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Review Article

Current distribution and status of *Lantana camara* and its biological control agents in Australia, with recommendations for further biocontrol introductions into other countries

M. D. Day[1], S. Broughton[2] and M. A. Hannan-Jones[1]
[1]Alan Fletcher Research Station, Department of Natural Resources and Mines, PO Box 36, Sherwood, Queensland 4075, Australia
[2]Entomology, Western Australian Department of Agriculture, 3 Baron-Hay Court, South Perth, Western Australia 6151, Australia

Abstract

The results of surveys conducted in Australia over a five-year period to determine the distribution of *Lantana camara* (lantana) and its introduced biological control agents are reviewed and discussed. The relative merits and drawbacks of each species are summarized for the benefit of other countries wishing to consider biological control programmes against lantana. Lantana is found in coastal and sub-coastal areas from far-north Queensland to southern New South Wales (NSW). Small populations of the weed have been reported around Darwin in the Northern Territory (NT) and Perth in Western Australia (WA). For the purpose of this review, lantana is classified into five varietal groups, based on flower colour. The pink flowering group is the most common and widespread. It is the only variety found in southern NSW and in high altitude subtropical areas. The pink-edged red flowering varietal group is the next most common, being found from central NSW to far-north Queensland. The three remaining varietal groups, red, white and orange, are less common and limited in their distribution. Of the 30 biological control agents that have been introduced into Australia, 16 have established. The most widespread and damaging agents are *Octotoma scabripennis*, *Uroplata girardi*, and *Teleonemia scrupulosa*. *Leptobyrsa decora* is very damaging to lantana seasonally but has a very limited distribution, being found at only a few sites in high altitude tropical regions. Two agents, *Plagiohammus spinipennis* and *Teleonemia harleyi* previously reported as established, were not found in the surveys. Despite the establishment of 16 agents, lantana is not under adequate control in Australia. Climate is probably the major factor that prevents populations of insects from being maintained at consistently high enough levels to control the weed.

Introduction

Lantana camara L. (Verbenaceae) is a native of tropical America. It and unknown other *Lantana* species were cultivated in glasshouses in Europe producing hybrids which were often referred to as '*Lantana camara*'. Over 600 named varieties (or cultivars) worldwide now exist (Howard, 1969) and many of these have become weeds in over 50 countries throughout the tropics (Parsons & Cuthbertson, 2001). Recent molecular studies suggest that some of these weedy forms have close affinities to *Lantana urticifolia* Miller (Scott *et al.*, 2002) and others have been subsequently identified as *L. urticifolia* × *L. camara* using morphological characteristics (R. Sanders, pers. comm.). As the origins of many weedy lantanas are not known, we refer to them by the common name 'lantana' in this paper.

Lantana was introduced into Australia in the mid 1800s (Swarbrick, 1986) and is now considered a major weed in coastal and subcoastal areas between Cairns in far-north Queensland, and Sydney, New South Wales (NSW) (Smith & Smith, 1982; Swarbrick *et al.*, 1998; Parsons & Cuthbertson, 2001). Lantana infests natural ecosystems, where it can become the dominant understorey species (Lamb, 1991), block natural succession processes and reduce biodiversity (Fensham *et al.*, 1994). In agricultural areas, it out-competes native pastures, reduces productivity, interferes with mustering and causes illness and death of livestock (Culvenor, 1985).

Biological control of lantana began in 1902, when 23 insect species from Mexico were introduced into Hawaii (Perkins & Swezey, 1924). Australia began biological control of lantana in 1914, with the introduction of four species that had established in Hawaii (Swarbrick *et al.*, 1998). Thirty agents have now been introduced into Australia, with up to 18 agents reported as established (Julien & Griffiths, 1998). However, biological control of lantana in Australia is only partially successful, with earlier reports suggesting that poor control was the result of many agents showing a preference for only some of the varieties (Diatloff & Haseler, 1965; Harley, 1973; Julien & Griffiths, 1998).

The paucity of recent information on the distribution of the different varieties of lantana and the cultivar preferences, distribution, relative abundance and impact of introduced biological control agents in Australia led to extensive surveys being conducted over a five-year period (1996-2001).

This paper reviews the results of these surveys and summarizes the current status of each agent now established in Australia. Drawing also on previously published results from Australia and experiences in other countries, biological and methodological reasons for the various successes and failures are discussed. Reasons for not achieving biological control of lantana in Australia are identified and further agents for consideration are noted. Based on this information, recommendations are given on the suitability of the agents established in Australia for use in other countries where lantana is a problem.

Field Surveys

Distribution of Lantana

From 1996-2001, lantana plants and/or thickets have been examined for biological control agents throughout the weed's range in eastern Australia. Sites surveyed included field release sites of biocontrol agents, sites *en route* to and from release sites, and numerous others

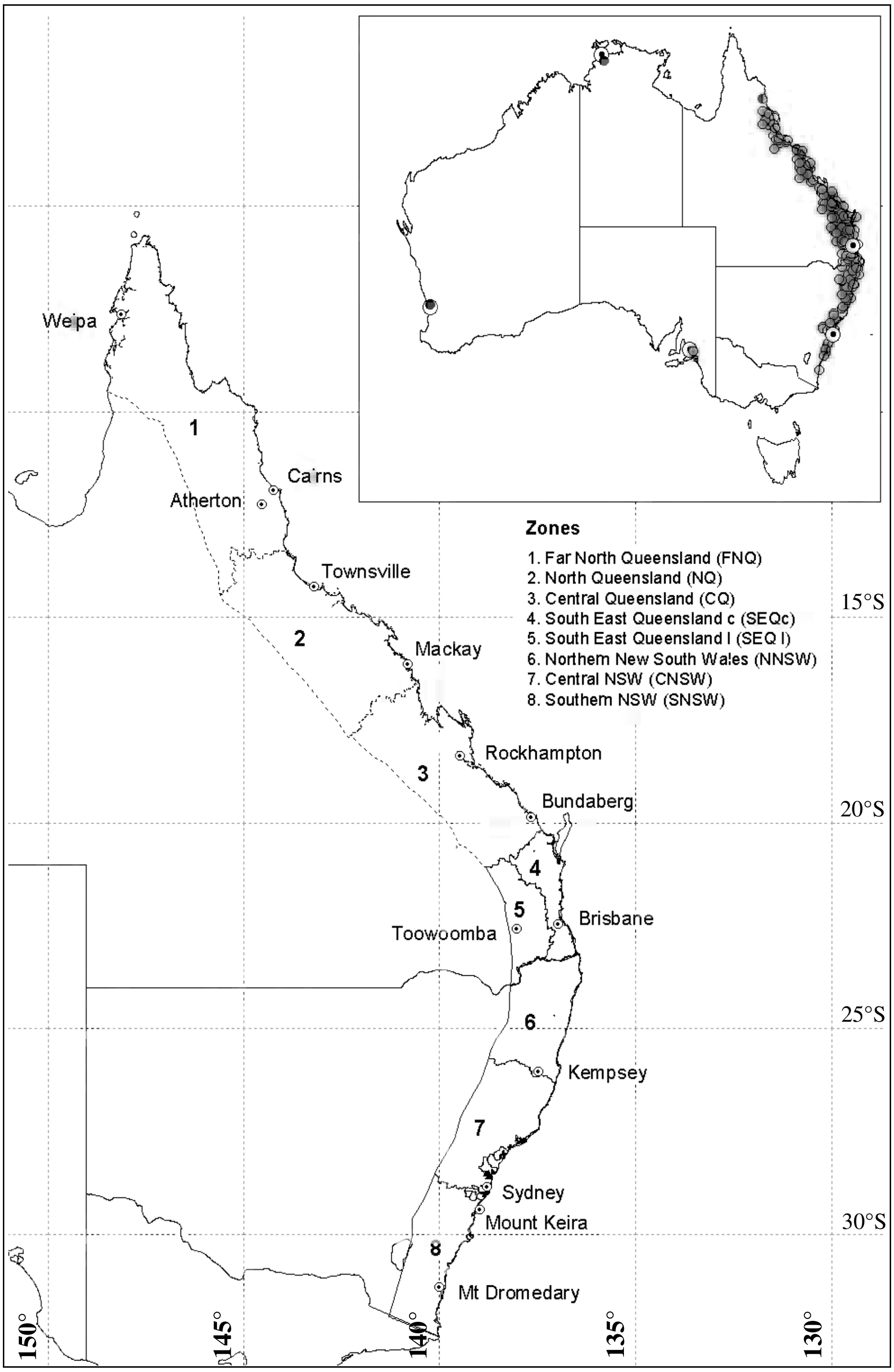

Figure 1. Eastern Australia showing division into eight survey zones. Inset: distribution of lantana in Australia.

