. The main stage is the urediniospores, although teliospores can be found on lantana growing in high altitudes (Barreto *et al*. 1995). Leaf infections are in the form of dark purplish brown lesions that can be irregular in shape. Severe lesions cause defoliation and infected plants are less vigorous and stunted (Tomley & Evans 1992).

Potential as a biocontrol agent

P. tuberculatum was released in Australia in 2001 and appears to have established at various sites. However, prolonged drought over most of eastern Australia has impeded its release and establishment in most areas. In Brazil, it can cause severe leaf necrosis resulting in defoliation leading to reduced vigour (Tomley & Evans 1992; Barreto *et al*. 1995). In Australia, the rust appears to be highly host-specific, attacking only the common pink-flowering variety (Tomley & Riding 2002). Detailed field assessment of this agent is needed before recommendations can be made on its value to other countries.

10.28 *Pseudopyrausta santatalis* (Barnes & McDunnough) (Lepidoptera: Pyralidae)

Natural distribution

Pseudopyrausta santatalis was found in Mexico on *L. camara*, *L. urticifolia*, *L. urticoides* and *L. hirsuta* (Palmer & Pullen 1995). It has also been found on *L. camara* in US, Columbia and Venezuela (Harley 1956b). There is no information on from which species of lantana it was collected to start laboratory cultures.

Biology

P. santatalis adults lay eggs on the underside of leaves. Larvae feed on the young leaves and more mature larvae feed on the growing tips inside webbing. Larvae feed for about two

Figure 62. *Salbia haemorrhoidalis*: (a) adult; (b) larva.

Figure 63. *Salbia haemorrhoidalis* damage to lantana (Brisbane, Queensland, Australia).

weeks and pupation occurs in dried leaves or in the leaf litter. Adults live for about two weeks (Harley 1956b).

Potential as a biocontrol agent

P. santatalis was introduced into Hawaii from Mexico in 1954, but failed to establish (Gardner & Davis 1982). Hawaiian stocks were released in Fiji in 1954 and Pohnpei in 1955 (Rao *et al*. 1971; Schreiner 1989). It failed to become established in Fiji following the release of 600 adults and 2000 larvae (Rao *et al*. 1971) and entomological surveys of lantana throughout Micronesia have failed to find the species (Denton *et al*. 1991).

Rearing *P. santatalis* moths was difficult, due to high mortality caused by bacterial and fungal diseases in the laboratory (Parham *et al*. 1956) which may account for the relatively short rearing program. *P. santatalis* completed development on three species in host-specificity testing: *Perilla frutescens* (L.) Britton (Lamiaceae); apple, *Malus sylvestris* (L.) Miller (Rosaceae); and soy bean *Glycine max* (L.) Merrill (Fabaceae). Development on all three species was significantly lower than that on lantana (Harley 1956b). The insect is not host-specific and therefore is not recommended for release.

10.29 *Salbia haemorrhoidalis* Guenée (Lepidoptera: Pyralidae)

Natural distribution

Salbia haemorrhoidalis was found in Central America (Waterhouse & Norris 1987), the Caribbean and Florida, US (Krauss 1962) on *L. camara*, *L. urticifolia*, *L. tiliifolia* and *L. hirsuta* (section *Camara*) and *L. undulata* (section *Calliorheas*) (Palmer & Pullen 1995). Laboratory cultures originated from populations occurring in Cuba and US, but it is not known from which species of lantana.

Biology

S. haemorrhoidalis adults feed on flowers and lay eggs on the underside of leaves. The larvae feed within folded leaves, which they fasten together with silk. Pupation occurs in cocoons spun in the leaf litter under the plant. Development from egg to adult takes 5–6 weeks (Harley 1956c).

Potential as a biocontrol agent

S. haemorrhoidalis was introduced into Hawaii in 1956. It established rapidly and was regarded as the only outstanding lepidopterous defoliator of lantana in Hawaii (Davis *et al*. 1992). Most of the damage occurred during the winter months, complementing *Teleonemia scrupulosa* which reached its highest densities in summer (Andres & Goeden 1971). Numbers of the moth have subsequently decreased (Harley 1971) and a combination of parasitism and the spread of *Hypena laceratalis* are believed to restrict population numbers (Callan 1964; Davis *et al*. 1992).

S. haemorrhoidalis has established successfully following its release in Australia (Haseler 1963), Fiji (Rao *et al*. 1971), Pohnpei (Denton *et al*. 1991), Mauritius and Uganda (Greathead 1971a), and South Africa (Baars & Neser 1999). However, in each of these places, it exerts little control on lantana (Cilliers & Neser 1991; Denton *et al*. 1991; Baars & Neser 1999). In Kenya, it failed to establish because only four individuals were released (Greathead 1971a) and has failed to establish in India (Muniappan & Viraktamath 1986), Zambia (Löyttyniemi 1982), and on Yap, Guam and Palau (Muniappan 1989; Denton *et al*. 1991).

One factor that has been identified as influencing establishment is the selection of suitable release sites. In Uganda, other biocontrol agents had heavily defoliated the lantana at one release site and as a result there may have been

insufficient new growth on which *S. haemorrhoidalis* could feed (Greathead 1971a). In Australia, the moth was mainly released in the warm high rainfall regions of northern Australia where there was ample new growth. Although *S. haemorrhoidalis* also established in southern Queensland, it failed to establish at many sites in the region where lantana often became seasonally dry and leafless. Recent surveys reported *S. haemorrhoidalis* at only a few sites in south-east Queensland (Day *et al.* 2003).

Another factor that may influence its establishment was the varieties of lantana present. Diatloff and Haseler (1965) reported that *S. haemorrhoidalis* appeared to prefer red-flowering varieties to the common pink variety. However, recent surveys have found the moth attacking all varieties present and in some areas it is the only agent damaging the pink-flowering variety (Day *et al*. 2003). Populations did not establish on Guam, Palau and in other countries. Many countries encountered difficulties in the rearing or importing sufficient numbers for release, with high mortality occurring during transit (Greathead 1971a; Rao *et al.* 1971).

Parasitism has been suggested as the main reason why the moth has failed to reach damaging population levels in many of the countries in which it has been released (Haseler 1963; Taylor 1989), although no study has confirmed this.

Provided that large numbers of moths can be released in healthy condition and in suitable sites, establishment rates of *S. haemorrhoidalis* are good. However, while it does contribute to the feeding damage caused by the complex of insects established in many countries, it is not regarded as a high priority agent.

10.30 *Septoria* sp. (Blastales: Sphaeropsidaceae)

Natural distribution

Septoria sp. was collected from *L. camara* in Ibarra, Ecuador (Trujillo & Norman 1995). The extent of its geographic and host range is unknown.

Biology

Septoria sp. is a leaf-spot fungus. Initial symptoms of chlorotic spots appear two weeks after inoculation becoming necrotic lesions after four weeks. Defoliation can occur after six weeks (Trujillo & Norman 1995). No other information is available

Potential as a biocontrol agent

Septoria sp. was released in Hawaii in 1997, although the status of the pathogen on these islands has not been reported (Thomas & Ellison 1999). Testing has indicated that it is capable of infecting and damaging Hawaiian varieties of lantana, but

Figure 64. *Septoria* sp.: (a) spores; (b) damage to lantana (Kokee, Kauai, Hawaii, US).

not *L. montevidensis* or any other plants tested (Trujillo & Norman 1995). This species differs morphologically from *S. lantanae* Gaerman from Puerto Rico with which it has been previously confused (Trujillo & Norman 1995).

10.31 *Strymon bazochii* (Godart) (Lepidoptera: Lycaenidae)

Natural distribution

Strymon bazochii was found on *L. camara* and *L. urticifolia* in Mexico (Palmer & Pullen 1995) and laboratory cultures originated from populations occurring on *L. urticifolia*.

Biology

S. bazochii adults feed on nectar and oviposit in the inflorescences. The larvae feed on the flowers, with each larva feeding in one or more inflorescences (Swezey 1924; Zimmerman 1958). Little else is known of the biology of this species.

Potential as a biocontrol agent

S. bazochii was one of the agents imported into Hawaii by Koebele in 1902 in his endeavour to establish flower-feeding and seed-feeding insects. It successfully established in Hawaii, where Swezey (1924) noted that in regions where the butterflies were abundant nearly every lantana flower contained either larvae or eggs. These large numbers are never seen in Hawaii today and *S. bazochii* appears to have a negligible impact on seed production (Harley 1971). The butterfly was successfully introduced into Fiji but, as in Hawaii, it is of little value in controlling lantana. Egg parasites are believed to be one reason for the butterfly's decline in Hawaii and Fiji. Swezey (1924) reported that 26 out of 29 eggs examined were destroyed by egg parasites. In Australia, *S. bazochii* failed to establish after its release in 1914 (Julien & Griffiths 1998).

Figure 65. *Strymon bazochii* adult.

Larvae of *S. bazochii* have been reported feeding on basil *Ocimum basilicum* L. (Lamiaceae) and *Hyptis pectinata* (L.) Poiteau (Lamiaceae) in Hawaii (Zimmerman 1958). The lack of host specificity and low impact makes this species unsuitable for further release.

10.32 *Teleonemia bifasciata* Champion (Hemiptera: Tingidae)

Natural distribution

Teleonemia bifasciata was collected from Trinidad (Mann 1954b) but it was also found in Brazil, Panama, Guatemala and Windward Islands (Drake & Ruhoff 1965). There is no information about which species of lantana it occurs on or from which species it was collected.

Biology

No information is available on the biology of *T. bifasciata*.

Potential as a biocontrol agent

T. bifasciata was collected from Brazil and released in small numbers (about 100) in Hawaii in 1954 (Julien & Griffiths 1998). It failed to establish and no other information is available. *T. bifasciata* is rarely recognised in reviews of bio-control attempts in Hawaii.

10.33 *Teleonemia elata* Drake (Hemiptera: Tingidae)

Natural distribution

Teleonemia elata was found in Brazil, Chile, Paraguay and Peru on *L. tiliifolia* and *L. glutinosa* (Harley & Kassulke 1971).

Laboratory cultures originated from populations occurring in Brazil, but there is no information on which species of lantana was involved.

Biology

T. elata adults feed on leaves, buds and flowers, causing wilting and death of apical portions of stems. The nymphs feed on the upper surface of leaves, causing the death and abscission of foliage. The life cycle is completed in 42 days in summer and 61 days in winter (Harley & Kassulke 1971).

Potential as a biocontrol agent

T. elata is one of several tingids that were released in Australia following the success of *T. scrupulosa* (Taylor 1989). *T. elata* was imported into Australia from Brazil in 1969 (Harley 1971), and released in large numbers at various locations along the coast of Queensland (CSIRO unpublished records). It failed to establish in Australia (Harley 1971) as well as in the Cook Islands, South Africa, Uganda and Zambia (Löyttyniemi 1982; Julien & Griffiths 1998).

T. elata appeared to show preferences for certain lantana varieties (Harley & Kassulke 1971; Harley 1971), however, this was not confirmed in the field. Tingids are dominant components of the fauna attacking lantana in its native range and therefore have potential to be useful biocontrol agents. However, better appreciation for the reasons that most tingids have failed to establish when released as biocontrol agents needs to be gained if we are to fully utilise this group.

10.34 *Teleonemia harleyi* (Froeschner) (Hemiptera: Tingidae)

Natural distribution

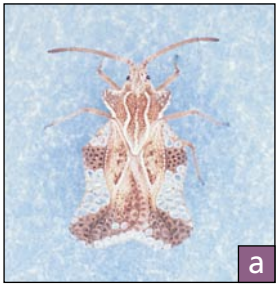
Teleonemia harleyi was found in Trinidad (Harley & Kassulke 1973) but no information is available indicating which species of lantana it was collected from or occurs on.

Biology

T. harleyi eggs are inserted singly or in small groups into flower stalks, young stems, petioles or main veins where they cause conspicuous swellings. Nymphs emerge after 9–10 days and actively move around the plant. The nymphs are not gregarious and feed mostly on flowers and meristem tissue, causing death of the buds and flowers. Nymphs complete development in 16 days. *T. harleyi* destroys all flowers when colonies are caged on plants (Harley & Kassulke 1973).

Potential as a biocontrol agent

T. harleyi was introduced into Australia in 1972. However, only a total of 245 individuals were released at four sites around Brisbane, Queensland (CSIRO unpublished records).



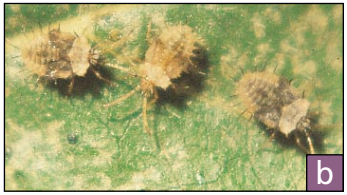


Figure 66.
Teleonemia elata:
(a) adult; (b) nymphs.

Figure 67.
Teleonemia harleyi:
(a) adult; (b) damage to flowers.

It is believed to have established at one site (Julien & Griffiths 1998), although recent surveys have failed to find the agent at this or any other site (Day *et al*. 2003). It is possible that due to its morphological similarity with *T. scrupulosa*, it could have been confused with *T. scrupulosa* and therefore overlooked.

T. harleyi has only been released in Australia. Laboratory studies indicate that it will attack all naturalised lantana taxa (Harley & Kassulke 1973). Further information on its status in Australia would be useful before release occurs in other countries.

10.35 *Teleonemia prolixa* Stål (Hemiptera: Tingidae)

Natural distribution

Teleonemia prolixa was found from Argentina to Mexico and the West Indies on *L. tiliifolia* and *L. glutinosa* (Harley & Kassulke 1975; Winder & Harley 1983) and *Acacia riparia* Kunth (Fabaceae) and *Cinchona* sp. (Rubiaceae) (Drake & Ruhoff 1965). Laboratory cultures originated from populations occurring in Brazil, but it is not known from which species of lantana.

Biology

T. prolixa feeds on flowers, young leaves and stalks. It has similar behaviour to the other flower-feeding species, *T. harleyi* (Harley & Kassulke 1975). Eggs are laid in flower stalks or in the midrib of young leaves; nymphs feed for about two weeks; adults can live for several months (Harley & Kassulke 1975).

Figure 68. *Teleonemia prolixa* adult.

Potential as a biocontrol agent

T. prolixa was released in Queensland in 1974 (Harley & Kassulke 1975), mainly around Brisbane in the south-east and at a few sites around Cairns in the north. It was not released in New South Wales due to rearing difficulties (Taylor 1989). It failed to establish in Queensland and has not been released in any other country. *T. prolixa* showed a clear preference for pink-edged red varieties in laboratory trials, while a population was unable to be sustained either on the common pink variety or *L. montevidensis* (Harley & Kassulke 1975).

10.36 *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae)

Natural distribution

Teleonemia scrupulosa was found throughout Mexico and Central and South America (Waterhouse & Norris 1987) and is a dominant component of the lantana fauna in its native range (Mann 1954b). It has a wide host range, being collected from *L. camara*, *L. urticifolia*, *L. urticoides* and *L. hirsuta* in Mexico and US and *L. tiliifolia* and *L. glutinosa* in Brazil (Winder & Harley 1983; Palmer & Pullen 1995). Laboratory cultures originated from populations occurring in Mexico, but it is not known from which species of lantana.

Biology

T. scrupulosa adults and nymphs feed in colonies, primarily on the under surface of leaves where they suck the cell contents (Khan 1945) although they often feed on flowers and growing tips of stems (Fyfe 1937). The feeding by adults and nymphs cause the formation of chlorotic and necrotic lesions and leaf malformation, curling and defoliation (Gupta & Pawar 1984; Waterhouse & Norris 1987). The occurrence of additional damage to plant parts removed from the

feeding site suggests that salivary toxins may have a systemic effect (Khan 1945; Harley & Kassulke 1971). Eggs are partially inserted into the midrib and main veins on the underside of leaves (Fyfe 1937). The life cycle is short, taking about a month, with 10–11 overlapping generations a year (Simmonds 1929; Gupta & Pawar 1984; Waterhouse & Norris 1987).