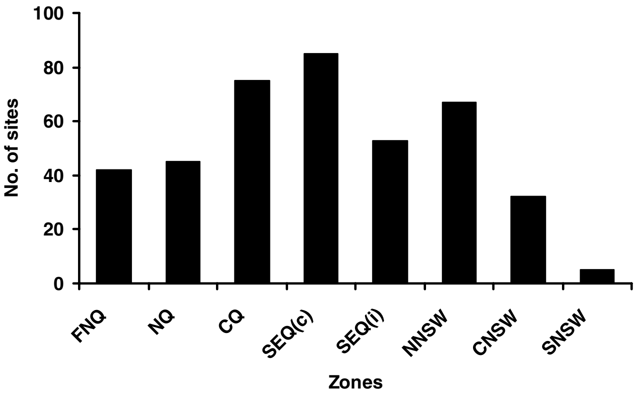

Figure 2. The number of different sites in each zone that were sampled irrespective of the number of lantana phenotypes present. Zones are FNQ = far-north Queensland, NQ = north Queensland, CQ = central Queensland, SEQ(c) = coastal southeast Queensland, SEQ(i) = inland southeast Queensland, NNSW = northern New South Wales, CNSW = central New South Wales and SNSW = southern New South Wales.

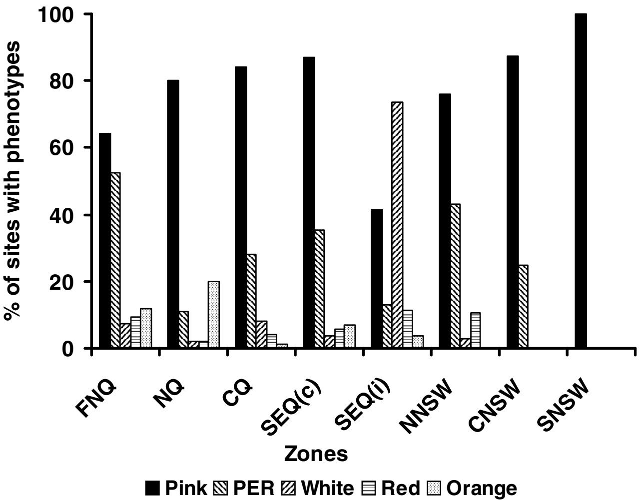

Figure 3. The percent of sites sampled in each zone (see Fig. 1) where each lantana varietal group was present. PER = pink-edged red.

visited during dedicated survey trips throughout eastern Australia. Many sites, especially release sites, were sampled more than once. However, many others, distant from the base of operations at the Alan Fletcher Research Station (27°31'S 152°58'E) in Brisbane, were only sampled once.

Twenty-nine varieties of lantana are reported to be present in Australia (Smith & Smith, 1982). Some biocontrol agents have been reported as showing preference for some varieties over others (Diatloff & Haseler, 1965; Harley & Kassulke, 1974). However, the variation of lantana encountered in the surveys was considerable and plants did not fit easily into named varieties. Thus, plants were classified into only five groups based on flower colour: pink, pink-edged red, red, white and orange. If plants were not flowering at the time of a survey, cuttings were taken and grown in a glasshouse until they flowered.

The surveys sampled 404 sites over the five-year period and the area in which lantana occurs in eastern Australia is divided into eight zones to assist in defining distribution patterns of plant varieties and agents (Fig. 1). More sites were sampled in southern and central Queensland and northern NSW, within several hundred kilometres of Brisbane while infestations further from Brisbane were sampled less frequently (Fig. 2).

Lantana is found in a diverse range of climatic and geographic areas. It occurs from Cow Bay (16°13'S 145°25'E) in far-north Queensland to Mt Dromedary (36°17'S 150°05'E) in southern NSW, a distance of approximately 3000 km. Lantana is also found around Perth (31°57'S 115°50'E) in Western Australia (WA) and has been reported around Darwin (12°27'S 130°52'E) in the Northern Territory (NT) (Fig. 1), but it is not considered a major weed in those areas. It is found at sea level throughout its distribution to altitudes of 1100 m near Ravenshoe (17°37'S 145°28'E) in far-north Queensland. Lantana occurs in areas receiving more than 4000 mm rainfall annually at Tully (17°56'S 145°55'E) in far-north Queensland, to areas receiving only 700 mm rainfall annually at Ravenswood (20°04'S 146°53'E) in north Queensland.

Lantana is found in a range of land uses including open grazing lands, forestry areas, national parks, rainforest edges, and along roads, creeks and fence lines, and are also cultivated as ornamentals in parks and gardens. Infestations range from single bushes to dense monocultures, replacing native vegetation or pasture species.

The pink flowering varietal group is the most common (Fig. 3) and widespread (Fig. 4A) in all but one zone in eastern Australia and consequently has been the most frequently sampled. Plants of this group are particularly common in the wet tropics. Pink flowering lantana is the only varietal group found in cooler regions, south of Sydney (34°01'S 151°04'E), at altitudes greater than 400 m south of 27°S latitude, and at altitudes greater than 200 m south of 30°S. The pink flowering varieties are also found in warm to hot, dry areas in central Queensland from Monto (24°51'S 151°08'E) to Ravenswood (Fig. 2).

The pink-edged red varietal group is the next most common (Fig. 3) and widespread variety (Fig. 4B). Apart from a few isolated patches around Pelaw Main (32°49'S 151°29'E), northwest of Sydney in central NSW, plants belonging to this group are generally found in the warmer coastal regions from Kempsey (31°05'S 152°50'E) in northern NSW to Kuranda (16°50'S 145°40'E) in far-north Queensland. They are generally confined to areas lower than 400 m altitude, except in far-north Queensland (17°S) where they occur up to 1100 m. Although this varietal group is less abundant and widespread than pink flowering lantana, it is of principal concern to graziers, as plants from this group are responsible for stock poisoning in Australia, resulting in up to 1500 cattle deaths annually (Culvenor, 1985).

The remaining three varietal groups of lantana (white, red and orange) have more limited distributions. The white flowering group commonly referred to as 'Helidon White', is the most common and abundant variety present throughout the inland southeast region of Queensland from Kooralgin (26°55'S 151°54'E) south to Mt Sylvia (27°40'S 152°11'E) and west to Haden (27°13'S 151°53'E). Smaller infestations have also been found around Urbenville (28°29'S 152°33'E) in northern NSW and Gracemere (23°27'S 150°28'E) in central Queensland (Figs. 3 & 5A). The red flowering varieties have a very patchy distribution, with the largest infestations found around Mt Sylvia. Smaller infestations are present in most other zones. However, red flowering varieties are not found in central and southern NSW (Figs. 3 & 5B). The orange flowering group also has a patchy distribution, with small infestations present throughout Queensland. However, it has not been found anywhere in NSW (Figs. 3 & 5C).