Potential as a biocontrol agent

T. scrupulosa is one of the most damaging of the lantana insects utilised in lantana biocontrol programs. It was one of the original insects introduced into Hawaii by Koebele in 1902 (Swezey 1923) and has since been released in most countries where lantana is considered a weed. It was released in Fiji in 1928, Vanuatu in 1935, Australia, Western Samoa and New Caledonia in 1936, Tonga in 1937, Indonesia in 1940, India in 1941, throughout Micronesia in 1948, Kenya in 1953, Tanzania and Zanzibar in 1958, Uganda and Palau in 1960, South Africa, Zimbabwe and Madagascar in 1961, Zambia in 1962, Northern Mariana Islands in 1963, Guam in 1969, Ghana and St Helena in 1971, Ascension Island and Papua New Guinea in 1973, Solomon Islands in 1993 and Niue in 1994 (Julien & Griffiths 1998).

The establishment rate for these introductions has been very high. The only place where it has certainly failed to establish is on Yap (Muniappan 1989). *T. scrupulosa* appears not to have established in Zimbabwe, but proper surveys

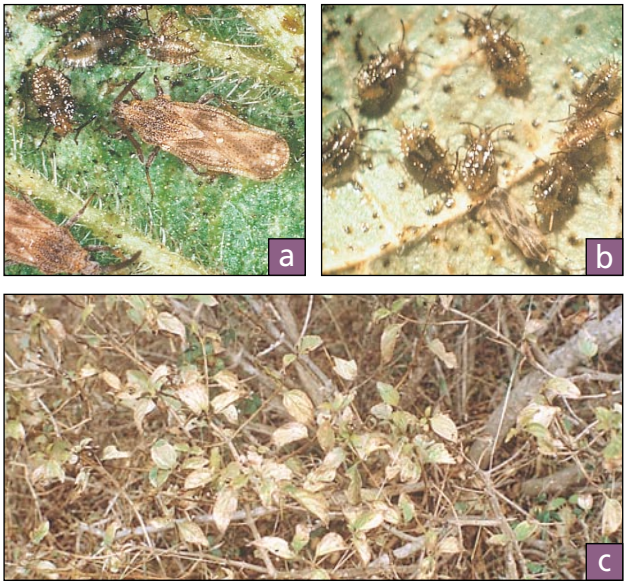


Figure 69.
Teleonemia scrupulosa: (a) adult and nymphs; (b) nymph cluster; (c) damage to leaves.

Figure 70.
Teleonemia scrupulosa damage to lantana at: (a) Yarraman; (b) Gracemere (Queensland, Australia).

have not been conducted. Its status on Niue is not known. In both India and Indonesia, its establishment was accidental. Colonies kept under quarantine were destroyed following fears that *T. scrupulosa* might damage teak *Tectona grandis* (Gardner 1944). However, in both countries, small numbers of the tingid escaped and managed to establish (Roonwal 1952; van der Vecht 1953; Rao *et al*. 1971; Muniappan & Viraktamath 1986). Its fortuitous spread has been recorded in Malaysia and the Philippines (Rao *et al*. 1971; Cock & Godfray 1985) and Mauritius (Greathead 1971a) where it readily spread throughout islands within each group (Denton *et al*. 1991).

The failure of *T. scrupulosa* to establish on Yap may be due to the lantana variety present. Schreiner (1989) notes that the orange-flowering variety occurring in Micronesia was attacked less than the purple-flowering varieties. Yap contains only the orange variety and while *T. scrupulosa* was believed to be present there in 1986 (Schreiner 1989), Muniappan failed to find it in 1989. In other countries such as Australia and South Africa, *T. scrupulosa* only attacks a proportion of the lantana varieties present (Diatloff & Haseler 1965; Harley & Kassulke 1971; Radunz 1971; Harley 1973; Harley *et al*. 1979; Cilliers 1987; Day *et al*. 2003). In Australia, *T. scrupulosa* prefers the white-flowering, red-flowering and pink-edged red-flowering lantanas. While it will feed on the common pink lantana, it is not as abundant as it is on the other varieties (Day *et al*. 2003).

Figure 71.
Teleonemia scrupulosa damage to *Myoporum sandwicense* (Hawaii, US).

T. scrupulosa has probably reached its full distribution in Australia (Taylor 1989), occurring in small numbers around Sydney and being common around Cairns in the north. It is more common in the warm drier areas and has caused seasonal defoliation to lantana infestations around central and southern Queensland (Day *et al*. 2003) with the most damaging populations occurring in the period midsummer to autumn (Haseler 1966; Willson 1968; Bisht & Bhatnagar 1979; Harley *et al*. 1979; Cilliers 1987). While feeding on flowers directly does little to impair the reproductive ability of lantana (Harley *et al*. 1979), the stress to the plant caused by leaf damage is known to affect flower and seed production significantly (Harley 1970; Rao *et al*. 1971; Muniappan *et al*. 1996).

When tingid populations are large, seasonal defoliation readily occurs, and when insect attack is combined with other stresses, such as drought, plants may be killed (Harley & Kassulke 1971). However, in many regions, lantana is able to compensate for this attack and *T. scrupulosa* is incapable of killing the weed (Swezey 1924; Greathead 1968, 1971b; Harley *et al*. 1979; Sen-Sarma & Mishra 1986; Sharma 1988). Tinged populations can undergo rapid crashes once plants have become defoliated, or with the onset of adverse weather as discussed below. Following such crashes, populations can take 2–4 months (three generations) to return to damaging levels (Khan 1945; Harley *et al*. 1979).

Environmental factors can greatly affect populations of *T. scrupulosa*. During the dry winter months, lantana drops its leaves and its growth is stalled due to frosts, low temperatures

and low winter rainfall (Harley *et al*. 1979). When the mean temperature is below 16°C, *T. scrupulosa* eggs and adults may overwinter while nymphs experience high mortality when mean temperatures are below 14°C (Harley & Kassulke 1971). Rainfall can reduce *T. scrupulosa* populations, with persistent rainy periods drowning the bugs and washing them from the leaves (Fyfe 1935; Khan 1945). Furthermore an undescribed parasitic fungus has been observed to attack T. *scrupulosa* in India and Fiji following prolonged rainy seasons (Fyfe 1935; Khan 1945).

Since its escape in India and Indonesia, *T. scrupulosa* has not significantly damaged teak as was once feared. However, it has attacked some non-target plants in various countries where it has been released. For example, widespread concern over the safety of the tingid developed after it was observed to be attacking sesame *Sesamum indicum* in Uganda (Greathead 1971b). However, this only occurred after an explosion in the population of the insect on nearby lantana, resulting in defoliation of its host plant. The poor survival rate of nymphs on sesame, an annual crop, suggests there is little danger of the development of a strain adapted to that crop (Davies & Greathead 1967).

Minor feeding has been recorded on *Myoporum sandwicense* A. Gray (Myoporaceae) and *Xanthium* sp. (Asteraceae) in Hawaii, ebony *Brya ebenus* (L.) DC (Fabaceae) in the US and *L. alba* (Verbenaceae) in the Antilles (Davies & Greathead 1967) and Australia. Laboratory studies in Australia show that while populations can be supported on *L. alba*, *T. scrupulosa* prefers and performs better on lantana (Gray 1998). Apart from *L. alba*, feeding on non-target plants has only been incidental and has only occurred when large populations had developed on lantana and there was insufficient food available. However, *T. scrupulosa* cannot maintain populations on these non-target plants.

Parasites and predators do not play a major role in regulating *T. scrupulosa* populations. However, in Fiji, generalist predators such as ants, spiders and the bug *Germalus pacificus* Kirkaldy (Lygaeidae) have been implicated in its failure to develop damaging populations (Simmonds 1929).

Teleonemia scrupulosa would be a useful introduction into regions where it is not present. However, as it has been found on several non-target species, host-specificity studies should be undertaken in the target country before its importation.

10.37 *Tmolus echion* (Druce) (Lepidoptera: Lycaenidae)

Natural distribution

Tmolus echion was found in Mexico on *L. camara* (Palmer & Pullen 1995).

Biology

T. echion is similar in habits to *Strymon bazochii*. Larvae feed on flowers, thus reducing seed production, but no other information on its biology is available.

Potential as a biocontrol agent

T. echion was among the eight insects successfully introduced into Hawaii by Koebele in 1902 (Swezey 1923). It is not common and has little impact on lantana seed production (Harley 1971). It was introduced into Fiji in small numbers in 1922, but it failed to become established (Rao *et al*. 1971).

In Hawaii, it is heavily attacked by native parasites, preventing the build up of large populations (Swezey 1924). *Tmolus echion* feeds on eggplant *Solanum melongena* L. (Solanaceae), pepper pods *Capsicum annuum* L. (Solanaceae) and the flowers of *Cordia sebestena* L. (Boraginaceae) (Swezey 1924). Due to its ability to attack other plant species and its minimal impact on seed production, it is not recommended for introduction into other countries.

10.38 *Uroplata fulvopustulata* Baly (Coleoptera: Chrysomelidae)

Natural distribution

Uroplata fulvopustulata was found from Colombia to Mexico and Costa Rica (Krauss 1962; Winder 1984; Palmer & Pullen 1995) on *L. camara*, *L. hispida* (section *Camara*) and *L. trifolia* (section *Calliorheas*). It was mostly found in low-lying, tropical regions and was uncommon in highland areas (Diatloff 1975). It has been referred to as three distinct species in the past and as a result, historical host records are misleading (Diatloff 1975; Winder 1984). Laboratory cultures originated from populations occurring on *L. urticifolia* in Costa Rica.

Biology

U. fulvopustulata adults prefer to feed on, and oviposit in, young but fully expanded leaves. Larvae mine the leaves and up to four larvae can develop in a large leaf. A greater number of larvae in one leaf may result in premature shedding of the leaf before the larvae have matured (Diatloff 1975). Larvae may die, as they are unable to transfer between leaves. In Costa Rica, the larval period varies considerably, depending on leaf quality, from 30–42 days (succulent leaves) to 60 days (small, hard leaves), with average development from egg to adult taking 56 days. There are three generations a year in Panama and Costa Rica and adults can survive the dry winter by entering a facultative diapause (Diatloff 1975).

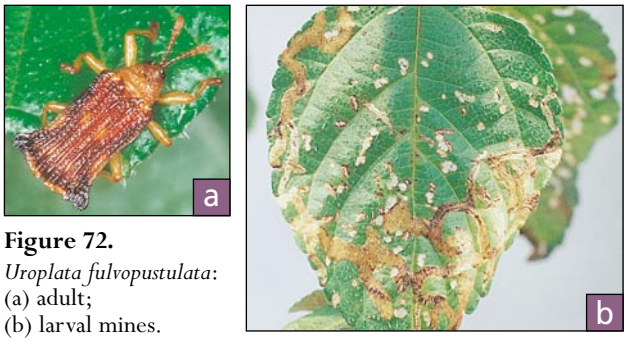


Figure 72.
Uroplata fulvopustulata:
(a) adult;
(b) larval mines.

Potential as a biocontrol agent

U. fulvopustulata was introduced to Australia in 1976 following the success of two other hispine beetles *U. girardi* and *Octotoma scabripennis*. In Australia, it was released extensively throughout Queensland and in smaller numbers in New South Wales. However, it has established only in north Queensland (Broughton 1998; Day *et al*. 2003). Climate is almost certainly the limiting factor, although low numbers released in NSW may have contributed to its failure to establish there (Taylor 1989). It has been released, although unsuccessfully, in Fiji and South Africa (Julien & Griffiths 1998), and the reasons for its failure to establish in these countries are not known. While parasites have been recorded from the species in its native range (Krauss 1962), these appear to play only a minor role in the control of field populations (Diatloff 1975).

Uroplata fulvopustulata may be a promising species for humid, tropical regions of the world, where *Octotoma scabripennis* or *Uroplata girardi* are less effective.

10.39 *Uroplata girardi* Pic (Coleoptera: Chrysomelidae)

Natural distribution

Uroplata girardi was found in Brazil, Paraguay and Argentina on *L. tiliifolia* and *L. glutinosa* (Krauss 1964). Laboratory cultures originated from populations occurring on *L. tiliifolia* in Brazil.

Biology

U. girardi adults feed on the upper leaf surface and scarify areas of the leaf tip causing it to curl providing shelter for the insect (Harley 1971). The larvae mine the leaves of lantana, feeding on the mesophyll layers and leaving the upper and

lower epidermal layers intact. There are usually one or two mines per leaf, with each containing one larva (Bennett & Maraj 1967). The lifecycle takes 31–52 days (Callan 1964) and there are normally about three generations per season. Adults may enter a facultative diapause during the winter when plants are dry (Harley 1969).

Potential as a biocontrol agent

U. girardi was the second hispine beetle introduced into Hawaii and, together with *O. scabripennis*, is the most successful agent used in lantana biocontrol projects (Broughton 2000a; Day *et al*. 2003). It has been introduced into 26 countries and is successfully established in 24 (Julien & Griffiths 1998). Its apparent failure to establish in two countries, Tanzania and St Helena, is probably due to insufficient numbers released or adverse weather conditions following release (Julien & Griffiths 1998). However, as no recent surveys have been conducted, the status of *U. girardi* in these countries cannot be confirmed.

Populations of *U. girardi* in some places — for example, Hawaii, Uganda, India and Micronesia — were slow to build up (Greathead 1971b; Sen-Sarma & Mishra 1986; Denton *et al*. 1991), while in other countries — for example, Australia and the Solomon Islands — the populations expanded rapidly following their introduction (Harley 1969; Scott 1998). In Australia, it is probably approaching the limits of its potential distribution, but may still move into new areas within its current range. *U. girardi* is tolerant of most environmental conditions, and is found from Sydney to Cooktown; however it prefers open, sunny situations, especially the warm, humid areas of the tropics (Day *et al*. 2003).

In South Africa, *U. girardi* is rare in inland regions or coastal areas that experience low rainfall (Baars & Neser 1999). A new strain from a cooler region of South America was imported into South Africa to improve control in elevated regions and it is believed to be spreading successfully (Cilliers & Neser 1991). *U. girardi* can perform well on lantana growing in semi-shade (Krauss 1962; Waterhouse & Norris 1987; Denton *et al*. 1991); indeed under these conditions it is better able to control lantana which is less vigorous under such situations (Kamath 1979). Damage caused by *U. girardi*, as with other leaf-feeding insects released on lantana, is insufficient to kill lantana bushes. However, seasonally, it can cause severe defoliation in plants resulting in a reduction in flowering and seed production (Day *et al*. 2003).

Figure 73.
Uroplata girardi:
(a) adult;
(b) larval mines.

Figure 74.
Uroplata girardi damage to lantana (Queensland, Australia).

Figure 75.
Uroplata lantanae adult.

Like other hispines, *U. girardi* can suffer some parasitism, but in many areas the insect does not appear to be greatly affected by parasites (Waterhouse & Norris 1987; Taylor 1989, Broughton 2001) with large populations developing on a seasonal basis. Generalist predators however, such as birds, ants and spiders are thought to be limiting population expansion in some areas (Sen-Sarma & Mishra 1986; Taylor 1989). As *U. girardi* is host-specific and can be very damaging, it would be a worthwhile agent to introduce into countries where it is not present.

10.40 *Uroplata lantanae* Buzzi & Winder (Coleoptera: Chrysomelidae)

Natural distribution

Uroplata lantanae is found in the temperate regions of Brazil on *L. tiliifolia* (Buzzi & Winder 1980; Winder 1984).

Biology

Like the other hispine beetles, *U. lantanae* adults feed on the upper surface of leaves and the larvae mine the leaves. The life cycle from egg to adult takes 48–54 days between October and January in Brazil, with only one generation per year (Winder 1984). However, in quarantine in Australia, up to three generations per year were completed. In Brazil, up to 24 per cent of leaves were attacked. Adults preferred taller plants and oviposited on higher branches (Winder 1984); isolated plants were favoured over plants growing among other understorey species.

Potential as a biocontrol agent

U. lantanae was introduced into Australia for cooler ecoclimatic zones not utilised by the other hispine beetles (Harley 1969). Over 6000 adults were released throughout eastern Australia from 1977 (Winder 1984); however, the species failed to become established (Julien & Griffiths 1998). *U. lantanae* was released in South Africa in low numbers and also failed to establish; it was slow to reproduce and in the insectary, adults diapause from late April to October in the leaf litter at the bottom of the cage (Taylor 1989).