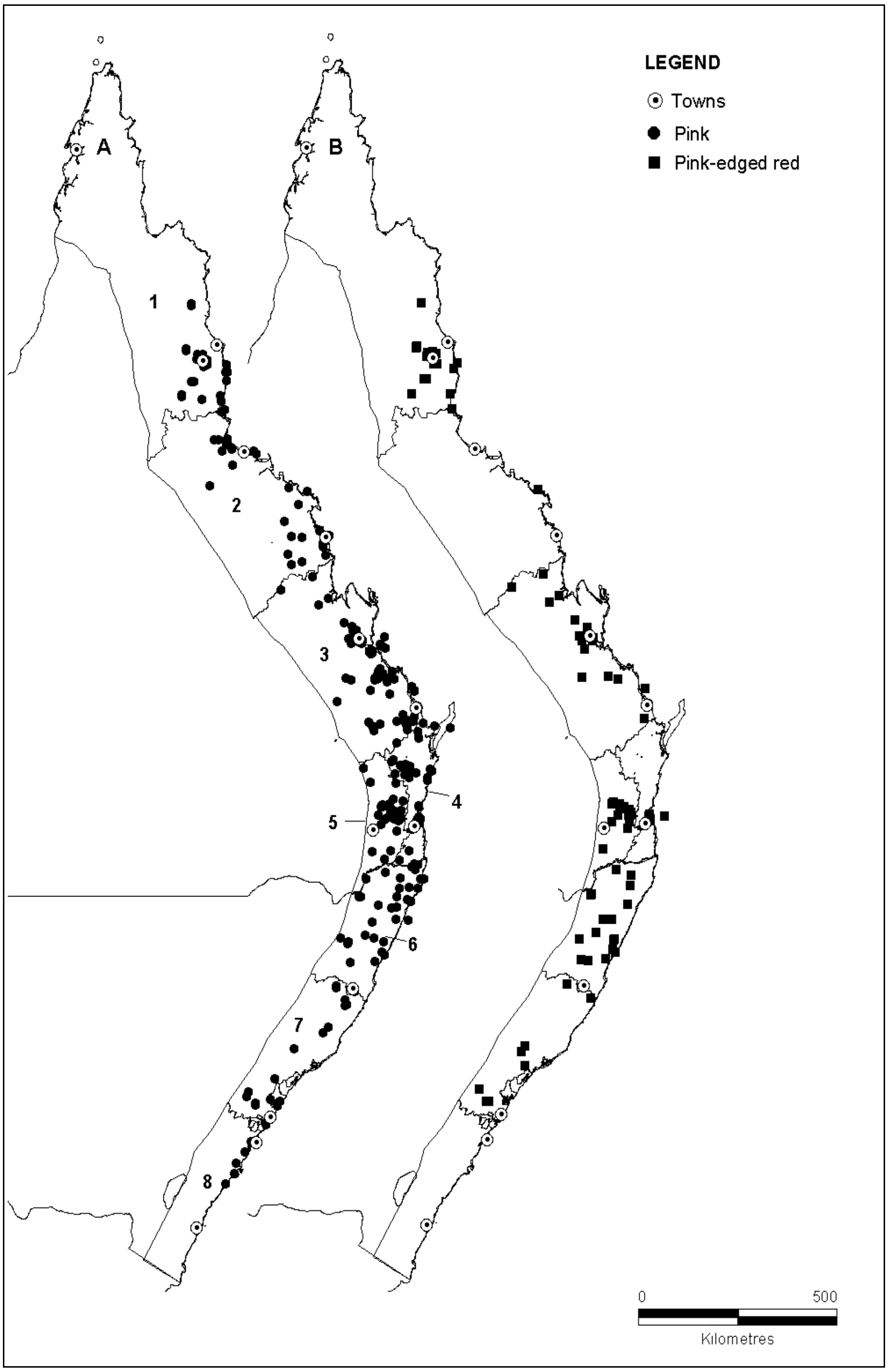

Figure 4. Distribution of the lantana varieties (A) common pink and (B) pink-edged red in eastern Australia (prepared using Arcview®).

Distribution of Biological Control Agents

The surveys investigated the presence/absence of agents, and their relative abundance and damage inflicted on lantana. However, as surveys were not conducted regularly and some sites were only sampled once, measuring the impact of agents on each plant or infestation was difficult.

Sixteen of the 30 biological control agents introduced into Australia were found during the surveys, although some species had very limited distributions (Fig 6). Two agents, the tingid *Teleonemia harleyi* Froeschner and the cerambycid *Plagiohammus spinipennis* Thomson, previously reported to have established (Taylor, 1989; Julien & Griffiths, 1998), were not found, despite numerous attempts to locate them (Table 1). All agents found are most abundant in late summer and autumn (March-May), when populations have had time to increase following warm temperatures and summer rainfall. Damage to plants is also greatest at this time, with many infestations becoming substantially defoliated and exhibiting little new growth, flowers or seed.

Despite the occasional substantial damage to individual plants by the various control agents, lantana is not under adequate control in Australia. During the dry, winter months, plants can often become leafless and be void of flowers and seeds and insect numbers can dramatically decrease (Broughton, 2000a). Some agents enter diapause, while populations of other species probably retreat to areas where plants are able to retain leaves and produce flowers. Lantana plants can readily recover from defoliation in the spring after rain,

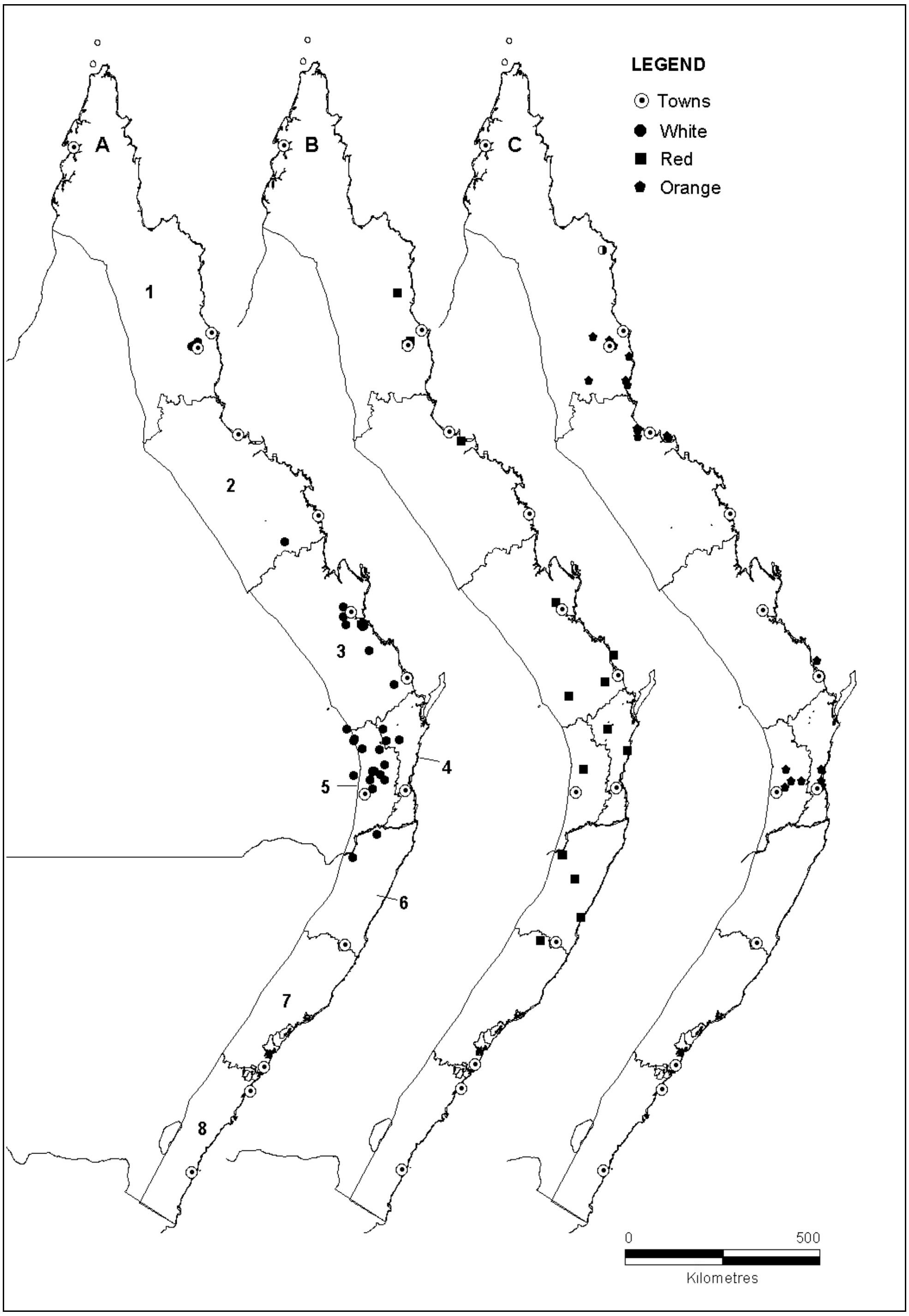

Figure 5. Distribution of the lantana varieties (A) white, (B) red and (C) orange in eastern Australia (prepared using Arcview®).

when insect numbers are low and before insect populations can increase to damaging levels. Therefore, some biological control agents can seasonally damage lantana, but insect populations are not maintained at levels high enough to consistently control the weed.