In addition to low reproductive rates, *U. lantanae* showed distinct preferences for certain lantana varieties. The beetle performed poorly in the laboratory on common pink, but could complete its lifecycle on pink-edged reds in the insectary (Winder 1984). Its failure to establish in the field is believed to be due to its inability to maintain populations on Australia's naturalised lantana (Sands & Harley 1980; Winder 1980). Consequently this species is probably of little value in future biocontrol programs in Australia.

11. Species imported, but not released

Many insects have been imported for biological control of lantana, but not released. Often, there were not enough to start a colony or for host-specificity studies to be conducted. Only a few examples occur where the insect was not released because it was not host-specific, and these were mainly in countries where lantana is native. The following insects were studied, but not released.

11.1 *Diastema morata* Schaus (Lepidoptera: Noctuidae)

This moth was found in Mexico at Merida, Yucatan, Tehuacan and Puebla. The larvae feed on leaves, but there are no records of the host *Lantana* species. It was imported into Hawaii, but the small number collected precluded a population being established (Krauss 1962). It has not been considered as a priority for further study.

11.2 *Hepialus* sp. (Lepidoptera: Hepialidae)

This stem-boring moth was recognised by Koebele (1903) as one of the most destructive enemies of lantana in Mexico, especially in the higher-rainfall regions of the east coast of Mexico. The larvae bore into the branches, forming new

tunnels with each moult. Pupation occurs in a tunnel in larger roots (Koebele 1903). Koebele sent this species from Mexico to Hawaii in 1902. However, few individuals survived the journey and it proved difficult to breed in the laboratory (Perkins & Swezey 1924). There were later concerns over its host-specificity, because Koebele had observed what he believed to be this species feeding on a range of woody plant species in Mexico and concluded that it would be unsafe to release (Koebele 1903).

Because this insect can be quite destructive, there is potential for it to be added to the suite of insects currently being considered for further study. However, the identity of this insect is unclear and W. Palmer (NRM, pers. comm.) believes that it may be *Phassus argentiferus* Walker (see section 11.7, below). The taxonomic status of this agent should be clarified before any future work on it is conducted.

11.3 *Langsdorfia franckii* Hübner (Lepidoptera: Cossidae)

Larvae of this moth can cause substantial damage to the stems and roots of lantana plants. However, propagation of this species in Hawaii was very difficult. Consequently, no host specificity testing was conducted and no releases were made (Krauss 1962; Gardner & Davis 1982).

11.4 *Octotoma gundlachi* Suffrian (Coleoptera: Chrysomelidae)

This beetle was found in Cuba, where adults feed on leaves and the larvae form mines in the leaves (Vaurie 1956). This species was sent by Krauss from Cuba to Hawaii in 1953, but was not reared successfully (Krauss 1962). Consequently, host-specificity studies were not conducted and the insect was not released (Krauss 1964; Gardner & Davis 1982).

11.5 *Oedionychus* sp. (Coleoptera: Chrysomelidae)

Krauss sent 46 larvae of an unidentified *Oedionychus* from Mexico to Hawaii in 1953, but a laboratory population failed to establish (Krauss 1953b). No other information is available on this species. Surveys by Winder and Harley (1983) and Palmer and Pullen (1995) found several species of *Oedionychus*, but these have not been fully identified and have not been studied further.

11.6 *Omophoita albicollis* Fabricius (Coleoptera: Chrysomelidae)

This beetle was imported into South Africa from Mexico. The adults feed voraciously on flowers and leaves, and they deposit eggs in the leaf litter. Host-specificity trials indicated that larvae could develop on several indigenous species of *Lippia* and *Phyla*, as well as several indigenous and economically important species in the Lamiaceae. However, it was subsequently rejected for release in South Africa and the laboratory culture was terminated (Baars & Neser 1999).

11.7 *Phassus argentiferus* Walker (Lepidoptera: Hepialidae)

This moth has been found in Veracruz and Morelos, Mexico, and in Costa Rica. The larvae were observed to tunnel into stems and roots killing branches and stems of several lantana species. The insect attacked several other plant species such as *Rubus* sp. (Rosaceae), *Coffea arabica* L. (Rubiaceae), *Salvia* sp. (Lamiaceae) and *Ricinus* sp. (Euphorbiaceae) (Diatloff NRM, pers. comm.); it was never released (Krauss 1962).

11.8 *Teleonemia validicornis* Stål (Hemiptera: Tingidae)

This tingid was imported into Australia from Brazil in 1972 (Harley & Kassulke 1974b). While it had been recorded on various hosts in its native range (Colombia, Surinam, French Guiana, Guyana, Brazil, Argentina, Venezuela, Panama and

Curacao), its host-specificity was tested in greater detail under quarantine conditions in Australia (Harley & Kassulke 1974b). The laboratory material was collected from lantana and the bug was found to breed freely on the widely cultivated ornamental tree, *Jacaranda mimosifolia* D. Don (Bignoniaceae), which it appeared to prefer over lantana (Harley & Kassulke 1974b). Consequently, *T. validicornis* was not released in Australia.

12. Factors influencing biocontrol of lantana

Despite a century of research into the biological control of lantana, albeit sporadically, and the release of 41 agents worldwide, lantana is still not under adequate control. Landholders in most areas continue to rely heavily on conventional non-biological control methods.

In many instances where biocontrol is not working, agents have not established; but in most situations, agents have established but are not causing significant damage to the weed. Six factors have been suggested as influencing successful biocontrol of lantana (Broughton 2000a; Day & Neser 2000):

- the *Lantana* species from which potential agents were collected;
- the variety of the target weedy lantana;
- climatic and geographical distribution of lantana;
- plant biology and ecology;
- release techniques or strategies; and
- parasitism.

These factors will now be discussed. Figure 76 highlights the steps of a biological control of weeds program and details possible reasons that agents are rejected or, if accepted, are not successful in establishing and controlling the weed.

12.1 Taxonomy

Sheppard (1992) suggests that genetically variable weeds are more difficult to control through biological means than weeds that are genetically homogeneous. In genetically variable weeds, varieties may differ in their suitability to particular biocontrol agents. If this statement holds true, then the hybrid nature of lantana naturalised throughout the tropics poses major challenges for biological control programs. As the weedy taxa of lantana are not indigenous anywhere, the problem is to identify the most suitable *Lantana* species on which to concentrate exploratory efforts in the natural range (Day & Neser 2000).

In most biocontrol programs, potential agents of a particular weed are found on the same species in its 'natural range' and are therefore suited to the same plant in its weedy environment. Potential agents collected from species in their native range, other than that of their target host, may not be adapted to the new host and therefore fail to establish (Day & Neser 2000). Biocontrol agents collected from different *L. camara* varieties or other species in the genus may all be considered 'new associations' when deployed against lantana taxa in their naturalised range. Consequently, the interactions between various natural enemies and the different lantana varieties can be complex and difficult to predict (Baars & Neser 1999).

Several authors have argued that new associations are generally more effective as biological control agents than long-established associations where the host plant has developed some resistance to the enemy (Hokkanen & Pimentel 1984; Sheppard 1992). Based on this reasoning, lantana should be easier to control as a result of its hybrid nature and not more difficult. However, despite a long history of releasing agents, lantana is clearly not under adequate biological control (Day & Neser 2000).

The 'new association argument', as it pertains to weed biocontrol programs, has been disputed by several authors (Goeden & Kok 1986; Simberloff & Stiling 1996). Myers *et al*. (1989) believe that plants respond to insect attack, not by developing defensive mechanisms as suggested by Hokkanen and Pimentel (1984), but by reacting to damage by producing more shoots and vegetative material. Agents should be collected from the target species where possible,

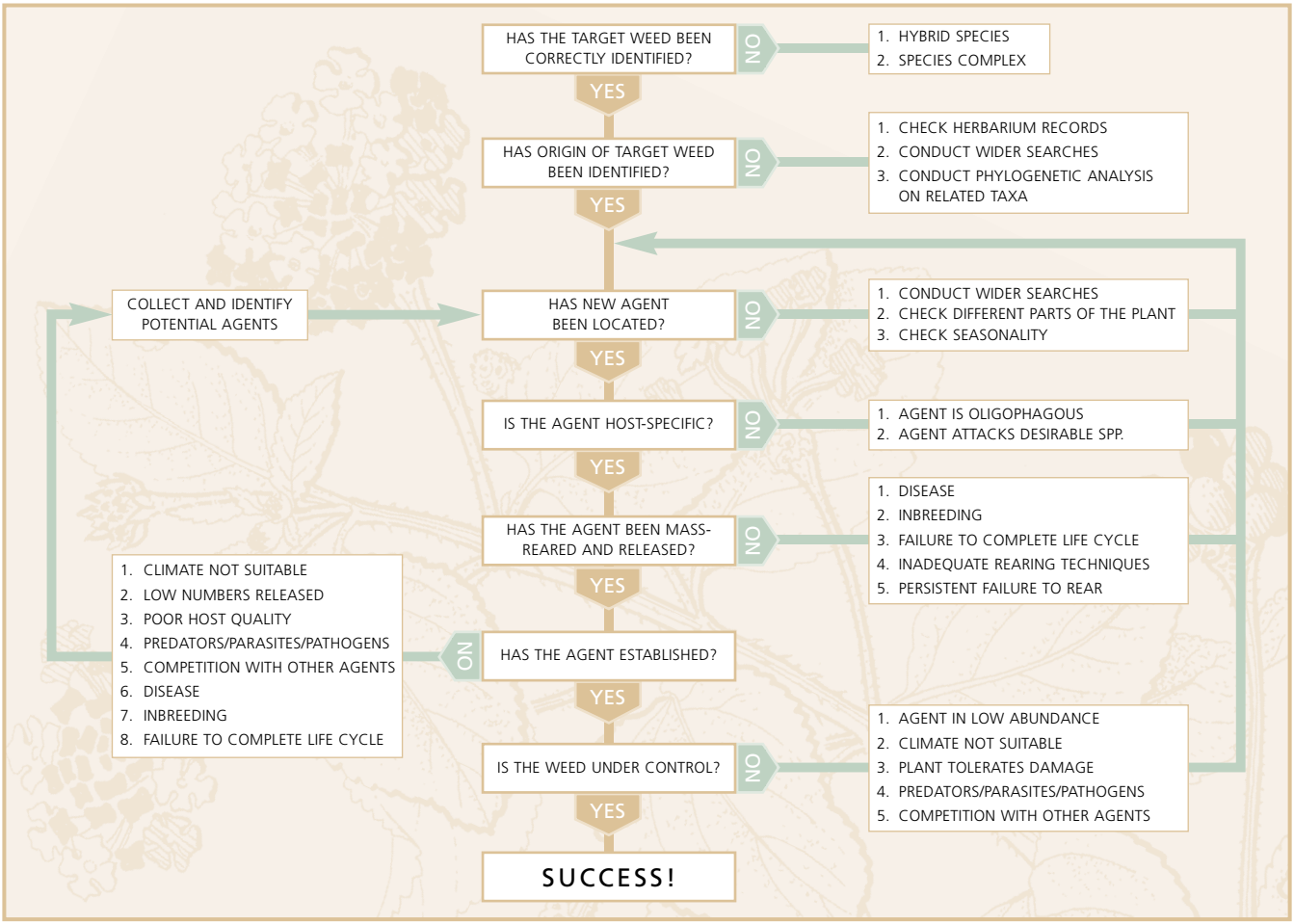


Figure 76.
Algorithm of a typical biological control program, and possible reasons that potential agents are not successful.

as the insect would be better adapted to the host. Other plant species may not have all the necessary nutrients for insects to develop, survive and produce fecund adults and thus to build up into large populations, or such plants may contain chemicals detrimental to the insect (Corbet 1985). In addition, these 'new association' plant species may be fed upon in cages in a laboratory, but may not be recognised as potential hosts by the agent in the field (Day & Neser 2000).

The importance of the identity of the host *Lantana* species, when searching for potential biocontrol agents, is highlighted by the observation that different *Lantana* species are known to have different assemblages of phytophagous fauna associated with them. In Mexico and US, only four species out of 261 insect and mite species identified, were common to all four species of *Lantana* sampled (*L. camara*, *L. urticifolia*, *L. urticoides* and *L. hirsuta*). Only 15 insect and mite species were common to three of the four *Lantana* species, while 24 insect and mite species were common to two of the four (Palmer & Pullen 1995).

Surveys by Winder and Harley (1983) in Brazil found that none of the 345 insect species collected from the four species of *Lantana* surveyed (*L. tiliifolia* and *L. glutinosa* (section *Camara*) and *L. fucata* and *L. undulata* (section *Calliorheas*)), were common to all four species. Only 25 species (8%) of the 335 insect species found on the two *Lantana* species in section *Camara* in Brazil were common to both. These observations are even more interesting given that Sanders (1998, pers. comm.) considers that *L. tiliifolia* and *L. glutinosa* are synonymous subspecies of *L. urticifolia*, suggesting that more research is needed into the taxonomy of the group to avoid collecting from inappropriate species.

When considering all insect and mite species collected from the various species of *Lantana* from South America to North America and the Caribbean, only 19 species (4%) are common to both regions and only 68 (12%) occur on more than one lantana species (Winder & Harley 1983; Palmer & Pullen 1995). However, the surveys sampled some *Lantana* species more often than others, so uncommon insects occurring on the less sampled species may have been missed.

With each species of *Lantana* having its own associated fauna, it appears that potential agents should be collected from the most closely related *Lantana* species to the taxa found in the target country. However, little is known of the relationship between the various *Lantana* taxa in different countries and their affinity with American varieties.

Work undertaken by Scott (1998) has indicated that the pink-flowering taxa from Australia, Fiji and Vanuatu are genetically more similar to each other than those taxa from other regions such as Hawaii and the Solomon Islands. He identified similarities between the common pink-flowering taxa in Australia, Fiji and Vanuatu and *L. urticifolia* from Mexico and suggested that this species may have been the main progenitor of the varieties common in the three countries. In addition, Munir (1996) suggested that *L. camara* from Australia had a close affinity to *Lantana moritziana* Otto & Dietrich, a species that Sanders considers a synonym of *L. urticifolia*. More recently in 2002, Sanders used morphological characteristics to identify over 50 lantana specimens representing five varieties from Australia as *L. urticifolia* x *L. camara*. These identifications support the DNA studies undertaken by Scott (1998). Previously, lantana in Australia and elsewhere outside the New World were thought to be *L. camara*.

The studies by Scott (1998) showed that the taxa from the Solomon Islands were very similar genetically to those from Maui, Hawaii. Six years earlier, Harley (1992) predicted this relationship based solely on morphological features. Using the key devised by Smith and Smith (1982), he identified taxa from Vanuatu and Fiji to be dominated by the Australian 'common pink' and 'common pink-edged red' (Fiji only). In contrast, he recognised taxa in the Solomons as being mostly the 'Hawaiian pink' variety.

Apart from the DNA studies performed on the lantana from Australia, Vanuatu, Fiji, Hawaii and the Solomons, little is known of the relationship between naturalised varieties in other countries and the American taxa. It is believed that Papua New Guinea's lantana taxa are related to taxa from the Philippines and Malaysia and are different from the taxa found in Australia (Waterhouse 1970). The lantana occurring in Africa is thought to be unique (Wells & Stirton 1988), although recently several varieties were identified as being similar to those occurring in Australia (Sanders BRIT, pers. comm.).

Past collections of biological control agents in Brazil and Mexico have been conducted from a number of *Lantana* species, with mixed success in control campaigns. Only two agents out of eight introduced from Brazil, where *L. tiliifolia* was the main host plant, established in Australia. In contrast, 12 of the 18 agents collected from Central America, Mexico and the Caribbean where *L. urticifolia* was the predominant host, established (Day & Neser 2000). Similar analysis for other regions such as South Africa or Hawaii have not been conducted, as the identity of lantana has not been studied in as much detail. In addition, many agents in South Africa were only released in small numbers and this may be more significant in determining lack of establishment success than differences in host variety (Cilliers & Neser 1991).

Given the problems with collecting potential agents from the most closely related species of *Lantana* and how lantana from each country may have different affinities, an alternative solution would be to collect potential agents found to occur naturally on a number of species of *Lantana* in their native range. The rationale behind this is that insects found on several species (oligophagous insects) may have a broad host range and develop on lantana varieties in different target countries. Eighteen of the 41 introduced agents were found on three or more species of lantana in their native range. Of these, 15 (83%) established. In Australia, 11 out of 13 agents in this category, successfully established. In comparison, 14 introduced agents were collected from one or two lantana species and only five (36%) established. Only two out of 12 agents (17%) found on only one or two lantana species in their native range established in Australia. *Teleonemia scrupulosa* that has been collected from six species of lantana and can develop on several closely related genera such as *Lippia* established in 29 of the 31 countries in which it was introduced. *Caly- comyza lantana* and *Hypena laceratalis* that have hosts in both the sections *Camara* and *Calliorheas* have established in all 15 countries in which they were introduced (Table 4). The host plants of several biological control agents could not be determined, while field establishment of other agents have not been confirmed.

The main problem with selecting agents that have a broad enough host range to accept several lantana varieties in a target country is that they may not be sufficiently host-specific to lantana for release in some countries. Two examples occur in South Africa where the stem-sucking bug *Aconophora compressa* and the leaf-feeding beetle *Omophoita albicollis*, collected from several lantana species in their native range (Palmer & Pullen 1995), attacked native species of *Lantana*, *Lippia* and *Phyla* in host-specificity

experiments. Consequently laboratory cultures in South Africa were destroyed and the insects were not released (Baars & Neser 1999).

These analyses, together with the DNA studies and the taxonomic findings, suggest that future collections of potential agents for release, in Australia, Fiji and Vanuatu at least, would have a greater chance of establishment if collected from *L. urticifolia*. The parentage of lantana taxa naturalised in South Africa, India and many other countries is less clear. More work is needed to determine the relationships of naturalised lantana in these countries with *Lantana* spp. in their native range. Without such information, it would be difficult to select and predict the successful establishment of agents in these regions.

12.2 Varietal differences

There are over 650 named varieties of lantana worldwide (Howard 1969), with the different varieties possibly having different progenitors (Scott 1998). Given that the different species of lantana have differing assemblages of insects associated with them in their native range, it is not surprising that some agents have been reported to show preference for, or perform better on, some varieties than others (Diatloff & Haseler 1965; Harley & Kassulke 1971; Harley *et al*. 1979; Winder 1984). *Plagiohammus spinipennis*, *Eutreta xanthochaeta* and *Strymon bazochii* have established and are widespread in Hawaii; all three have failed to establish in Australia, despite several attempts. As discussed earlier, *Lantana* in Hawaii may have different progenitors to that in Australia and other places, and this may at least partly explain different establishment success.

Even within a country, agents have shown differences in their preference for, or performance on, particular varieties. Ten of the 41 agents introduced to control lantana have shown some degree of preference for certain varieties (Table 3) within a country. Of these ten agents, six were collected from *L. tiliifolia* in Brazil and failed to establish. Three agents (*Aconophora compressa*, *Falconia intermedia* and *Teleonemia scrupulosa*) were collected from species other than *L. tiliifolia* and established. In some instances, preference was shown in the laboratory and as establishment was not successful, comparative assessment in the field could not be conducted. Conversely, of the agents that did not show any preference to one or more lantana varieties, only one (*Teleonemia harleyi* which was released in low numbers) did not establish.

Most of the observations of agents showing preferences for one or more *Lantana* varieties were made in Australia (29 varieties) or South Africa (over 40 varieties). In Hawaii and the Solomons, most lantana infestations are attributed to only one *Lantana* variety and therefore preference by agents is not displayed nor expected. This is believed to be one of the reasons why biocontrol of lantana has been more successful in Hawaii than elsewhere (Harley 1973).

Insects are not the only agents to show preference for particular varieties. Many rusts are highly specific and will only attack certain varieties. *Prospodium tuberculatum* only affects the common pink-flowering taxa in Australia (Tomley 2000), while another rust, *Puccinia lantanae* Farlow, attacks the common pink-edged red flowering lantana (A. Tomley NRM, pers. comm.).

To complicate the problem of varieties further, the horticultural industry is producing more varieties for home gardens and landscaping. These varieties generally produce less seed, but can be propagated vegetatively. If these cultivated varieties hybridise with the naturalised varieties then new varieties are produced with an increase in genetic diversity, further

restricting the potential for successful biocontrol. If the vegetative reproductive capabilities of naturalised lantana are enhanced, it may prove very difficult to limit the future spread of the weed through biological means. In addition, fertile tetraploid or diploid forms are still grown in many developing countries, such as India (Ojha & Dayal 1992) and the Pacific Islands (Harley 1992).

The continuing introduction of new varieties is potentially most damaging on the island groups that are presently infested with only one or a few varieties, and therefore efforts should be made to eliminate any early infestations of new varieties in island groups.

To address the issue of varietal preference, preference and performance trials should be conducted on potential agents to determine:

- whether any local varieties can support populations of the agent; and, if so,
- which varieties are favoured by the agent.

Such studies will determine whether rearing and release programs are worth implementing in that country, and on which varieties releases should be conducted (Day & Neser 2000). As an example, *Charidotis pygmaea* was introduced into Australia to control *L. camara* and *L. montevidensis* in the early 1990s. Preference trials showed that the agent was incapable of sustaining populations on any *L. camara* taxa naturalised in Australia. However, populations could be sustained on *L. montevidensis*, which is also considered a weed. Consequently releases were conducted on this plant and not on *L. camara* (Day *et al*. 1999).

12.3 Climate

Climate is probably the single most important factor determining the distribution of insects and the effectiveness of biocontrol agents. Climate can have several direct physiological effects on biocontrol agents, the target plant and their interaction.

Temperature and photoperiod can affect host-location behaviour of adults (Papaj & Rausher 1983), while low temperatures may slow vital physiological processes, reduce the potential rate of population growth and induce diapause in some species. Low temperatures can lead to inactivity, making an insect more vulnerable to predation. An example of the effect of temperature is the behaviour of *Cactoblastis cactorum* Bergroth. This insect can control *Opuntia* spp. in Queensland, but is less effective in southern New South Wales and Victoria where it is considerably cooler (Hosking *et al*. 1988).

Rain can also have an important influence on the populations of introduced agents. Heavy rain adversely affects populations of the tingids, *Teleonemia scrupulosa* and *Leptobyrsa decora*, with young nymphs being washed from leaves (Khan 1945; Rao *et al*. 1971; Mishra & Sen-Sarma 1986; Sen-Sarma & Mishra 1986). Other factors such as wind and humidity are likely to have important physiological effects on agents being released (Denton *et al*. 1991; Baars & Neser 1999).

Lantana occupies a wide range of habitats over a broad geographical distribution in many countries where it has been introduced. Consequently, climatic conditions can vary widely throughout the naturalised range of lantana affecting the distribution of biocontrol agents (Figure 77). In Australia, lantana is found from tropical areas in far northern Queensland to temperate areas in southern NSW and only two agents, *Lantanophaga pusillidactyla* and

Ophiomyia lantanae are found in most areas. These two agents have established in almost every country to which they were introduced (Table 4).

More often agents are limited in their distribution. There are several biocontrol agents that currently occupy very restricted geographical ranges. *Leptobyrsa decora* and *Uroplata fulvopustulata* are only found in tropical north Queensland, while *Octotoma championi* occurs in temperate southern New South Wales and a few sites in the cooler more protected areas of the tablelands of north Queensland (Day *et al*. 2003). In addition, *T. scrupulosa* is often found in dry areas or on north-facing slopes but is rarely found on south-facing slopes or on lantana growing under canopy (Figure 78). There are some areas in Australia, particularly the more southern higher-altitude areas, where lantana grows very well and there are no agents present.

Similar observations have been reported in South Africa, Hawaii and Fiji. *Octotoma scabripennis* prefers the warm, moist coastal regions in South Africa than the drier inland areas. In Hawaii, *T. scrupulosa* and *L. decora* are found in the dry areas to the west but not in the cooler, wetter regions of the east. Similarly, on the main island of Fiji, Viti Levu, there are fewer species of control agents present in the cool eastern mountainous areas than in the warm, flat areas to the west.

The effect of climate can alter plant characteristics that would otherwise make it suitable for natural enemies. Frosts or seasonally dry conditions cause defoliation of plants making them unsuitable for leaf-feeding insects. Consequently, leaf-feeding insects are more effective as control agents in warm, moist sites where lantana retains foliage all year round (Day & Neser 2000). Dry conditions can result in fewer succulent new shoots, and in Hawaii, stem-boring insects such as *P. spinipennis* have much higher mortality at drier sites (Harley & Kunimoto 1969).

Not only do insect populations vary spatially and temporally according to climatic conditions, but the susceptibility of lantana to damage caused by these insects appears to be climatically dependent. Successful control of lantana has been reported in drier areas of some countries, where the combined stresses of drought and large populations of *T. scrupulosa* and other agents have been sufficient to kill mature plants (Swezey 1924; Fullaway 1959; Andres & Goeden 1971; Willson 1985). Likewise, lantana growing beneath established pine plantations in Fiji has been largely controlled through the damage caused by *U. girardi* in combination with reduced vigour associated with low light conditions (S.N. Lal MAFF, pers. comm.).

Perennial plants such as lantana are rarely killed through damage caused by defoliating insects (Harris 1971; Crawley 1989). There are many cases documenting agents such as *T. scrupulosa*, *U. girardi* and *O. scabripennis* causing the defoliation of lantana plants, only to have the plant regrow once the insect populations have diminished (Greathead 1968; Harley *et al*. 1979; Muniappan & Viraktamath 1986; Baars & Neser 1999; Day *et al*. 2003).

As a result of the direct and indirect effects of climate on biocontrol agents, it is important to recognise local conditions as being fundamental to the successful establishment of prospective biocontrol agents. Potential agents should be collected from sites in their native range that closely resemble the areas in which they are to be released. Many species have been observed to occupy limited geographical or climatic ranges in their native range (e.g.*Uroplata fulvopustulata* (Diatloff 1975); fungal pathogens (Tomley & Evans 1992);

and *U. lantanae* (Winder 1984)). As lantana is frequently widespread and is not separated by major geographical barriers in its native range, it is probable that these species are constrained to their geographic ranges by climate. If the climate in the naturalised range of lantana is greatly different to that where the agents occur naturally, it is less likely that they will establish successfully (Sutherst *et al*. 1999).

Furthermore, selecting agents from eco-climatically similar regions may be important for more widespread agents. It is thought that widely spread insect species often comprise a number of strains, which are variously adapted to the local conditions in which they occur (Simmonds 1963; Messenger & van der Bosh 1971; Frick & Johnson 1972; Sands & Harley 1980; Neser & Cilliers 1989). Consequently, different strains within an insect species may mean that if collections are not conducted throughout its range, it may not establish in all areas of the naturalised range. This hypothesis remains to be critically tested.

In the past, different strains of previously introduced lantana agents have been released in an attempt to broaden their ecological preferences (Haseler 1966; Cilliers & Neser 1991). In these instances the new strains were released into areas already containing other strains. Neither the successful integration of new strains into the area, nor any resulting range expansions of the agent has ever been demonstrated. Releases of new strains should be made either into regions not yet containing strains of the agent, or alternatively at a time that immediately precedes a seasonal population increase of the agent. These techniques would enable the new strains to build up in numbers, without the new genetic material being diluted by the strains already present. The effectiveness of introducing new strains of already existing agents is difficult to measure unless the incorporation of new genetic material into the population can be monitored (Neser & Cilliers 1989).

Macroclimate matching of potential release sites in the naturalised range with the collection area of the agent can be achieved using climatic modelling computer programs

Figure 77.
Insect abundance varies with climate: (a) Lantana is undamaged in cool, high altitude areas (Gibraltar Range National Park, west of Grafton, NSW); (b) Lantana is attacked by *Octotoma scabripennis* in warm, low coastal areas (Grafton, NSW, Australia).

such as CLIMEX (Sutherst *et al*. 1999). These programs can predict which areas of the naturalised range are eco-climatically similar to the agent's native range and hence suitable areas for introduction (Day & Hannan-Jones 1999). A major limitation with CLIMEX is that it is only a guide to general areas that may be suitable and particular release sites within an area may vary in their suitability for the agent. Closely matching potential release locations with sites from which the insects were collected or using knowledge of the agents' full habitat requirements would improve the chance of establishment. Unfortunately, we rarely know these requirements. Even so, releasing large numbers of agents in a range of sites within the eco-climatically suitable area may increase the chance of establishment in at least one site.

Another method suggested to overcome problems with climate, is to artificially select laboratory strains of agents to improve their resistance to environmental extremes. Laboratory ecotypes can display acclimatisation to temperature, light and humidity (Mackauer 1980) and establishment success may potentially be improved if individuals are artificially selected in the laboratory for conditions that mimic the local environment (Debach 1958). However, the usefulness of this technique has been refuted (Simmonds 1963; Messenger & van der Bosh 1971).

There are two difficulties that restrict the practical value of laboratory selection procedures to produce new climatically adapted strains of agents. The first is the adequate definition of the qualities required. The second is that deliberate selection for required characteristics is likely to be accompanied by involuntary selection for associated characteristics that could be disadvantageous in nature (Wilson 1960). Selective breeding involves the restriction of variability, and adaptation and adaptability are antagonistic (Simmonds 1963). This technique has so far not been shown to be practical (Messenger & van der Bosh 1971). However, it is useful to conduct trials with insects reared in the lab under different temperature regimes to determine developmental thresholds and to determine development parameters that could prove useful in selecting possible release sites and in interpreting field data (C. Clech & M. Day, unpublished data).

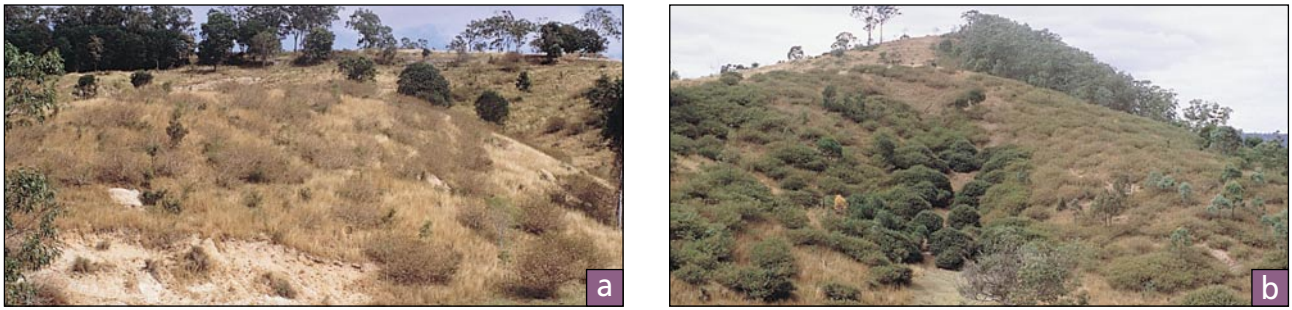


Figure 78.
Aspect can affect the abundance of *Teleonemia scrupulosa*: (a) on a hot, dry northern slope; (b) on a cool southern slope (Kooralgin, Queensland, Australia).

Genetic variability in the introduced population should be maximised to enhance its potential for acclimatisation. While a strain may not be perfectly pre-adapted, it may successfully establish provided that it contains the essential genetic diversity to enable it to adapt to local conditions. Maximising genetic diversity is achieved through:

- collecting a large sample of colony founders from the source population;
- preventing bottlenecks occurring in laboratory populations; and
- avoiding artificial selective changes through rearing conditions occurring in laboratory cultures.

Teleonemia scrupulosa is one agent that may have suffered as a result of founder effects. The original Hawaiian collections were made in a limited area of Mexico. Subsequently each country that imported the species did so from another country utilising it, rather than from the native range of lantana. As a result, each time collections are made for distribution to another country, the new *T. scrupulosa* population undergoes a further 'founder event' as only a small random subset of the total genetic material is incorporated into the new population. The reduction in diversity continues to occur when further subsets of this new population are sent to other areas. For example, the Mexican material present on Ascension Island was brought there via Hawaii, Fiji, Australia, India and St Helena (Julien & Griffiths 1998).

While this is an extreme example, it highlights an important threat to potentially useful biocontrol agents. Fortunately, *T. scrupulosa* is effectively controlling lantana in Ascension Island (Julien & Griffiths 1998) and there do not appear to be any obvious problems due to inbreeding. However, Harley & Kassulke (1971) suggested that varietal preferences of *T. scrupulosa* and its susceptibility to cold or wet weather may be a result of the limited genetic variation within naturalised strains of the species.