Climate appears to play a significant role in the distribution of all agents on lantana. Most agents are more abundant north of 31ºS where winter temperatures are warmer. South of 31ºS, agents are found in low numbers and their populations do not necessarily increase to damaging numbers, even over summer. Altitude also influences the distribution and abundance of agents. In the regions south of 29ºS, slight rises in elevation (~200 m above sea level) can cause a significant reduction in agent abundance and damage to lantana plants. Further south at sea level, shading by tree canopy can reduce temperatures and light, leading to a substantial reduction in insect numbers compared to sites where lantana is growing in open conditions.

Apart from temperature, rainfall and humidity also appear to influence insect distribution and/or abundance. Many areas in the inland southeast region of Queensland and central Queensland, experience low rainfall (700 mm/year) and as a result, some of the agents, e.g. leaf-feeding Lepidoptera, are only found in low numbers or only during the wetter months. Other agents, such as some of the Hemiptera, prefer drier conditions and are less frequently found in coastal regions where it is wetter, or in humid areas where lantana grows under a dense canopy.

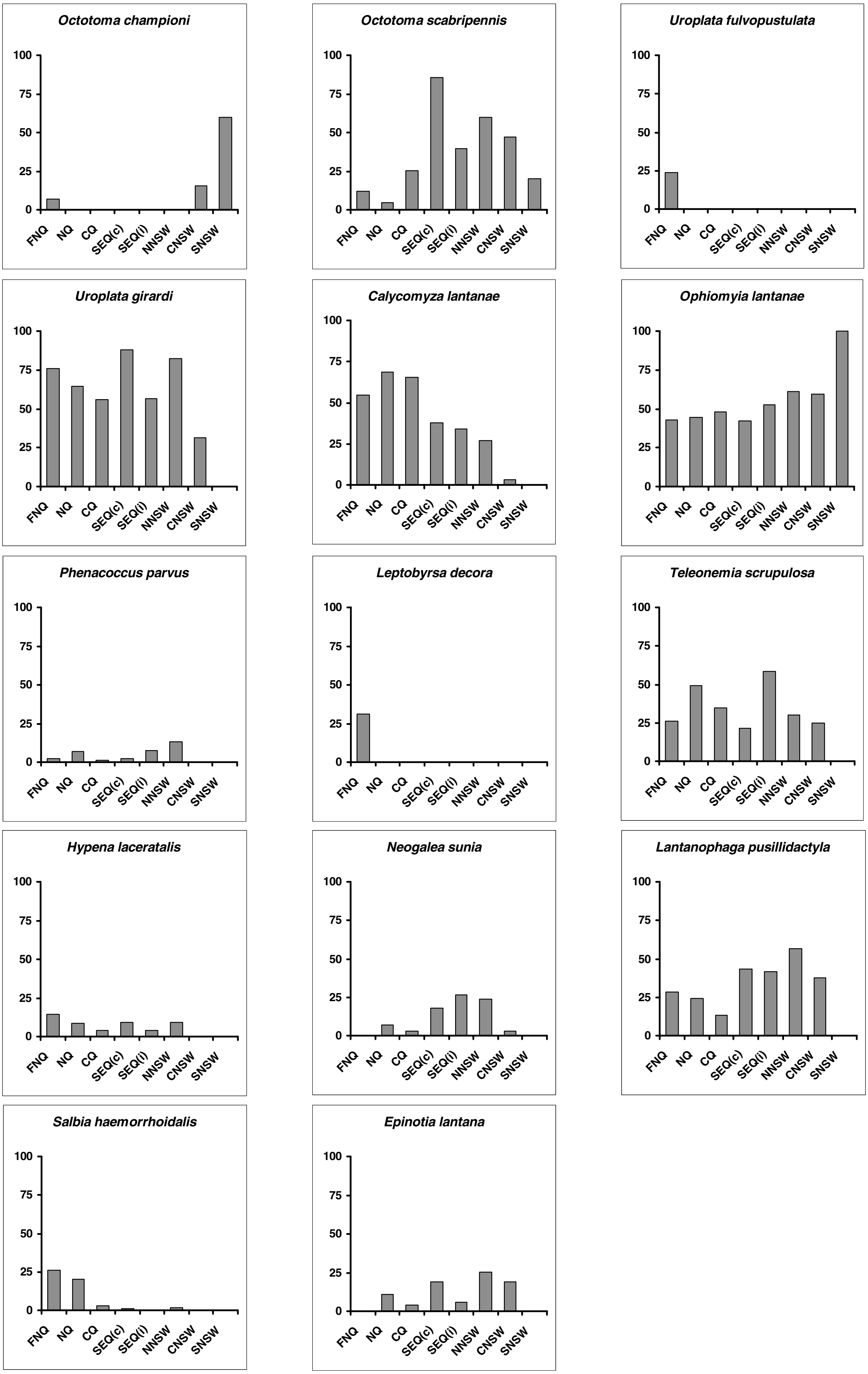

Figure 6. The percent of sites sampled in each zone (see Fig. 1) where each lantana biocontrol agent was present.

Table 1. Biological control agents of lantana released in Australia and their guild, origin, date of introduction and status.

Order	Family	Species	Guild	Country of origin	Date introduced	Status in Australia
Coleoptera	Cerambycidae	*Aerenicopsis championi*	stem borer	Mexico	1995	not established
		Plagiohammus spinipennis	stem borer	Mexico	1967	not established
	Chrysomelidae	*Alagoasa parana*	leaf feeder	Brazil	1981, 1997	not established
		Charidotis pygmaea	leaf feeder	Brazil	1994	not established
		Octotoma championi	leaf miner	Costa Rica	1975	established
		Octotoma scabripennis	leaf miner	Mexico	1966	established
		Uroplata fulvopustulata	leaf miner	Costa Rica	1976	established
		Uroplata girardi	leaf miner	Brazil	1966, 1974	established
		Uroplata lantanae	leaf miner	Brazil	1977	not established
Diptera	Agromyzidae	*Calycomyza lantanae*	leaf miner	Trinidad	1974	established
		Ophiomyia lantanae	fruit feeder	Mexico	1914, 1917	established
	Tephritidae	*Eutreta xanthochaeta*	stem gall former	Mexico	1914, 1971	not established
Hemiptera	Membracidae	*Aconophora compressa*	stem sucker	Mexico	1995	established
	Miridae	*Falconia intermedia*	leaf sucker	Jamaica	2000	too early
	Pseudococcidae	*Phenacoccus parvus*	leaf & stem sucker	unknown	1988	established
	Tingidae	*Leptobyrsa decora*	leaf sucker	Colombia	1969	established
		Teleonemia elata	leaf sucker	Brazil	1969	not established
		Teleonemia harleyi	leaf sucker	Trinidad	1969	not established
		Teleonemia prolixa	flower & bud feeder	Brazil	1974	not established
		Teleonemia scrupulosa	leaf sucker	Mexico	1936, 1969	established
Lepidoptera	Depressariidae	*Ectaga garcia*	leaf feeder	Brazil	1993, 1997	not established
	Lycaenidae	*Strymon bazochii*	flower feeder	Mexico	1914	not established
	Noctuidae	*Autoplusia illustrata*	leaf feeder	Colombia	1976	not established
		Diastema tigris	leaf feeder	Panama	1965	not established
		Hypena laceratalis	leaf feeder	Kenya	1965	established
		Neogalea sunia	leaf feeder	USA	1957	established
	Pterophoridae	*Lantanophaga pusillidactyla*	flower feeder	Mexico	1936	established
	Pyralidae	*Salbia haemorrhoidalis*	leaf feeder	Cuba	1958	established
	Tortricidae	*Epinotia lantana*	flower feeder	Mexico	1914	established
Uredinales	Puccinaceae	*Prospodium tuberculatum*	leaf rust	Brazil	2001	established

Several agents have a very limited distribution. The status and distribution of each agent found in the surveys are documented below, grouped by insect order then genus, together with information for agents previously recorded as established and for several agents that have recently been introduced. Biological and methodological factors affecting the success or otherwise of each agent are considered, including those related to rearing and field survival. Experiences with each agent in Australia and elsewhere are discussed in relation to its suitability for introduction to new countries.