To overcome possible inbreeding, new strains of *T. scrupulosa* were collected in the 1950s and 1960s; they were imported into many countries that already contained the Mexican-Hawaiian strain (Krauss 1962; Harley & Kassulke 1971; Harley 1973). However, no studies were conducted to examine the incorporation of this new genetic material into existing populations and it is not known whether these new strains successfully established. No improvements were noticed in the control exerted by the bug following the introduction of these new strains.

There are several anecdotal reports of agents colonising regions in which they once failed to establish. These have been interpreted as evidence for post-release adaptation or acclimatisation. Examples include *C. lantanae* in Australia (Taylor 1989) and South Africa (Cilliers & Neser 1991) and the hispines *O. scabripennis* and *U. girardi* in Australia (Taylor 1989). However, it is difficult to distinguish such 'range expansions' from other confounding processes such as exponential population increases in areas that were always inhabited, but at undetectable levels (Vitelli *et al*. 1996; Mo *et al*. 2000). There is currently no experimental evidence for climatic range expansions occurring in lantana insect populations as a result of post-release adaptations.

12.4 Plant biology and ecology

Leaf-feeding insects have been able to control many weeds, or at least severely retard plant growth and flowering, and thus limit the competitive ability of the weed and reduce its ability to spread. For example, *Cordia curassavica* (Jacquin) Roemer and Schultes (Ehretiaceae) in Malaysia and Mauritius is controlled by the chrysomelid *Metrogaleruca obscura* (Degeer) (Julien & Griffiths 1998).

However, leaf-feeding insects rarely kill perennial weeds. Over half of the agents released on lantana have been leaf-feeding insects and it is clear that they have not been able to control lantana successfully in many areas. In response to seasonal variation and plant quality, insect populations tend to increase during summer when plants are healthy and fall during winter when temperatures decrease and plants are often without leaves. Any damage that agents such as *Teleonemia scrupulosa*, *Octotoma scabripennis* or *Uroplata girardi* do to lantana is only on a seasonal basis and the plant can recover. Even in the absence of natural enemies, lantana has the ability to survive defoliation when stressed either as a result of the dry winter months and/or frost, and to re-shoot and flower following spring rains and warmer temperatures (Figure 79).

Some insects such as *O. scabripennis* and *U. girardi* can survive winter by diapausing. For many others such as the leaf-feeding and flower-feeding lepidoptera, there is no diapause stage. Consequently, in the spring when lantana plants begin to recover, many of the insects are present in only low numbers or they colonise plants from elsewhere. Populations of agents then slowly build up, and by late summer can reach levels that can severely damage plants. However, the damage is not sustained as insect numbers again begin to decrease with the onset of winter. Therefore, insect numbers tend to follow plant abundance and health, so control of the weed is not achieved because insect numbers are not maintained at levels high enough to damage the plant continually.

As a result of plant condition being linked to seasons and the ability for plants to recover from defoliation, it is unlikely that leaf-feeding agents will ever control lantana by themselves.

Seed-feeding and flower-feeding insects also have limited impact on lantana. An individual lantana plant has the ability to produce thousands of flowers and seeds each season. Although there have been several flower- and seed- feeding agents e.g. *Lantanophaga pusillidactyla*, *Epinotia lantana* and *Ophiomyia lantanae* released on lantana and damaging up to 80 per cent of flowers and/or fruit (Muniappan 1989), large amounts of viable seed can still be produced, especially

Figure 79.
Effect of season on lantana: (a) plants can become leafless in winter; (b) plants can recover and have healthy foliage after rain in summer (The Gap, Queensland, Australia).

early in the season when the insects have yet to build up into damaging populations. Birds and mammals feeding on the unaffected fruit disperse the seed, creating new infestations.

Only a few agents that attack the stems (for example *Aconophora compressa*, *Eutreta xanthochaeta* and *Plagiohammus spinipennis*) have been released on lantana, and they have established in limited areas (Julien & Griffiths 1998; Day *et al*. 2003). In addition, only one root-feeding agent, *Parevander xanthomelas* has been released on lantana. The advantage of utilising stem-boring or root-feeding agents is that they do not require the plant to be in leaf all year round. Stem-boring or root-feeding insects attack the carbohydrate reserves of a plant and disrupt translocation. They often have life histories where adults emerge in summer when there is fresh leaf growth upon which to feed while the larvae feed in the stems or on the roots, respectively, during winter when the plant can be devoid of leaves. Releasing both types of agents may overcome the problems that other agents face when lantana loses its leaves during dry spells.

Populations of most of the agents released on lantana appear to respond to the health of the plant, especially early in the growing season, rather than suppress the weed as in the case of other biocontrol of weed programs. Life histories of many of the established agents are such that they are not able to respond quickly enough when lantana recovers following rain and warm weather. This is particularly true of the leaf- and flower-feeding insects. To offset this rapid recovery of lantana, agents that have rapid population growth should be utilised.

As discussed earlier, three pathogens have been recently released on lantana: *Septoria* sp. in Hawaii; *Prospodium tuberculatum* in Australia; and *Mycovellosiella lantanae* in South Africa (Thomas & Ellison 2000; Tomley 2000; A. Den Breeÿen PPRI, pers. comm.). The advantages of using pathogens are that they have a short life-cycle, a high capacity to reproduce and disperse, and a resting stage to overcome unfavourable conditions. The impact of these three agents, and whether they can overcome the intricacies of lantana's biology is still to be determined.

12.5 Parasitism and predation

The importance of parasites and predators in reducing biocontrol agent populations has rarely been investigated but frequently alluded to as a cause of 'failure'. Newly introduced biocontrol agents may undergo rapid population explosions causing severe defoliation to the target weed, only to suffer a subsequent population crash after which the population never reaches the same size again (Fullaway 1959; Gardner & Davis 1982; Cilliers & Neser 1991; Denton *et al*. 1991). It has been suggested that seasonal changes in climate, or alternatively, reduced food supplies due to heavy defoliation, causes these reductions in agents' effectiveness in controlling weeds. However, it is expected that insect populations should be able to reach these initial levels again, provided climatic conditions are suitable and the weed has recovered from its attack. As this does not always occur, other factors are probably involved.

There are numerous anecdotal reports of parasites attacking lantana insects, particularly Lepidoptera and Diptera. *Autoplusia illustrata*, *Calycomyza lantanae*, *Eutreta xanthochaeta*, *Hypena laceratalis*, *Neogalea sunia*, *Octotoma scabripennis*, *Ophiomyia lantanae*, *Salbia haemorrhoidalis*, *Strymon bazochii* and *Uroplata girardi* have all experienced some parasitism in the field (Swezey 1924; Haseler 1963; Greathead 1971a; Harley & Kassulke 1974a; Diatloff 1976; Winder 1982; Waterhouse & Norris 1987; Duan *et al*. 1998; Baars & Neser 1999; Broughton 2001).

A series of studies undertaken by Duan and coworkers (Duan & Messing 1996; Duan, Purcell & Messing 1997; Duan, Ahmad, Joshi & Messing 1997; Duan *et al*. 1998) revealed that *E. xanthochaeta* was attacked by parasitoids introduced into Hawaii to combat fruit flies. However, parasitism rates in the wild were very low (Duan & Messing 1996) and the gall fly larvae experienced high levels of mortality from non-parasite-induced reasons (Duan *et al*. 1998). They concluded that the fruit fly parasitoid probably does not play a role in reducing or regulating populations of *E. xanthochaeta* because parasitism rates were independent of host density (Duan *et al*. 1998). In addition, the levels of parasitism of *P. spinipennis* in Hawaii varied between sites and accounted for only ten per cent of the overall mortality at the site with the highest parasitism rates (Harley & Kunimoto 1969).

As noted above, in Brazil levels of parasitism of *O. lantanae* varied from high to low (Winder 1982). The low numbers of *O. lantanae* in Brazil when compared to numbers in the exotic range could be attributed to parasitism in the native range keeping fly populations in check (Winder 1982). However, the potential importance of parasites was not substantiated with any experimental studies examining the actual degree to which parasitism limited population increase. In species with high fecundity and where there is high mortality associated with intraspecific competition for resources, an increase in parasitism is likely to have little impact on the numbers of larvae surviving to maturity. This is because those larvae that escape parasitism would have higher survival rates due to reduced competition. Parasitism is likely to have the greatest impact on populations in which the intrinsic reproductive potential of the species involved is the limiting factor affecting population expansion.

For many other species, there is either nothing recorded about their levels of parasitism (*Charidotis pygmaea*, *Diastema tigris*, *Ectaga garcia*, *Epinotia lantana*, *Lantanophaga pusillidactyla*), or the published literature contains conflicting statements regarding their susceptibility/resistance to parasites. A good example of the latter situation is *Teleonemia scrupulosa*. While tingids are believed to be almost free of parasites, even in their country of origin (Harley & Kassulke 1971, 1973), predation by *Germalus pacificus* and parasitism by an unidentified fungus have been implicated in mortality of the species in Fiji and India respectively (Simmonds 1929; Khan 1945).

The role of natural enemies in the regulation of insect populations is generally greater in areas where climate, edaphic and other factors favour a diverse and productive flora and fauna (Rabb 1971). Islands tend to have lower biodiversity than continental landmasses and the success of biocontrol of lantana reported from island areas may in part be due to the lower number of species of native parasites and predators found there. Species such as *Salibia haemorrhoidalis*, *Hypena laceratalis*, *Strymon bazochii* and *Eutreta xanthochaeta* that are subject to parasitism have either established on islands, but not elsewhere, or reached higher population densities on islands than on continental land masses (Julien & Griffiths 1998).

It is probable that parasitism has been used as an excuse for the failure of agents to control a weed or to build up to large numbers when no other explanation can be deduced. When agents are imported into countries for release, they usually undergo a quarantine period, when they are screened for parasites and diseases to ensure that they are introduced without their natural enemies (Buckingham 1992). In early biocontrol attempts, this method was not fully effective (Perkins & Swezey 1924) and may account for some parasites being introduced with biocontrol agents in their new environment and attacking them. The more likely situation, however, is that the parasites attacking agents in the introduced

country are native species that have either wide host ranges, or are associated with indigenous species closely related to the biocontrol agents. To overcome this possibility it has been suggested that we should avoid selecting agents in genera that have representatives native to the region of introduction (Harris 1980).

Lantana insects collected from the Americas are generally not closely related to species occurring in the Old World and those species apparently free of parasites in their native range are rarely parasitised in their new environment. Therefore, parasites and predators attacking biocontrol insects in their new environment are likely to be generalist species, making it difficult to predict which biocontrol agents are likely to be parasitised in the target country.

While the effect of parasites is little understood, the impact of diseases on agent populations is even more poorly known. Certainly, many species have been heavily attacked by disease while being cultured (Parham *et al*. 1956) and undetected pathogens may inadvertently be released with the insect (Allen 1980). The effects of both parasites and disease on biocontrol agents require further attention.

12.6 Release techniques

Some biocontrol agents of lantana have not established due, almost certainly, to either the release of insufficient numbers or the use of inappropriate release techniques. There are limited data available for earlier releases concerning the numbers of insects liberated and the release procedures used (Day & Neser 2000). More recently, data are available on release sites with respect to altitude, number of insects released, the use of cages (including size and material used), time of day and weather conditions at the time of release.

There are many recent papers proposing release methods to maximise establishment (for example Grevstad 1996; Memmott *et al*. 1996; Shea & Possingham 2000). Release techniques should be based on the agent's biology, behaviour and the most suitable life stage for release (Figure 80). For most agents, adults are the most appropriate, as they are more mobile than immatures and seek favourable feeding and/or oviposition sites (Day & Neser 2000). Immatures, on the other hand, are less mobile and their fate is often dependent on being released in suitable areas. Higher establishment rates were obtained when *Neogalea sunia* was released as adults compared with when larvae were used (Haseler 1963).

Figure 80.
Release methods: (a) cage (Monto, Queensland, Australia); (b) releasing adult *Aconophora compressa* on cut stems (Coleyville, Queensland, Australia); (c) releasing *Falconia intermedia* (South Africa).

Where insects have a long life cycle, or there is high mortality in either the prepupal or pupal stage, it is often more practical to release immatures. The cerambycid, *Plagiohammus spinipennis* failed to establish in most countries where it was released, and it is thought that this is due to its univoltine life cycle and high larval mortality (Harley & Kunimoto 1969; Waterhouse & Norris 1987). The stem-borer *Aerenicopsis championi* is also a univoltine insect and is difficult to rear in high numbers. The rearing method is labour intensive and there is high mortality in the pupal stage. The insect was first released as adults but now trials releasing large numbers of mature larvae placed in holes drilled in the stems of lantana have been conducted in Australia. The numbers released are critical as synchrony of adult emergence is vital for successful mating and establishment to occur. The stem-boring moth *Carmenta mimosa* Eichlin & Passoa, an agent for *Mimosa pigra* L. (Mimosaceae), was successfully released using this method (M. Day, pers. comm.).

Widely dispersing species such as some Lepidoptera can be released into field cages initially, to maximise mating success (Day & Neser 2000). While there is no experimental evidence that caged releases have achieved higher rates of establishment in any biocontrol agent, caged releases allow for a greater ease of finding any surviving individuals, eggs and/or larvae at the release sites (Day & McAndrew 2002). If insects cannot be found following open releases, it is difficult to state that establishment has failed, because the insect may be present at very low population densities. Many examples exist of insects which have not been observed in the field for several years before becoming sufficiently abundant to be seen some time later (McClay *et al.* 1990; McFadyen 1992; Mo *et al.* 2000). While it may be premature to infer establishment from the persistence of insects in cages soon after release, failure to establish is readily discerned in this way.

To overcome the problem of finding a mate when individuals are released in low numbers, previously mated adults can be used. Newly mated adults do not need to spend time finding a mate and have the potential to lay their full complement of eggs, other factors aside, in the most appropriate sites for oviposition and larval development. Grevstad (1996) found that successful establishment was significantly higher when releasing mated adults than when releasing unmated adults. While releasing mated adults may facilitate establishment, there is still the problem of detecting whether the insect has established until field populations are present in significant numbers.

The minimum number of individuals released to maximise the chance of establishment depends on the insect species. For many biocontrol agents, there is little information available to assist in determining the ideal number of individuals to release. Shea & Possingham (2000) suggest that in the early stages of a release program, a mixture of a few large releases and many smaller releases should be conducted. Releasing different numbers of individuals at many sites and monitoring their progress may determine an optimal release size. This means that subsequent releases could be made using the lowest number of individuals that achieve establishment, and may increase the total number of releases that can be achieved. For instance, if 1000 insects are being released at any one time, but only 250 individuals are needed to gain establishment, then releasing this smaller number at any one time would enable the insect to be released at four times as many sites.

Grevstad (1999) achieved complete establishment by releasing 540 individuals of the beetle *Galerucella pusilla* (Duft- schmidt) on purple loosestrife *Lythrum salicaria* L. (Lythraceae). Establishment was also achieved by releasing only 60 individuals

but there was a much lower success rate. Species, such as *Teleonemia scrupulosa*, which are highly fecund and have a relatively short generation time, has managed to establish in the field following the release of relatively few individuals (<200). Conversely, cerambycids require many more individuals to achieve establishment to ensure synchrony of emerging adults. For agents such as flower and seed feeders that react strongly to a variable environment, the insects rely on suitable oviposition sites being available and establishment is more likely to succeed when many small releases over a period of time are conducted rather than a single large release (Grevstad 1996).

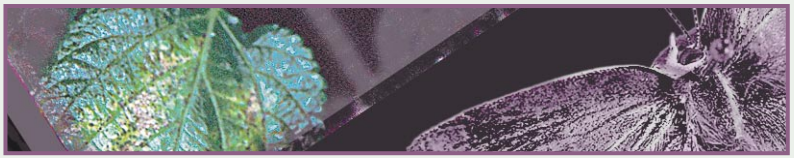
A less apparent reason for poor establishment is the quality of food available. Plants that are stressed through drought or frost are obviously less healthy but some plants may lack sufficient nutrients that are vital for oviposition and development of young. A well-documented case concerns the beetle *Cyrtobagous salviniae* Calder & Sands that was released to control *Salvinia molesta* D.S. Mitchell (Salviniaceae) in Australia and elsewhere. Attempts to get the beetle to establish in lagoons on the Sepik River, Papua New Guinea (PNG) failed until bags of fertiliser were dumped into the release site improving the quality of plants. Consequently the insect established at the site and was later spread to other lagoons. This action ultimately led to the successful control of salvinia in PNG (Room & Thomas 1985).