Coleoptera

Aerenicopsis championi Bates (Cerambycidae)

This univoltine stem-boring beetle was released in low numbers as adults and larvae at a few sites in southern Queensland and northern NSW (Palmer *et al.*, 2000). The insect does not appear to have established at any site. High mortality in the pupal and mature larval stages in the mass-rearing programme prevented large numbers being produced for release. New rearing and release methods are currently being investigated and some release sites near Brisbane are still being monitored.

Aerenicopsis championi has the potential to be an effective agent if it can become established. Adults emerge in spring with the onset of warmer temperatures and rain. They feed on the first or second pairs of leaves, removing the mid-vein and laying eggs in the tips of branches. Larvae tunnel down the branches, killing stems and stunting the plant, resulting in smaller bushes and allowing more desirable plant species to establish. Larvae feed for 6-9 months and pupation occurs in the stem. Attempts to introduce *A. championi* into other countries should be delayed until its establishment and potential in Australia has been assessed.

Plagiohammus spinipennis (Thomson) (Cerambycidae)

This stem-boring beetle was introduced into Australia, following its success in Hawaii. Although thousands of adults were reared and released throughout Queensland and NSW over a 15-year period, the insect was reported to have established at only one site, at Willawarrin (152º38'S 30º56'E) in central NSW (Taylor, 1989). Several visits were made to this site over a three-year period in the 1990s. No larvae or adults were found and the managers of the property have not seen the insect since it was last released in the mid 1980s. The managers also reported that severe fires killed lantana plants in and around the release site in 1999.

Given that *P. spinipennis* has a poor record for establishment elsewhere, it is possible that the insects found previously at this central NSW site were progeny from newly released individuals and that the population was in fact reducing rather than establishing. We propose that *P. spinipennis* is no longer present at this release site and that it has died out in Australia.

Plagiohammus spinipennis has been released in several other countries but has only established in Hawaii, where it assists in the control of lantana in dry areas. As *P. spinipennis* is labour intensive to rear in large numbers, it is not recommended as a priority agent for release in other countries.

Alagoasa parana Samuelson (Chrysomelidae)

This univoltine leaf-feeding beetle was released at only a few sites in Queensland and NSW in 1980, as it was difficult to mass rear (Winder *et al.*, 1988; Taylor, 1989). The insect was thought to have established near Mt Glorious (27º19'S 152º45'E), northwest of Brisbane, but a fire destroyed plants in the area and the insect has not been found again (D. P. A. Sands, pers. comm.).

The beetle was re-introduced in 1997 and 1998. However, it was still difficult to rear in large numbers in the laboratory and glasshouse. A number of rearing methods were investigated, including the use of potted plants and various pupation mediums, but high mortality continued to occur in the pupal and late larval stages. In addition, newly emerged adults enter a facultative diapause stage, where they remain for six months. High mortality has been experienced during this stage as well, with less than 50% of adults surviving to the next spring and laying eggs. This equates to 10-15% of eggs completing development and surviving to egg-laying adults 12 months later.

To overcome these rearing difficulties, adults have been imported and mature first generation larvae released in the field. In 1998-1999, over 2500 first generation adults and late instar larvae were released at each of three sites; one near Grafton (29º37'S 152º56'E) in northern NSW and two near Brisbane. Both adult and larval stages initially fed on lantana, but *A. parana* has not been found at any site during the following seasons.

The rearing and release programme of *A. parana* has ceased in Australia due the lack of field establishment, the difficulties in rearing the insect in large numbers and its ability to complete only one generation per year. Therefore, *A. parana* is not recommended for introduction or release in other countries.

Charidotis pygmaea Klug (Chrysomelidae)

This leaf-feeding beetle was introduced to control *L. camara* and creeping lantana *Lantana montevidensis* (Sprengel) Briquet. *Lantana montevidensis* is predominantly a garden plant, but a weedy form has invaded pastures of central Queensland. Early releases were conducted on both species. Subsequent laboratory preference experiments showed that the beetle preferred *L. montevidensis* and it was then reared and released on this species only (Day *et al.*, 1999). *Charidotis pygmaea* was released at 40 sites throughout southern and central Queensland. It failed to establish on either species, probably due to the unsuitability of host plants and/or climate (Day & McAndrew, 2002). Therefore, *C. pygmaea* is not recommended as a priority agent for other countries.

Octotoma championi Baly (Chrysomelidae)

This is one of five leaf-mining hispine beetles introduced to Australia (Broughton, 1998). It has been released throughout NSW and Queensland and was thought to have established only around Sydney (Taylor, 1989; Broughton, 1998; Julien & Griffiths, 1998). More recently, the beetle has been found at several locations, albeit in low numbers, from Mt Dromedary north to Terrigal (33º26'S 151º26'E) in central NSW. It has also been found in low numbers at several sites on the Atherton Tableland (17º30'S 145º30'E) in far-north Queensland, with altitudes between 750 and 850 m (Fig. 6). It has not been found at any site between central NSW and northern Queensland.

Octotoma championi is mainly found on the pink flowering lantana, the predominant variety of central and southern NSW. However, it is also found on the pink-edged red flowering variety on the Atherton Tableland.

Octotoma championi is found in only low numbers and causing minimal damage to lantana. It has not established in the other three countries where it was introduced (Julien & Griffiths, 1998), and therefore is not recommended as a priority agent for other countries wishing to control lantana.

Octotoma scabripennis Guérin-Méneville (Chrysomelidae)

This is one of the most widely distributed and damaging agents present on lantana in Australia (Broughton, 1998). It is found from Wollongong (34º25'S 150º54'E) in southern NSW to the Atherton Tableland (Fig. 6). The beetle has been reported around Darwin, but it is not known how it arrived there. It is most abundant from Kempsey to Bundaberg (24º52'S 152º20'E) in Queensland. It prefers mild climates, generally being found along the coast. It is uncommon at latitudes south of 32ºS or at altitudes greater than 200 m south of 29ºS. *Octotoma scabripennis* is only found at a few sites north of 24ºS, at high altitudes where temperatures are milder.

Octotoma scabripennis can cause severe defoliation of plants on a seasonal basis, particularly near Grafton and Brisbane. Damage is greatest in late summer and autumn, with affected plants containing over ten adults per branch and producing very few flowers. Insect numbers decrease in winter when conditions become cool and dry and plants become leafless and void of flowers. While plants can be severely damaged seasonally by *O. scabripennis*, lantana infestations are not necessarily permanently suppressed nor is control achieved. In marginal areas such as southern NSW or at higher altitudes, damage to lantana is minimal. *Octotoma scabripennis* is found on all Australian lantana varietal groups.

Octotoma scabripennis has established in six of the 12 countries in which it has been introduced. In those countries with other established agents, it achieves partial to moderate control of lantana (Julien & Griffiths, 1998). It is one of the most beneficial agents to introduce into countries where lantana is a problem. It has fed slightly on several plant species in host specificity tests namely, *Sesamum indicum* L., (sesame; Pedaliaceae) *Vigna unguiculata* (L.) Walpers and *Phaseolus vulgaris* L. (common bean; Fabaceae) and *Tectona grandis* L.f. (teak; Lamiaceae), although there was no oviposition (Harley, 1969). Thus, countries considering the introduction of this agent should conduct host specificity testing to determine its risk to desirable plant species first.

Uroplata fulvopustulata **Baly (Chrysomelidae)**

This is one of three leaf-mining hispine beetles from the genus *Uroplata* to be introduced into Australia. It is found only in far-north Queensland, usually in moderate numbers, despite being released in northern NSW and throughout Queensland. However, large numbers causing moderate damage have been observed around Tinaroo (17º08'S 145º32'E) on the Atherton Tableland. It is found on pink-edged red and pink flowering varieties of lantana. The other lantana varieties are not present in the areas in which the beetle occurs.