Competition among introduced agents has been proposed as one factor leading to the failure of agents to establish and or control a weed species (McEvoy 2002). Where agents have established but failed to substantially reduce the abundance or biomass of the target weed, a usual response is to seek another agent, rather than determine why the agent remains at low levels of abundance or why the damage inflicted fails to have a more substantial effect. If initial introductions result in some established agents, subsequent introductions may still fail for various reasons as expressed in Figure 76. This will lead to the erroneous proposition that failure to establish is causally related to the number of species successfully introduced, particularly if the weed is not reduced in abundance.

New agents for biocontrol are generally sought because the current agents are at low levels of abundance and/or having a minimal impact on the target weed. It is difficult to envisage how current agents, occurring at very low levels of abundance, either prevent the new agent from establishing or limits its abundance once established. The negative correlation between failure to establish (or control) versus number of species introduced is likely to be due to one or more of the many factors that can lead to failure (Figure 76) rather than to competition *per se*. Crawley (1986) suggested that the factors that limit the effectiveness of biocontrol agents (some were limited by more than one factor) were climate (44% of cases), predators (22%), parasitoids (11%), disease (8%), host incompatibility (33%) and competition (12%). Only controlled exclusion experiments at many sites will help resolve this issue (Denno *et al*. 1995).

Introduction of additional agents is likely to continue in classic biological control campaigns. Such programs should strive to experimentally test competition impacts. Releasing new agents at sites with and without existing agents and controlling for other establishment factors will determine the influence of competition on establishment. Using insecticides, herbicides and fertilizer experimentally to manipulate the plant-herbivore-predator interactions would help determine the influence of these factors on both agent establishment and weed control.

Part III: Future Directions



Part III. Future Directions

13. Control and management

For most countries where lantana is a problem, increasing the species of biological control agents would improve control. There are many countries where lantana is present, but not any of the biocontrol agents (Table 5), while many other countries have released only a few agents of the 41 that have been tried (Table 4).

Country	Potential Weediness
American Samoa	Unknown
Angola	High
Azores Is. (Portugal)	Unknown
Cambodia	High
Cameroon	High
Canary Is. (Spain)	Unknown
China	Moderate
Cote d'Ivoire	High
Democratic Republic of Congo	High
Ethiopia	Moderate
French Polynesia	High
Futuna Is. & Wallis Is.	Unknown
Galapagos Is. (Ecuador)	Unknown
Guinea	Moderate
Kiribati	Unknown
Liberia	Moderate
Madeira Is. (Portugal)	Unknown
Mozambique	High
Nauru	Unknown
Nigeria	High
Reunion Is. (France)	Unknown
Saudi Arabia	Low
Senegal	Low
Seychelles Is.	Unknown
Spain	Low
Turkey	Low
Tuvalu	Unknown

Based on EI values in Appendix courtesy of P. Mackey, DNRM 2002.

Table 5.
Countries that have lantana, and no recorded control agents.

Teleonemia scrupulosa, *Octotoma scabripennis*, *Uroplata girardi* and *Ophiomyia lantanae* have proved to be damaging agents in many countries, and could be introduced where they are not already present. *Calycomyza lantanae*, *Hypena laceratalis*, *Epinotia lantana* and *Lantanophaga pusillidactyla* are not as damaging as the aforementioned agents, but could assist in controlling lantana in countries where only a few agents are present. *Aconophora compressa* and *Leptobyrsa decora* are damaging but appear to have specialised climatic requirements. In addition, there are three pathogens that have been recently released that could be tried in other countries once their impact on lantana has been assessed in their introduced country. All the above agents have been found to be generally host-specific but some host-specificity testing, especially of plant species peculiar to particular countries is recommended prior to the importation of any agent. This will ensure that the agent is not a risk to valuable plant species.

For countries such as Australia and South Africa that have imported many biocontrol agents, new and more effective agents need to be located in their host range and trialed. Particular characteristics worth considering when importing new agents are: the agents' ability to develop on the lantana variety being targeted; agents being adapted to the climate in which it will be released; and agents that attack the parts of the plant such as roots and stems, upon which few agents have been released.

As biological control research is a long-term proposition, more immediate control solutions need to be developed. At present there is little information on the integrated control and large-scale, long-term management of lantana. Potential biocontrol agents and the possibilities of integrated control will now be discussed.

13.1 Selecting future lantana biological control agents

There are many papers published on what makes a good biological control agent and some authors have offered a method for assessing agents or conducting exploration (Harris 1973; Goeden 1983; Hokkanen & Pimentel 1984; Wapshere *et al*. 1989). Such methods consider guild, life history and behaviour of the agent and how they affect the plant in terms of biomass removal or the reduction of seed set (Harris 1973; Winder & Harley 1982). While these papers offer a guide, the intrinsic nature of the target weed will limit the effectiveness of any system. In addition, it is difficult to predict how a potential agent will perform once released. Factors such as climate, habitat, altitude and the impact of predators and/or parasitoids are all influential in determining the effectiveness of an agent (Wapshere *et al*. 1989).

In Koebele's original insect collections for release in Hawaii, he concentrated his exploration efforts on species that attack the fruits and/or flowers of lantana (Koebele 1903). Subsequently, the majority of the initial insects sent to Hawaii, were flower feeders on the premise that once infestations were physically removed, flower and seed feeders would contribute to the low establishment rates experienced by lantana. Harley (1984) recognises three situations where the suppression of reproduction is important for the control of woody weeds, namely when:

- the weed occupies only a portion of its potential range and is spreading by seed;
- there is a conflict of interest and existing stands are of some benefit, but an increase in their density is undesirable; and
- a weed may be easily killed by herbicide application but control is short-lived because of re-infestation by seeds.

For lantana, the importance of the situations outlined by Harley (1984) is less relevant. In most countries, lantana has been established for a long period of time and lantana has now probably reached its potential geographic range. In addition, while lantana does have minor uses in some countries, it is generally considered a pest and the removal of existing stands is desired. Finally, lantana infestations commonly occur in inaccessible areas where the costs of conventional control exceed the value of the land. Because lantana has a low germination rate, regeneration by seed following herbicide applications is of minor importance, compared to regrowth from basal shoots. Therefore suppressing flowering is less important than reducing the regrowth from shoots. In this instance, the introduction of tip- or shoot-feeding insects may be more desirable.

The effect of flower-feeding and fruit-feeding insects on seed loss appears to be limited because insect numbers do not have an impact during high-flowering periods. Flower- and fruit-feeders are satiated when flowers and/or fruit are abundant, resulting in many seeds being unaffected. Conversely, seed losses by the agents are greatest when flowers and/or fruit are scarce (Crawley 1989). Very large numbers of flowers and fruit are produced simultaneously over large areas in response to rainfall and this food supply is generally short-lived, with insufficient time for such agents to build up into large and damaging numbers. Thus, they may be less useful as biocontrol agents than earlier anticipated.

Studies in Guam indicate that leaf-feeding insects account for greater reductions in seed-set than the flower-feeders and seed-feeders (Muniappan 1996). Also, there are many native insects that feed occasionally on lantana flowers and do not appear to impact heavily on seed production (Day *et al*. 2003). However, flower-feeding and fruit-feeding

insects such as *Epinotia lantana*, *Lantanophaga pusillidactyla* and *Ophiomyia lantanae* have been effective in a few regions such as Guam and some islands of Micronesia (Denton *et al*. 1991).

Several authors have suggested that the control of perennial weeds such as lantana cannot be solely achieved through the release of flower-feeding and seed-feeding insects, as existing stands of the weed are not affected (Crawley 1989; Hoffmann & Moran 1998) and the prime concern in the control of any perennial weed is the destruction of existing plants (Harris 1971). Defoliating insects have proved very useful on a number of weeds e.g. *Zygogramma bicolorata* Pallister on *Parthenium hysterophorus* L. (Aster- aceae) (Dhileepan *et al*. 2000), but leaf-feeders are limited in their impact on lantana. Seasonal changes in both climate and the condition of lantana mean that few leaf-feeding agents are likely to be able to sustain large populations all year round sufficient to kill plants or control the weed.

While it is easy to show that herbivorous insects affect plant performance, it is more difficult to demonstrate that insect herbivory affects plant population dynamics (Crawley 1989). Lantana infestations have decreased in size in certain countries, following the release of biocontrol agents, but only in dry areas, where regular droughts place additional pressure on the plant. In wetter regions, continuous feeding pressure is required for lantana to be killed. Therefore, if lantana is to be controlled, this additional pressure must be applied through the introduction of new and more effective agents.

There have been many surveys conducted in the Americas for biological control agents for lantana (for example Koebele 1903; Krauss 1953b; Winder & Harley 1983; Palmer & Pullen 1995). The number of insects and mites from each of the major guilds found on lantana from these surveys is shown in Figure 81 which also shows the number of agents that have been released and established. Leaf-feeding insects make up the majority of insects released while other guilds are largely untried.

It is important to find new agents that show tolerance for cooler climates and higher rainfall, as well as those able to tolerate heatwaves and droughts. There is also a current shift in the selection of agents, with insects that form galls, stem-borers, root-feeders and pathogens preferred over leaf-feeding insects. This is because the activity of these agents is independent of the condition of the foliage, have life cycles that are more suitable to seasonal variation and the condition of the plant or, in the case with pathogens, have very short generation times. The stem-boring and root-feeding insects are able to attack the actual stores of carbohydrates, reducing the ability of the plant to recover from heavy attack. Unfortunately, few insects have been found to attack lantana stems or roots in the Americas (Koebele 1903; Krauss 1953a; Winder & Harley 1983; Palmer & Pullen 1995). *Parevander xanthomelas* (only released in Hawaii) and *Longitarsus* sp. that is currently being studied in South Africa (A. Urban PPRI, pers. comm.) both attack the roots of lantana.

There have been two stem-boring beetles introduced to control lantana, *Plagiohammus spinipennis* and *Aerenicopsis championi*, but both have proved difficult to establish. One factor limiting the ease with which these species are established is their long lifecycle. Cerambycid borers are typically univoltine and so are difficult to rear in large numbers in the insectary. Thus for the first year in the field, the population is limited by the number of insects released. This long period of small population size, coupled with high mortality of larvae, makes the insect highly prone to dying out, due to stochastic events or where females fail to find a mate. Never-

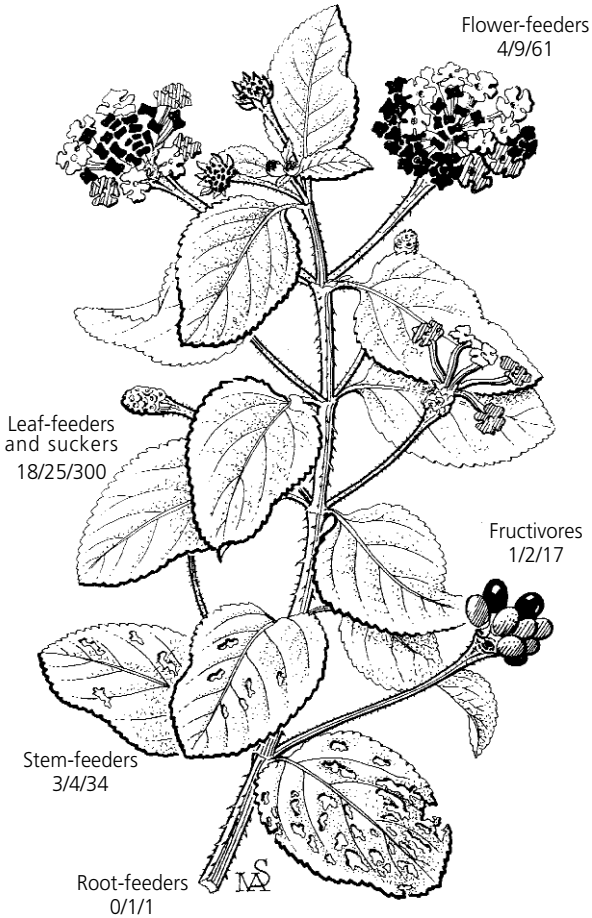


Figure 81.
The number of agents (1) established and (2) released on each part of lantana; and (3) the number of insects found attacking each part of lantana in the native range

Based on surveys by Winder & Harley 1983; Palmer & Pullen 1995.

Drawing courtesy of Queensland Department of Natural Resources and Mines, (DNRM).

theless, *P. spinipennis* has proved to be a useful agent in Hawaii and it would be a valuable addition to the agents present in other countries, if a more efficient rearing method could be developed.

Only one gall-forming insect *Eutreta xanthochaeta* has been released, and it has only established in Hawaii. *Aceria lantanae* Cook, which is being studied in South Africa (Baars & Neser 1999) also forms galls. Gall-forming agents can act as physiological sinks and can deplete the plant of important food reserves, causing the plant to die or become stunted and cease flowering. Gall-forming agents have been used successfully in other biocontrol of weed programs, for example *Cecidochares connexa* (Macquart) (Tephritidae) on *Chromolaena odorata* (L.) King and Robinson (Asteraceae). Other insects that could be tried include those that diapause so there is a ready population once the growing season commences. The hispine beetles *Octotoma* spp. and *Uroplata* spp. all diapause and can cause seasonal damage to lantana. Further research information is required for many species. In particular, the tingids show great potential as agents but apart from *Teleonemia scrupulosa*, there have been problems achieving establishment of other species in the genus.

The use of pathogens in weed biological control is a fairly recent development. Pathogens have only been utilised as potential biocontrol agents in the last ten years or so. Previously, they have been under-utilised due to uncertainty regarding host specificity testing. Screening methods were considered less satisfactory for pathogens compared with insects (Willson 1993). In addition, pathogens were thought to change host preferences in their new environments (Waage & Greathead 1988). However, some pathogens, particularly rusts, are generally more specific than insects, attacking only particular varieties of a plant species (Evans 1995).

Harris (1973) suggests that we should be utilising more pathogens in biocontrol programs, because half the losses caused by pests in crops are the result of diseases. Field evidence has shown that pathogens that have been utilised as biocontrol agents can be very damaging to weeds. Several pathogens have been used successfully in Australia such as *Maravalia cryptostegiae* (Cummins) Ono on rubber vine *Cryptostegia grandiflora* (Roxburgh) Brown (Asclepiadaceae), *Puccinia abrupta* Dietz & Holway var. *partheniicola* (Jackson) Parmalee on *Parthenium hysterophorus* (Asteraceae), and *Puccinia xanthii* Schweinitz on Bathurst burr *Xanthium strumarium* L. (Asteraceae) (Julien & Griffiths 1998).

Pathogens appear to have very specific climatic requirements in their native range (Barreto *et al*. 1995), but will develop on cool, moist sites for which there are currently few biocontrol agents. Surveys carried out in Brazil have identified several species of fungi that are capable of causing significant damage to lantana (Tomley & Evans 1992; Barreto *et al*. 1995). These appear to be highly host-specific, with damage not seen on very closely related species of *Lantana* (Barreto *et al*. 1995); therefore they may not attack all of the naturalised varieties of lantana (Trujillo & Norman 1995; Tomley 2000).

Due to the wide geographical distribution of lantana, international cooperation is needed if biological control programs are to reach their full potential. Many countries infested by lantana do not have the resources or the expertise to carry out their own independent biological control programs (Ooi 1986). Even in developed countries, there are limited funds available for testing and releasing new agents from the Americas. Thus, many countries can benefit from the fundamental work carried out in Australia, Hawaii and South Africa, either through the importation of agents that have been shown to be safe and successful elsewhere (Greathead 1971a; Harris 1973; Wapshere 1985), or through the incidental spread of agents from neighbouring countries in which they were released (Rao *et al*. 1971; Löyttyniemi 1982; Cock & Godfray 1985; Muniappan *et al*. 1992).

13.2 Agents currently being considered for release

Surveys conducted by Winder and Harley (1983), Barreto *et al*. (1995), Palmer & Pullen (1995) and Pereira & Barreto (2000) have listed many species attacking lantana in tropical America. Subsequently, biocontrol practitioners have identified several potential agents worth investigating to improve the biological control of lantana. While the actual number of insects and/or pathogens found attacking lantana is quite high, the number considered to be specific enough for further study is much less. In addition, many potential agents may not be adapted climatically to the target country. Potential agents that are currently being studied for importation or release are discussed below.

13.2.1 *Aceria lantanae* Cook (Acari: Eriophyidae)

Mites have never been employed as biological control agents against lantana, despite many mite species showing a high degree of host-specificity. Mite populations can increase rapidly, and large numbers can be accommodated in small spaces. They can place huge physiological pressures on the plant such that the host will stop producing new shoots, flowers or seeds and they are known to carry viral plant diseases (Cromroy 1976; Craemer & Neser 1996). *Aceria lantanae* causes galls on leaves and inflorescences, resulting in stunted plants in Florida, Mexico, the Caribbean and Brazil (Flechtmann & Harley 1974; Craemer & Neser 1990). Although the mites inducing the two symptoms are regarded as morphologically identical, they appear to be distinct and may constitute separate strains or even species (Craemer &

Neser 1990; Baars & Neser 1999). Colonies of both strains from southern US are being studied as potential biocontrol agents in South Africa (Craemer & Neser 1990, 1996; Baars & Neser 1999). *Aceria lantanae* appears to be host-specific, inducing galls in only some lantana varieties but not attacking any of the native South African species of lantana (Urban *et al*. 2001). It is regarded as one of the highest priority agents for South Africa and Australia.

Mites require very specific conditions such as humidity and actively growing hosts for establishment to occur (Baars & Neser 1999). Contamination by other mites and glasshouse pests is common and difficult to overcome when handling such a microscopic organism (Craemer & Neser 1990). Their usefulness as a biocontrol agent in Australia at least has been questioned, as there are already a large number of indigenous and introduced mite species that attack lantana, without much effect on the plants (Walter 1999). Furthermore, native predatory mites and pathogenic fungi may keep the populations of these indigenous phytophagous mites in check and may do the same to any mite species introduced (Walter 1999). However, in its native range *A. lantanae* is very damaging to lantana, and predatory mites are also present in large numbers in the infested galls.

The suggestion that mites may make the plant unsuitable to other potentially damaging agents of lantana is countered by the observation that there is a wide range of natural enemies attacking lantana already infested with the mites in the native range (Craemer & Neser 1990). Other mite species that have been observed to cause significant damage to lantana in its native range include *Calacarus lantanae* Boczek and Chandrapatya, *Paraphytoptus magdalenae* Craemer, *Phyllocoptes lantanae* Abou-Awad and El-Banhawy (Craemer 1996) and *Rhynacus kraussi* Keifer (Flechtmann & Harley 1974), but these have not yet been studied in detail.

13.2.2 *Aerenica multipunctata* Le Peletier & Audinet-Serville (Coleoptera: Cerambycidae)

This stem-boring beetle was collected from Parana State, Brazil, where it was heavily attacking *L. tiliifolia*, resulting in reduced fruit production. It prefers smaller, secondary branches 0.5–1.7cm in diameter (Winder & Harley 1982). Although *A. multipunctata* has been imported into Australia for biological studies, host testing has not been conducted. Only one agent, *Plagiohammus spinipennis*, which attacks the stems of lantana has established and it has only established in Hawaii. Therefore, the use of stem-boring insects such as

Figure 82.
Aceria lantanae:
(a) an infected and a healthy flower;
(b) infected lantana flowers;
(c) infected lantana shoots and buds (Florida, US).

P. spinipennis and *Aerenicopsis championi* should be a high priority for many countries where lantana is not under adequate control.

13.2.3 *Alagoasa extrema* Jacoby (Coleoptera: Chrysomelidae)

Adults and larvae of this flea beetle from Mexico, feed on the leaves of lantana (Baars & Neser 1999). The benefits of importing and studying *A. extrema* when another flea beetle *Alagoasa parana* failed to establish, is that *A. extrema* was collected from *L. urticifolia*, a more closely related species to *L. camara* and can complete several generations each summer before it diapauses. *Alagoasa parana*, on the other hand, was collected from *L. tiliifolia* in Brazil and is univoltine (Winder *et al*. 1988). *Alagoasa extrema* is at an early stage of evaluation in South Africa and Australia (Baars & Neser 1999).

13.2.4 *Ceratobasidium lantanae-camarae* Evans, Barreto & Ellison (Tremellales: Ceratobasidiaceae)

Records from Brazil, Ecuador and Costa Rica indicate that this web-blight fungus has a wide distribution in the neotropics. It is favoured by lowland, humid tropical regions and was not recorded in surveys in southern Brazil (Barreto 1995) where it is more temperate. This fungus can be extremely damaging to its host plant and has the potential to be a very useful biocontrol agent. In the field, *C. lantanae-camarae* appears to have a narrow host range, not infecting *Lantana lilacina* Desfontaines (section *Calliorheas*) growing alongside heavily infected *L. camara* (Barreto *et al*. 1995). No comprehensive host testing has been done on this species under laboratory conditions.

13.2.5 *Coelocephalapion camarae* Kissinger (Coleoptera: Brentidae)

Adults feed on leaves and lay eggs in the petioles. The larvae bore into the petioles and induce small galls (Baars & Neser 1999). Galls on leaf petioles may cause small leaves to desiccate and abscise, while flower galls prevent the development of seeds. Research in South Africa shows that *C. camarae* can disrupt the transport of essential solutes and cause a reduction in dry weight of roots and shoots. The adults are long-lived and diapause during winter when plants can lose their leaves. The insect is awaiting approval to be released (Baars & Heystek 2001). It is not known if this species is the same as one of the *Apion* species imported into Hawaii in 1902, as no specimens of these earlier imports were preserved.

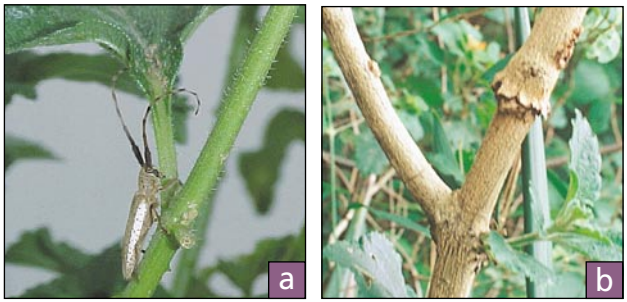


Figure 83.
Aerenica multipunctata:
(a) adult;
(b) larval damage to lantana plants (Brazil).

Figure 84.
Alagoasa extrema adult (PPRI, South Africa).

13.2.6 *Longitarsus* sp. (Coleoptera: Chrysomelidae)

Longitarsus sp. is a root-feeding flea beetle found in Trinidad, Florida and Mexico (Baars & Neser 1999). Adults feed on leaves and lay their eggs in the leaf litter. Larvae feed on the roots and pupate in the soil (Simelane 2001). The insect has many generations per year, but the adults diapause over winter when it is dry. *Longitarsus* sp. is considered a highly promising agent as it is one of only a few root-feeding insects to be studied for the biocontrol of lantana. The biology and host-specificity of *Longitarsus* sp. is currently being conducted at the Plant Protection Research Institute, South Africa. The beetle has been tested against 43 plant species, and so far appears safe for release (Simelane 2001).

13.2.7 *Puccinia lantanae* Farlow (Uredinales: Puccinaceae)

This rust fungus is common on *L. camara* in tropical areas of Brazil, but is scarce on this plant in subtropical regions. In cooler climates, *P. lantanae* remains damaging to *L. lilacina* (section *Calliorheas*). It is of potential interest for classical weed biocontrol in warmer, more humid regions (Barreto *et al*. 1995). Preliminary host-testing and varietal susceptibility tests have been conducted, and the rust is believed to have a narrow host range.

13.3 Integrated control techniques

Despite the efforts of entomologists worldwide, successful biological control of lantana has not been achieved. While biological control agents can seasonally damage plants, the plants usually recover when insect numbers decrease. The lack of success of the biocontrol program means that long-term management will rely on the integration of conventional and biocontrol techniques. The main conventional control methods are chemical, mechanical and fire. Table 6 provides a comparison of control techniques and recomendations on the integration of control.

Biological control agents and favourable climate can together sometimes severely damage lantana to the point that plants are defoliated or fail to flower and set seed. It is therefore important to study the best conventional control methods available to kill plants already weakened by biocontrol agents.

Figure 85.
Ceratobasidium lantanae-camarae:
(a) spores (Una, Brazil); (b) damage to lantana (Manaus, Brazil).

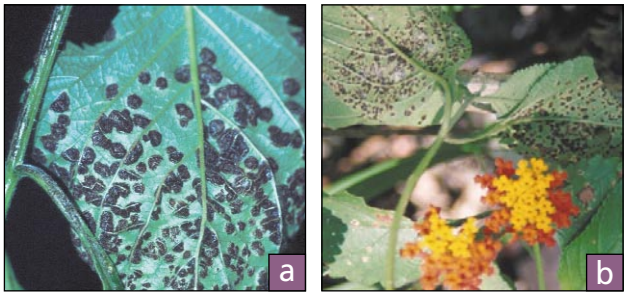


Figure 86.
Puccinia lantanae:
(a) spores; (b) damage to lantana (Brazil).

In the past, landholders have often been reluctant to implement chemical or fire control for fear of killing the biocontrol agents, which are at least keeping plants in check. If other control measures are not implemented, insect numbers drop with the onset of winter and when more favourable conditions occur, the plants re-shoot without the agents. A loss of biomass as a result of insect attack can improve the likelihood of successful removal through other methods. Several landholders in Australia have stated that plants suffering through heavy insect attack or drought are easier to access and remove by hand. Others have suggested that the leafless plants are more susceptible to fire and that the leaves dropped on the ground can supply fuel.

Mechanical clearing or manual removal are both effective ways of reducing lantana infestations. Both techniques are considered more successful during winter when the plants have less foliage, making access easier. It is also the time that many insects will be less effective. Follow up treatment using manual removal or use of herbicides will assist with permanent removal of a local infestation.

Fire is one of the cheapest methods for controlling lantana but may have a major effect on biocontrol insect numbers. Also, mature lantana often sprouts after it has been burnt so that infestations can recovery quickly. The timing of the fire can influence the end result. A hot summer fire will kill lantana plants, but a cool winter fire may only cause dieback to the lower stems. Fire however, provides an effective tool where biocontrol is having limited success and can be followed by chemical treatment of regrowth. Fire can be used over extensive areas but follow up using mechanical, manual removal or chemical control is necessary but not able to be used in large areas. The area burnt should be dependent on the land manager's capability for follow-up control.

Chemical control is very valuable, particularly following mechanical or biocontrol methods. However in treating plants heavily attacked by insects or suffering from drought means that if there are only a few leaves on the plants then there is less surface area for chemicals to be absorbed. So it is advisable to treat all the stems with the herbicide solution. Chemical control is often improved by application after rain and when it is warm (Hannan-Jones 1998).

Any controls implemented should reflect the landuse and type of natural vegetation in the infested area. While fire could be applied in many grazing situations, it may not be appropriate in conservation areas or in and around orchards or plantations. The use of chemicals is just as complex and also requires care.

All control methods require follow up treatment. Months or years of treating infestations are wasted if follow up treatments aren't applied. Therefore, the size of the infestation treated should be such that landholders can maintain the necessary level of control for a few seasons until seeds in the soil have germinated. This is likely to take about 2–3 years. After this time, regular spot control is still needed to remove new plants arising from seed brought in by birds from neighbouring areas.

13.4 Integrated control recommendations

In summary, the recommended approach is:

- determine what biocontrol insect species are present on the lantana infestation, and use the information in this book to determine whether there are more effective species for control;
- if the biocontrol agents are not providing adequate control, consider whether mechanical removal is suitable for the site — if so, consider attempting mechanical removal during winter or after major defoliation by biocontrol agents;

Control technique	When to use	When not to use	Comments
Biological Control	• If effective biocontrol agents are available and not already present.	If biocontrol agents affect other species deemed important.	Suggestions are provided in this book concerning the suitability of different biocontrol agents for different morphological forms of lantana growing under different climatic conditions.
Mechanical control	• If the area is suitable for access by machinery without significant damage and the action of the machinery will itself not lead to further land degradation.	Close to rivers, creeks and drainage lines, as damage to soil will impair water quality and increase erosion. If it is not possible to follow up with further treatments such as chemical or manual removal.	
Manual removal	• When labour is available and relatively cheap. • Where the area to be cleared is limited. • Where manual removal is being used as a follow-up technique after fire or mechanical removal.	Where the cost of labour outweighs land value.	Anecdotal evidence suggests that removal during winter, or when plant is under stress, increases the likelihood of success.
Fire regime	• Where the area is extensive and there is little risk of fire spreading	Where lantana may inappropriately increase the intensity and frequency of fire e.g. Rainforest environmental areas. Fire should not be used as a control technique unless follow-up treatment with chemical or manual removal is feasible.	Fire can be used to treat large areas of lantana infestation; but due to its short-term effects and the long-term potential for land degradation posed by frequent fire regimes, it must be carefully considered. The use of fire can also have a detrimental effect on biocontrol agents, which may have been keeping the species under some control. Care should be taken to ensure continued survival of some agents.
Chemical control	• Where the area to be cleared is limited and of high value • As a follow-up treatment after other control techniques • In the early stages of infestation or on the edge of the species range	Where the cost outweighs the land value.	Chemical control is very successful but has limited use because of its cost. It may be a particularly useful technique where the species is in the early stages of establishment.

Table 6.
Comparison of control techniques, and recommendations on the integration of control

- if the site is small or labour is available, consider hand-pulling individual plants when the biomass of plants is restricted;
- if the area is not environmentally sensitive and is not in a plantation or orchard, consider the use of fire — however, fire may reduce the success of biocontrol efforts and care should be taken to ensure some agents survive.

All conventional control methods require extensive follow-up with chemical and mechanical control, and this is an ongoing process.

14. Research

Research into integrated control is still in its infancy. Landholders are beginning to try new control regimes, which take advantage of prevailing conditions such as plant stress. These trials should be documented so that a matrix of control options for different areas and landuse can be prepared for others to use.

Three specific areas of research that may help to understand lantana taxonomy and biology in the hope that the information may be useful in achieving better control of lantana will now be discussed. They are:

- classification and identification of naturalised taxa;
- somatic mutations; and
- lantana ecology and biology.

14.1 Classification and identification of naturalised taxa

The first step in any biological control program should be to determine the correct identification of the target weed species and intraspecific taxa (Schroeder & Goeden 1986). Work on the biological control of lantana has been conducted since 1902, and yet this vital step has not been fully addressed. Part of the problem stems from not fully realising the complexity of the lantana group and its effect on biological control agents. In earlier exploration visits, agents were collected from morphologically similar plants to those in the naturalised range, and many such plants were collectively referred to as *L. camara*. Moldeneke & Moldeneke (1983) state that the name '*camara*' has been so loosely applied by collectors to so many different species that much of the information in the literature is incorrect or misleading unless verified by voucher specimens.

It is only recently with DNA studies and a more thorough appreciation of the complexities of the group that we are now seeing the affinities and taxonomic relationships of plants in this genus. Despite these recent advances, there is still scope for further research and a need to look at particular characteristics of specimens more closely to separate groups, because anomalies within the taxa still occur.

In the past, the recognition of varieties has been based on morphological features. Taxa have often been grouped for convenience on obvious morphological differences, such as presence/absence of thorns (Swarbrick 1986; Munir 1996), or broad flower colour (Diatloff & Haseler 1965; Everist 1974). Australian taxa are typically divided into groups based on their flowering colour — 'pinks', 'reds', 'whites' and 'oranges' (Haseler 1966; Everist 1974) — and may not be the characters that accurately separate the taxa into biologically meaningful groups from the perspective of a biological control agent (Scott *et al*. 1997). This method of classification has been fraught with problems as many varieties were distinguished by subtle differences in morphology. Further difficulties arise when somatic mutations occur (Smith & Smith 1982) or when hybrids are formed between morphologically similar varieties (Spies 1984; Cilliers & Neser 1991).