It is thought that the cooler temperatures further south may have contributed to the beetle's failure to establish in NSW (Taylor, 1989), while many release sites in Queensland experience a lengthy dry season or become too hot in summer.

Uroplata fulvopustulata has been introduced to only two other countries, Fiji and South Africa and has failed to establish in either country. As the insect is found at only a few sites and causes minor damage to lantana in Australia, it is not considered as a high priority agent for other countries.

Uroplata girardi **Pic (Chrysomelidae)**

This is one of the most widespread and damaging agents present on lantana in Australia (Broughton, 1998). It is found from Sydney to Cow Bay and has been reported around Darwin (Fig. 6). The beetle is generally found in low numbers south of Kempsey or at altitudes greater than 200 m south of 29ºS. It is more common in the warmer, drier areas, particularly in the subcoastal regions of southern and central Queensland. Here, it can be quite damaging and is often one of only a few agents present. *Uroplata girardi* is also found in shaded rainforest areas and at altitudes of 700 m at latitudes north of 27ºS, but the damage to the plants is usually minimal. It causes similar damage to that by *O. scabripennis* and the two species are often found together, resulting in substantial defoliation on a seasonal basis. Like *O. scabripennis*, populations of *U. girardi* decrease in the dry winter months and are not maintained at high enough levels to control lantana. The beetle is found on all lantana varieties.

Uroplata girardi has established in 24 of the 26 countries in which it has been introduced and in some countries, such as the Solomon Islands, it is the dominant agent damaging lantana (Scott, 1998). As *U. girardi* is widespread and damaging, it would be a very worthwhile agent to consider introducing for lantana control in countries where it is not already present.

Diptera

Calycomyza lantanae **(Frick) (Agromyzidae)**

This leaf-mining fly from Trinidad is found from Sydney to Cairns (16º50'S 145º41'E) (Fig. 6). It has also been reported around Darwin, although there has been no deliberate attempt to establish it there. It is more common in Queensland than NSW, as it prefers warm, moist areas, with populations building up over summer following rain. Populations are greatest in late summer and autumn. In some areas in the tropics, most of the leaves contain mines, while around Sydney and the more temperate areas, populations are usually smaller, resulting in little damage to plants.

Calycomyza lantanae is found on all five varietal groups of lantana, contradicting a report by Harley & Kassulke (1974), who suggested that it preferred the pink-edged red flowering varieties to the pink flowering varieties. This earlier report may have arisen as a consequence of *C. lantanae* not being abundant in cooler areas, where only the pink flowering varieties exist. Recent surveys indicate that the fly can heavily damage pink flowering lantana in warm, moist areas, such as those in most parts of coastal Queensland.

Calycomyza lantanae is also common on two other introduced species, *L. montevidensis* in southeast and central Queensland, and *Lippia alba* (Miller) N. E. Brown (Verbenaceae) in central Queensland. *Lippia alba* has only a limited distribution, being found near Blackwater (23º33'S 148º45'E) in central Queensland and in far-north Queensland in Lakefield National Park (15º15'S 144º11'E).

The fly has established in 15 countries worldwide. It has established in all countries in which it has been deliberately introduced, as well as in a number of other countries through natural spread (Julien & Griffiths, 1998). The female inserts its eggs into fresh leaves and the larvae feed between the upper and lower leaf surfaces, causing dark blotches to form. Pupation occurs in the leaf. The fly has the ability to increase in numbers very quickly under favourable conditions. While it is unlikely to control lantana on its own, it may make a valuable contribution in reducing the spread of lantana in tropical countries that have no or few lantana biocontrol agents. However, countries considering the introduction of *C. lantanae* are advised to conduct preliminary surveys to determine whether the agent is already present.

Ophiomyia lantanae **(Froggatt) (Agromyzidae)**

The seed-fly *O. lantanae* was one of the first agents to be introduced into Australia in 1914 and is now present in almost all areas where lantana occurs, including Darwin and Perth. The southerly limit of its distribution is Mt Dromedary, where it is found in low numbers, even in midsummer. It is also found in low numbers at altitudes greater than 200 m in temperate areas (29-31ºS). Further north, the fly is common in warm, humid areas where lantana flowers and sets seed readily (Fig. 6).

Ophiomyia lantanae is found on all lantana varietal groups. The fly can damage up to 85% of fruits in late summer or autumn, but is less common in winter when temperatures are cooler and flowering is reduced. It feeds on the fleshy pulp surrounding the seed but does not damage the embryos (Broughton, 1999). Fruit damaged by *O. lantanae* are thought to be less attractive to birds (Denton *et al.*, 1991), which are the main vectors for the spread of lantana. The germination rate of lantana seeds is generally increased if the seeds are passed through the gut of birds where the surrounding fleshy pericarp is removed (Beeson & Chatterjee, 1939; Swarbrick *et al.*, 1998). Consequently, the presence of *O. lantanae* may decrease the dispersal of lantana (Taylor, 1989). However, due to the enormous quantities of seed produced by lantana plants, there are still many fruits left undamaged by *O. lantanae*, even when populations of the fly are at their highest.

Ophiomyia lantanae has established in 23 of the 28 countries in which it was introduced. In most countries, it causes damage to fruits at levels similar to that in Australia. However, much of the information has not been quantified, and in other countries its status is unknown (Julien & Griffiths, 1998). It would be a worthwhile agent to introduce into countries where no or few agents have been introduced. Countries considering the introduction of this agent should conduct surveys to determine whether it is already present.

Hemiptera

Aconophora compressa Walker (Membracidae)

This stem-sucking bug has been found on several lantana varietal groups, at numerous sites around Brisbane, near where most of the rearing of the insect was conducted, and around Terrigal. In both areas, branches of affected plants have died and there appears to be reduced flowering and seeding compared to uninfested lantana growing nearby.

Around Brisbane, *A. compressa* has been found on pink and pink-edged red flowering bushes up to 10 km away from the points of release. At Terrigal, the insect is present on pink flowering lantana up to 0.5 km from the release site. It is also present in low numbers on pink flowering lantana at Jamberoo (34º39'S 150º47'E) in southern NSW and Iluka (29º23'S 153º21'E) in northern NSW, white flowering lantana around Kooralgin (26º55'S 151º54'E) in the inland southeast region of Queensland, and pink-edged red flowering lantana near Mt Fox (18º53'S 145º53'E) in north Queensland. First and possibly second generation (after release) nymphs and adults have been found at approximately 20 other sites in both Queensland and NSW. However, it is too early to determine if the insect has definitely established at these sites.

There have been major difficulties in achieving establishment of *A. compressa*, with populations at some earlier release sites being killed by heat waves (maximum day temperature >40ºC) or floods. At several sites around Wivenhoe Dam (27º20'S 152º36'E) northwest of Brisbane and Kooralgin, the insect appeared to establish and was slowly spreading, but populations were destroyed by adverse conditions. Populations tend to build up in winter and subside during the hot summer months. The insect has not established in areas that are high in humidity or when canopy cover is greater than about 50%.

In Brisbane, *A. compressa* has been found breeding on *Citharexylum spinosum* L. (fiddlewood, Verbenaceae), an introduced species used in parks and gardens in suburban areas. Occasional feeding by adults and nymphs has also been observed on several introduced species and one native species growing near large populations of *A. compressa*. These include: *Duranta erecta* L., *Stachytarpheta cayennensis* (Richard) Vahl, *Stachytarpheta mutabilis* (Jacquin) Vahl (Verbenaceae), *Jacaranda mimosifolia* D. Don. *Pandorea pandorana* (Andrews) Steenis, *Tecoma stans* (L.) Kunth (Bignoniaceae) and *Baccharis halimifolia* L. (Asteraceae). However, populations of *A. compressa* could not be sustained on these plants and damage was negligible (Day & Snow, unpublished data).

Aconophora compressa is no longer being reared for field release, although field monitoring of this agent will continue, to assess its ability to spread and colonize new areas. It shows potential as a damaging agent against lantana. However, its ability to feed on other closely related species may be of concern for countries where such species are native or deemed desirable. For example, entomologists in South Africa did not release *A. compressa*, as experiments showed that it has the potential to attack native species of *Lantana* and *Lippia* (A. Urban, pers. comm.). Countries considering the introduction of this agent should first conduct host specificity tests on closely related or desirable plant species.

Falconia intermedia (Distant) (Miridae)

This sap-sucking bug was approved for release in 2000. The insect has been released at approximately 50 sites throughout Queensland and parts of NSW. It failed to establish at some sites in both states due to heatwaves and/or drought. At other sites, such as in north Queensland, insects have appeared to persist for several generations. However, it is too early to determine its impact on lantana at those sites. In laboratory experiments, *F. intermedia* fed and laid eggs on all lantana varieties tested. However, development through to adult was poorer on the common pink flowering variety in Australia (Day & McAndrew, 2003).

In South Africa, the insect has established in a large number of sites and is reportedly causing substantial damage to lantana at some of these (Baars, 2000). It feeds on the intercellular tissue causing necrosis and premature abscission of leaves. Damaged plants can become stunted, producing fewer flowers and seeds. *Falconia intermedia* prefers warm, humid conditions and may be a suitable agent for tropical areas where lantana is in leaf all year round.

Phenacoccus parvus Morrison (Pseudococcidae)

This mealybug was reported to have been accidentally introduced into Australia in 1988. It quickly established and spread throughout southern Queensland (Marohasy, 1997). In the recent surveys, it was found in isolated populations from Kempsey to the Atherton Tableland, as well as around Perth (Fig. 6). *Phenacoccus parvus* is most common in northern NSW and southern Queensland, where it can periodically cause severe damage to plants. In the dry years of the mid 1990s, landholders in the inland southeast region of Queensland reported significant dieback of lantana due to the mealybug. In the late 1990s when normal rain patterns returned to the district, mealybug numbers reduced dramatically and lantana began to recover.

Damage by *P. parvus* was also very noticeable in northern NSW in the late 1990s, while a localized population was causing severe damage to plants on the Atherton Tableland in 2001. Elsewhere along the coastal and subcoastal regions, the mealybug has only appeared as small populations in localized areas.

Phenacoccus parvus has been reported attacking several economically important plants such as tomato and aubergine (eggplant) in the family Solanaceae (Marohasy, 1997) and is therefore not recommended for release in other countries.

Leptobyrsa decora Drake (Tingidae)

This species was released in large numbers throughout Queensland and NSW. However, it has been found at only five sites on the Atherton Tableland, at altitudes of about 750 m (Fig. 6). It reaches damaging numbers in late summer in open, sunny areas and plants attacked by *L. decora* have fewer leaves, flowers and seeds than uninfested lantana plants growing under similar conditions nearby. It is not found where lantana grows under dense canopy or in high rainfall areas. The tingid is found on the pink and pink-edged red flowering varieties of lantana. How it performs on the other varieties is not known as these were not found on the Tableland during the recent surveys. In NSW and southern Queensland, the winter period in which *L. decora* is non-reproductive is longer than in the tropics. This may partially explain why the insect has failed to establish in those areas (Taylor, 1989).

Leptobyrsa decora was released in 10 countries with varying success. It has established and is spreading slowly in Hawaii, but failed to establish in South Africa, Ghana and a number of countries in the South Pacific (Julien & Griffiths, 1998). The reasons for its failure in these countries are not fully understood. *Leptobyrsa decora* developed on *Tectona grandis* and as a consequence was not released in India (Muniappan & Viraktamath, 1986). Countries considering the introduction of this agent should conduct host specificity tests on desirable species first. Provided *L. decora* passes host specificity testing, it could be useful in controlling lantana in open, high altitude tropical regions similar to that of the Atherton Tableland.

Teleonemia harleyi Froeschner (Tingidae)

Only about 250 adults of this species were released in southeast Queensland (B. W. Willson, unpublished data) and it was reported to have established at only one site (Julien & Griffiths, 1998). However, several visits to the site from 1998-2000 failed to recover this agent. The tingid is very similar in appearance to the very common and widespread *Teleonemia scrupulosa*, so it is possible that *T. harleyi* may have been confused with *T. scrupulosa* and/or overlooked.

As a consequence of the low numbers released and the fact that the insect was not located despite several visits to the site during recent surveys, we propose that *T. harleyi* has not established in Australia. It has not been released in any other country and is not recommended for introduction to other countries.

Teleonemia scrupulosa Stål (Tingidae)

This is one of the most widespread and damaging agents of lantana. It is found from Sydney to Cairns (Fig. 6) and is present around Darwin. It prefers drier, more exposed regions and is rarely found in areas with high rainfall or where lantana grows under dense canopy. It is more common on north-facing than south-facing slopes. *Teleonemia scrupulosa* can cause substantial defoliation of lantana on a seasonal basis, resulting in plants producing fewer new shoots and flowers. It has been particularly damaging in the dry regions of central NSW and southern and central Queensland.

In central and north Queensland, lantana plants growing in exposed paddocks are heavily damaged by *T. scrupulosa*, while plants growing under trees lining the paddocks contain very few insects. Noticeable differences in abundance and attack are also observed in the inland southeast region of Queensland, where lantana plants growing on north-facing slopes are substantially more damaged by *T. scrupulosa* than plants on the cooler south-facing slopes.

Teleonemia scrupulosa is occasionally found in greater numbers (or is only present) on the pink-edged red or white flowering varieties compared to the pink flowering varieties growing at the same site. While these observations suggest that *T. scrupulosa* may prefer other varieties to the pink flowering variety, the tingid will heavily attack pink flowering lantana if growing in favourable climatic conditions where other varieties are not present. It has not been possible to determine the agent's preference for the white or pink-edged red flowering plants as the two varieties have rarely been found growing together.

Teleonemia scrupulosa has established in 29 of the 31 countries in which it has been introduced and is regarded as one of the most damaging agents on lantana (Muniappan *et al.*, 1996; Julien & Griffiths, 1998). It has been reported to feed on other plant species, namely *Myoporum sandwicense* A. Gray (Myoporaceae), *Xanthium* sp. (Asteraceae), *Brya ebenus* (L.) DC (Fabaceae), *Lippia alba* and *Sesamum indicum*, although it is not considered a problem on these species (Davies & Greathead, 1967). *Teleonemia scrupulosa* should be a high priority for any country where lantana is a problem. However, countries considering the introduction of this agent should first conduct host specificity testing on those plant species considered desirable.

Lepidoptera

Ectaga garcia Becker (Depressariidae)

This leaf-feeding moth was released as adults, pupae and larvae, using caged and uncaged techniques, at approximately 40 sites in Queensland and NSW. Subsequent monitoring of the release sites failed to confirm establishment at any site. Detailed studies of release sites near Brisbane and Grafton showed that less than 20% of first generation eggs developed to the pupal stage.

Ectaga garcia was collected from *Lantana tiliifolia* Chamisso and *Lantana fucata* Lindley in Brazil and it is possible that the low survival of eggs to adults may be attributed to lantana in Australia being a less suitable host (Day & Neser, 2000). The insect is not being considered for further work in Australia and it is not recommended for use in other countries where lantana is a problem.

Hypena laceratalis Walker (Noctuidae)

This moth was introduced from Kenya in 1964 but was later found to be already present in Australia. It is not known whether *H. laceratalis* is native to Australia or whether it was brought in accidentally on introduced plants. It is more common in the tropical and subtropical regions of Queensland, but small populations are found in NSW, south to Kempsey (Fig. 6). It does not show preference for any lantana variety, occurring on most varieties. Although it has never been recorded on the orange flowering varieties, this is probably a consequence of the limited distribution of orange flowering lantana and the limited number of times this varietal group has been sampled, rather than any preference by the moth (Fig. 3). *Hypena laceratalis* has also been found on *L. montevidensis* in moist areas around Brisbane and central Queensland.

Hypena laceratalis is most common late in the season, when plant growth is lush and insect populations have had a chance to increase over summer. Damage to lantana is seasonal and localized and, even under favourable conditions, is not sufficient to control lantana.