There is some controversy over the usefulness of the broad 'flower-colour groups' of lantana as taxonomic entities. Scott *et al*. (1997) analysed the genetic relationship between 'pinks' and 'pink-edged reds' from four regions along the east coast of Australia and found that geographical proximity is more important than flower colour in defining genetic similarity between populations. They found that within any one region there appeared to be some isolation of the two colour types, but that between regions flower colour had little phylogenetic significance. These results support findings that the same colour types in different regions vary in their toxicity to livestock and their susceptibility to attack by biocontrol agents (Diatloff & Haseler 1965; Everist 1974), suggesting that the varieties in different regions may have originated from different sources.

The differences in insect attack on two similar-flowering varieties in different regions, however, can also be attributed to other factors such as climate. Also, some agents have shown preference to some flowering varieties over others occurring in the same region. The common pink taxon of Australia is less preferred by some introduced biocontrol agents (Tomley 2000; Day *et al.* 2003) and is known to contain several secondary plant compounds not found in other Australian lantana taxa. The pink-flowering variety lacks plant compounds common to all other varieties (Hart *et al*. 1976; Sharma & Sharma 1989). In addition, different flowering varieties in the same region can vary in their toxicity to livestock. For example the common pink-flowering variety is regarded as non-toxic to livestock throughout eastern Australia, while the pink-edged red-flowering variety is considered highly toxic.

This preference by agents for some flowering lantana varieties and the differing levels of toxicity to livestock among varieties, suggests that flower colour could be used in distinguishing taxa. These observations suggest that there is a need to determine whether there is any connection between morphological features and chemical or physiological characteristics of the plant. However, given the variability within the *L. camara* complex, this would not be an easy task to address. Spies (1984) noted that in South Africa, there was no correlation between cytological data and plant morphology.

It is hoped that further DNA-testing combined with biochemical profiling and morphological studies will improve the understanding of the relationships of the taxa within the lantana complex. Clarifying the taxonomy of the genus and in particular the *Lantana* section *Camara* is an essential prerequisite for successful biological control. Our poor understanding of the taxonomy of the group to date has greatly hindered progress, with potential agents being collected from inappropriate taxa. In addition, by knowing the relatedness of the naturalised lantana between different countries, successful agents can be re-released into countries that have suitable varieties of lantana for the agents.

14.2 Somatic mutations

Occasionally, branches on lantana plants produce different flower colour types to the rest of the plant. Nothing is known of the taxonomic or evolutionary significance of these 'somatic mutations' and plants grown from cuttings taken from these mutant branches are morphologically similar to the mutant (M. Hannan-Jones NRM, pers. comm.). In addition, seeds from mutant branches have been found to produce plants similar to the mutant branch (Smith & Smith 1982). Consequently, it is possible that new taxa may become established from mutant branches. Smith & Smith (1982) recognised that these mutant branches may be reversion shoots representing the original parent material from which the plant that produced them was derived.

It is doubtful that such branches actually arise from one meristem cell containing a mutation on a gene-regulating flower colour. It is more likely that environmental 'switches' change the chromosomes being expressed (in polyploid taxa), so that different varieties (with possibly different chemistry and susceptibility to agents) may occur on the one plant. The chemistry of 'mutant' versus parent branches and the genetics involved have implications in biocontrol and other areas.

14.3 Lantana biology and ecology

Little is known about lantana's soil seed-bank dynamics. Anecdotal evidence suggests that seeds remain viable in the soil for about two years, but apparently no formal studies have been made. Such studies would assist in control in general and would govern how long follow-up treatments would need to be implemented following the removal of thickets by conventional means.

There is little information about the role of birds in dispersing lantana. Seed germination increases significantly if passed through the gut of birds, so information regarding the behaviour and feeding preferences of birds on lantana fruits may prove useful in terms of integrated control or selecting new agents. For instance, if birds move only a short distance after feeding then the application of integrated control techniques may be quite different to those situations where birds move large distances, spreading the seed further. Also, birds tend not to eat fruit damaged by the seedfly *Ophiomyia lantanae*, so the impact of flower-feeding and seed-feeding insects on lantana and the insect population levels that are needed to significantly reduce seed set or damage seed needs to be studied.

While there have been many studies trying to understand basic taxonomy and biology and many attempts at utilising biocontrol agents, there has been little progress made on what must be done to lantana to either kill the plant or at least reduce its vigour and seed set. Harris (1973) attempted to rate the different insect guilds in relation to their effectiveness as a biocontrol agent for weeds in general but such studies are limited when applied to lantana. Winder & van Emden (1980) and Broughton (2000b) studied various aspects of the impact of leaf-feeding insects, with both studies monitoring the effects of pruning plants at different levels and times. However, feeding by insects is a continuous process and quantitative studies that reflect this should be conducted in the field.

Finally, a better appreciation of the impact of each of the agents currently established is needed to determine their potential usefulness for other countries. So far, little information exists, apart from some earlier studies by Forno and Harley (1976), Winder (1980), Winder and Harley (1982) and some anecdotal reports. More recently, scientists in South Africa and Australia have been trying to address this deficiency. Through field assessment of agents and manipulative experiments, it should be possible to make decisions on which guilds of agents are best to focus on in the future and which agents are unlikely to help control lantana.

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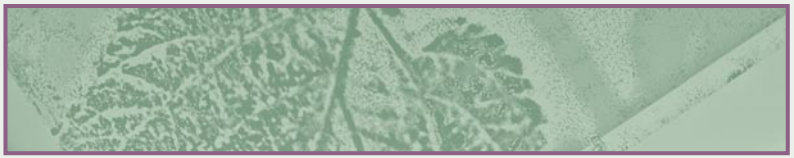

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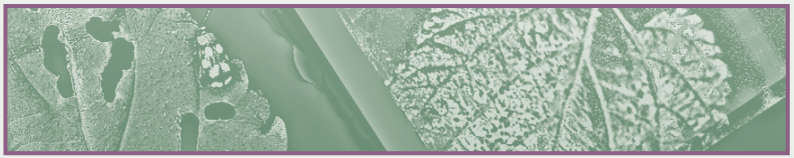
Appendix



Appendix

Countries and/or island groups: (1) where taxa within *Lantana* section *Camara* are found; or (2) which have locations where the Environmental Index>30 indicating that lantana could establish if introduced. (Environmental Index (EI) values could not be obtained for all countries or islands.)

Country/Island group	Lantana Status	No. of climatic stations				Total Locations	References
		EI<30	EI=30–50	EI=50–70	EI>70		
Algeria	Absent	27	2	0	0	29	
Angola	Introduced	2	11	9	6	28	Stirton 1977
Argentina	Native	10	4	1	1	16	Julien & Griffiths 1998
Ascension Is. (UK)	Introduced	–	–	–	–	–	Julien & Griffiths 1998
Australia	Introduced	191	19	16	3	229	Holm *et al*. 1991
Azores Is. (Portugal)	Introduced	–	–	–	–	–	
Bahamas	Native	–	–	–	–	–	Sanders 1987
Bangladesh	Absent	0	2	1	0	3	
Benin	Absent	0	2	4	1	7	
Bermuda	Native	–	–	–	–	–	Sanders 2001
Bolivia	Native	2	1	1	0	4	Holm *et al*. 1991
Botswana	Absent	7	1	0	0	8	
Brazil	Native	0	3	9	15	27	Holm *et al*. 1991
Burkina Faso	Absent	4	2	0	0	6	
Burundi	Absent	0	1	1	0	2	
Cambodia	Introduced	0	0	2	2	4	Holm *et al*. 1991
Cameroon	Introduced	2	0	4	6	12	Holm *et al*. 1991
Canary Is. (Spain)	Introduced	–	–	–	–	–	
Cape Verde Is.	Introduced	–	–	–	–	–	T. van Harten, pers. comm.
Central African Republic	Absent	1	0	5	4	10	
Chad	Absent	9	1	0	0	10	
Chile	Native	17	1	0	0	18	Flechtmann & Harley 1974
China	Introduced	59	8	9	9	85	Holm *et al*. 1991
Colombia	Native	0	1	0	0	1	Flechtmann & Harley 1974
Congo, The Republic of	Absent	0	0	0	10	10	
Cook Is.	Introduced	0	0	0	2	2	Waterhouse & Norris 1987
Costa Rica	Native	0	0	1	0	1	Holm *et al*. 1991
Cote d'Ivoire	Introduced	0	0	2	5	7	Holm *et al*. 1991
Cuba	Native	0	0	0	2	2	Mann 1954
Democratic Republic of Congo	Introduced	0	2	3	17	22	

* Countries that have lantana but have EI values < 30.
EI data was generated by using a CLIMEX analysis of potential lantana distribution, courtesy P. Mackey, DNRM 2002

Country/Island group	Lantana Status	No. of climatic stations				Total Locations	References
		EI<30	EI=30–50	EI=50–70	EI>70		
Dominican Republic	Native	0	0	0	1	1	Holm *et al*. 1991
Easter Is.	Absent	0	0	0	1	1	
Ecuador	Native	0	1	0	0	1	
El Salvador	Native	0	0	1	0	1	Mann 1954
Equatorial Guinea	Absent	0	0	0	1	1	
Ethiopia	Introduced	12	4	2	0	18	
Federated States of Micronesia	Introduced	–	–	–	–	–	Holm *et al*. 1991
Fiji	Introduced	0	0	0	1	1	Holm *et al*. 1991
French Guiana	Native	0	0	1	0	1	Harley, pers.comm.
Futuna Is. & Wallis Is.	Introduced	–	–	–	–	–	Waterhouse & Norris 1987
Gabon	Absent	0	0	1	6	7	
Galapagos Is. (Ecuador)	Introduced	–	–	–	–	–	Mauchamp *et al*. 1998
Gambia, The	Absent	1	1	0	0	2	
Ghana	Introduced	1	1	0	4	6	Holm *et al*. 1991
Guam (US)	Introduced	0	0	0	3	3	Waterhouse & Norris 1987
Guatemala	Native	0	2	1	1	4	Holm *et al*. 1991
Guinea	Introduced	2	5	1	1	9	Holm *et al*. 1991
Guyana	Native	0	0	0	1	1	
Haiti	Native	0	0	0	1	1	Sanders 1989
Hawaii (US)	Introduced	1	2	2	4	9	Holm *et al*. 1991
Honduras	Native	–	–	–	–	–	Holm *et al*. 1991
Hong Kong	Introduced	–	–	–	–	–	Holm *et al*. 1991
India	Introduced	24	12	7	0	43	Holm *et al*. 1991
Indonesia	Introduced	0	3	5	9	17	Holm *et al*. 1991
Israel*	Introduced	4	0	0	0	4	Holm *et al*. 1991
Italy	Absent	24	1	0	0	25	
Jamaica	Native	0	0	1	0	1	Holm *et al*. 1991
Kenya	Introduced	14	16	10	8	48	Holm *et al*. 1991
Kiribati	Introduced	–	–	–	–	–	Waterhouse & Norris 1987
Laos	Absent	0	2	4	0	6	
Lebanon	Absent	0	1	0	0	1	
Lesotho	Absent	3	1	0	0	4	

Country/Island group	Lantana Status	No. of climatic stations				Total Locations	References
		EI<30	EI=30–50	EI=50–70	EI>70		
Lesser Antilles	Native	0	0	1	3	4	Holm *et al*. 1991
Liberia	Introduced	0	1	0	0	1	Holm *et al*. 1991
Lord Howe Is. (Australia)	Introduced	0	0	0	1	1	
Madagascar	Introduced	7	10	5	5	27	Holm *et al*. 1991
Madeira Is. (Portugal)	Introduced	–	–	–	–	–	
Malawi	Absent	0	4	2	0	6	
Malaysia	Introduced	0	0	2	4	6	Holm *et al*. 1991
Mali	Absent	16	3	0	0	19	
Marshall Is. (US)	Introduced	0	0	0	1	1	Julien & Griffiths 1998
Mauritius	Introduced	–	–	–	–	–	Holm *et al*. 1991
Mexico	Native	29	16	5	2	52	Mann 1954
Monaco	Absent	0	1	0	0	1	
Morocco	Absent	14	1	0	0	15	
Mozambique	Introduced	6	6	8	6	26	Holm *et al*. 1991
Myanmar	Introduced	5	6	3	0	14	Julien & Griffiths 1998
Nauru	Introduced	–	–	–	–	–	
Nepal	Absent	0	1	0	0	1	
New Caledonia	Introduced	0	0	0	1	1	Waterhouse & Norris 1987
New Zealand (North Is.)	Introduced	25	3	0	0	28	Holm *et al*. 1991
Nicaragua	Native	–	–	–	–	–	Holm *et al*. 1991
Nigeria	Introduced	9	4	6	5	24	Holm *et al*. 1991
Niue	Introduced	–	–	–	–	–	Waterhouse & Norris 1987
Norfolk Is. (Australia)	Introduced	–	–	–	–	–	Waterhouse & Norris 1987
Northern Mariana Is. (US)	Introduced	–	–	–	–	–	Julien & Griffiths 1998
Palau (USA)	Introduced	0	0	1	0	1	Julien & Griffiths 1998
Panama	Native	0	0	1	1	2	Holm *et al*. 1991
Papua New Guinea	Introduced	0	1	1	5	7	Holm *et al*. 1991
Paraguay	Native	0	0	0	1	1	Krauss 1964
Peru*	Native	4	0	0	0	4	Harley 1974
Philippines	Introduced	0	0	3	5	8	Holm *et al*. 1991
Puerto Rico	Native	0	0	0	1	1	Holm *et al*. 1991
Republic of South Africa	Introduced	65	34	9	7	115	Holm *et al*. 1991

Country/Island group	Lantana Status	No. of climatic stations				Total Locations	References
		EI<30	EI=30–50	EI=50–70	EI>70		
Reunion Is. (France)	Introduced	–	–	–	–	–	
Saint Helena Is. (UK)	Introduced	–	–	–	–	–	Julien & Griffiths 1998
Saudi Arabia*	Introduced	2	0	0	0	2	Holm *et al*. 1991
Senegal	Introduced	6	1	0	0	7	Holm *et al*. 1991
Seychelles Is.	Introduced	–	–	–	–	–	Oosthuizen 1963
Sierra Leone	Absent	0	1	2	0	3	
Singapore	Introduced	0	0	0	1	1	Julien & Griffiths 1998
Solomon Is.	Introduced	–	–	–	–	–	Waterhouse & Norris 1987
Somalia	Absent	7	0	1	0	8	
Spain	Introduced	27	1	0	0	28	
Sri Lanka	Introduced	0	0	0	2	2	Holm *et al*. 1991
Sudan	Absent	15	5	0	1	21	
Suriname	Native	0	0	0	1	1	
Swaziland	Introduced	1	0	1	0	2	Day, pers. obs.
Tahiti	Introduced	0	0	0	1	1	Holm *et al*. 1991
Taiwan	Absent	0	0	0	2	2	
Tanzania	Introduced	1	14	14	9	38	Holm *et al*. 1991
Thailand	Introduced	0	5	9	3	17	Holm *et al*. 1991
Togo	Absent	0	1	1	3	5	
Tonga	Introduced	–	–	–	–	–	Waterhouse & Norris 1987
Trinidad and Tobago	Native	0	0	0	1	1	Holm *et al*. 1991
Turkey*	Introduced	13	0	0	0	13	Holm *et al*. 1991
Uganda	Introduced	0	0	3	10	13	Holm *et al*. 1991
Uruguay	Native	0	1	9	0	10	Harley, pers.comm.
United States of America	Native	145	8	7	8	168	Holm *et al*. 1991
Vanuatu	Introduced	0	0	0	1	1	Waterhouse & Norris 1987
Venezuela	Native	1	0	2	1	4	Krauss 1964
Vietnam	Introduced	0	0	7	6	13	Holm *et al*. 1991
Western Samoa	Introduced	0	0	0	1	1	Waterhouse & Norris 1987
Zambia	Introduced	0	17	1	0	18	Holm *et al*. 1991
Zanzibar	Introduced	–	–	–	–	–	Waterhouse & Norris 1987
Zimbabwe	Introduced	11	29	1	0	41	Holm *et al*. 1991

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