Hypena laceratalis has been introduced and established in 14 countries, with varying levels of success. In Indonesia, the Philippines and South Africa, it is thought that parasites might be limiting populations to levels where the agent is ineffective (Greathead, 1971; Cock & Godfray, 1985; Cilliers & Neser, 1991). In more remote islands, such as Hawaii, there are relatively few parasitic species present and *H. laceratalis* appears to be more damaging. *Hypena laceratalis* would be a valuable agent to introduce to other countries, if the parasitism levels there remain low.

Neogalea sunia (Guenée) (Noctuidae)

Neogalea sunia is found from Sydney, where it occurs in low numbers, to Mt Fox (Fig. 6). It is particularly common in the drier regions of northern NSW near Grafton and throughout the subcoastal regions of southern Queensland. Together with other biocontrol agents, *N. sunia* can seasonally defoliate plants, reducing the development of new shoots.

Neogalea sunia is found on all lantana varieties except for the orange flowering variety. This dispels earlier suggestions by Diatloff & Haseler (1965) that the moth prefers the red, pink-edged red and white flowering varieties to the pink flowering varieties. The orange variety has been found at only a limited number of locations and has therefore been sampled less frequently so *N. sunia* could easily have been missed. Larvae are well camouflaged, lying longitudinally along the stems during the day and thus are hard to detect. However, cocoons containing pupae are easily seen on the tips of branches, especially during the dry months when plants have lost much of their foliage.

Neogalea sunia has been introduced to five countries but has only established in Hawaii and New Caledonia (Julien & Griffiths, 1998). It is not known why it failed to establish in South Africa and Micronesia but it is not regarded as a high priority agent for other countries.

Lantanophaga pusillidactyla (Walker) (Pterophoridae)

This flower-feeding moth appears to have been accidentally introduced, possibly brought in on imported plants (Julien & Griffiths, 1998). It is one of the most widespread biological control agents for lantana in Australia, and is found on all varieties from Sydney to Cow Bay (Fig. 6). It is also been found on *Lippia alba* in central Queensland and is common on *Lantana montevidensis* in both naturalized populations and gardens in southern Queensland and northern NSW.

Lantanophaga pusillidactyla is more common in the warmer coastal regions but small numbers have been found in the temperate, higher altitude, subcoastal areas. Populations are greatest in late summer, although the agent appears to have limited impact on lantana, with plants still producing many seeds. Lantana plants flower profusely after rain and moth populations are unable to increase to the same extent, resulting in large numbers of undamaged flowers, producing many seeds.

Lantanophaga pusillidactyla has established in 11 countries worldwide. It has established in all countries in which it has been introduced and has naturally spread to several others. In most countries it causes minimal damage. However, in Micronesia, it assists *Epinotia lantana* in reducing seed production by up to 80% (Denton *et al*., 1991). *Lantanophaga pusillidactyla* may assist in the control of lantana in many regions. However, countries considering the introduction of this agent should conduct surveys to determine whether it is already present.

Salbia haemorrhoidalis Guenée (Pyralidae)

This is one of three leaf-feeding moths to have established in Australia. It is found from northern NSW to far-north Queensland (Fig. 6), being more abundant in the warm, moist tropical regions. *Salbia haemorrhoidalis* is the dominant agent present at some sites on the Atherton Tableland with altitudes between 700 and 750 m, and where lantana grows at the edge of rainforests or pine plantations. It is also common at altitudes of 750 m southwest of Ingham (18°39'S 146°04'E) in north Queensland. It is found around Brisbane, but not in the drier subcoastal regions of southern and central Queensland.

Salbia haemorrhoidalis is found on both pink and pink-edged red flowering lantana, dispelling earlier reports (Diatloff & Haseler, 1965) that it prefers the red and pink-edged red flowering varieties to the pink flowering varieties. The moth is also found on the less common orange and the red flowering varieties in north Queensland.

Salbia haemorrhoidalis has established in seven of the 13 countries in which it has been introduced. As it only causes moderate damage to lantana in a limited number of areas, it is not recommended as a high priority for introduction into other countries.

Epinotia lantana (Busck) (Tortricidae)

This was one of the four original agents imported into Australia in 1914. Larvae of the moth feed on flowers and/or bore into shoot tips or flower peduncles. The moth is found throughout most areas where lantana occurs. However, it is generally more common in warmer coastal districts of southeast Queensland and northern NSW. Its most southerly distribution is around Gosford (33°31'S 151°22'E) in central NSW, where it is found in only low densities (Fig. 6).

Although *E. lantana* can be seasonally abundant, the moth does not appear to have a significant impact on the plant. Even in areas where *E. lantana* is abundant, seed production is quite high. It has established in all nine countries in which it has been introduced, but control has been variable. The impact of *E. lantana* appears to be significant in tropical islands in the Pacific, and seed production has been reduced by up to 80% in Micronesia (Denton *et al*., 1991). *Epinotia lantana* may prove useful in tropical islands that have no or few lantana biocontrol agents present. However, countries considering the introduction of this agent, should conduct surveys to determine if it is already present.

Mycocetes

Prospodium tuberculatum (Spegazzini) Arthur (Uredinales, Puccinaceae)

This is the first rust and the 30th agent to be released on lantana in Australia. It was first released in 2001 and has now been released throughout Queensland and NSW. Releases are continuing in both states. Spores are wind-dispersed and attach to the underside of leaves. They cause premature abscission of leaves, resulting in a reduction of new growth and stunting of plants. *Prospodium tuberculatum* is highly specific, affecting only the common pink flowering variety in Australia (Tomley & Riding, 2002). So far, establishment has been confirmed in only southeast Queensland and northern NSW. It is too early to confirm whether the agent has established at other sites or what impact it will have on lantana (A. Tomley, pers. comm.). Countries wishing to import this agent are advised to wait until its effectiveness is evaluated. Pathogenicity testing on potential host varieties of lantana to determine if those varieties are susceptible should be conducted prior to importation.

Conclusion

The most widespread and damaging agents to lantana in Australia are *Octotoma scabripennis, Uroplata girardi* and *Teleonemia scrupulosa*. Several other agents, notably *Calycomyza lantanae, Epinotia lantana, Hypena laceratalis*, *Lantanophaga pusillidactyla* and *Ophiomyia lantanae* are also widespread and seasonally abundant, but have less impact on lantana. *Leptobyrsa decora* is also very damaging but has a limited distribution, preferring the high altitude tropical regions. Although 16 agents have established on lantana in Australia and many are quite widespread, it is clear that the weed is still not under adequate control.

Climate appears to play a significant role in controlling the distribution and abundance of agents, with many species having only a limited geographical range or being only seasonally abundant and damaging. The long dry winters in eastern Australia can cause defoliation of lantana, causing leaf-feeding insect numbers to decline. Plants are able to re-shoot following warm weather and spring rains and, without the presence of large numbers of insects, can once more dominate other vegetation. Plants become severely damaged again late in the season once insect numbers have increased. Therefore, climate and the weed's response to climate appear to limit the ability of agents to increase and maintain population levels sufficiently high to control lantana (Broughton, 2000b).

Research into the biocontrol of lantana is continuing, with several new agents being studied in either Australia or South Africa. These agents include the budmite *Aceria lantanae* (Cook) (Acari, Eriophyidae), the petiole galling apionid *Coelocephalapion camarae* Kissinger (Col., Brentidae), the leaf-feeding beetle *Alagoasa extrema* Jacoby (Col., Chrysomelidae), the herring-bone leaf-miner *Ophiomyia camarae* Spencer (Dipt., Agromyzidae), the root-feeding beetle *Longitarsus* sp. (Chrysomelidae) and two plant pathogens *Mycovellosiella lantanae* (Chupp) Deighton (Mycosphaerellales: Mycosphaerellaceae) and *Puccinia lantanae* Farlow (Uredinales, Puccinaceae) (Baars & Neser, 1999). It is hoped that these agents, if approved for release, will further damage lantana and achieve better control of the plant in Australia. In countries where lantana is a major problem, and few, if any agents have established, some of the more widespread and damaging agents established in Australia or elsewhere could be introduced to assist in the control of lantana. These should include *Octotoma scabripennis, U. girardi* and *T. scrupulosa*. Countries wishing to import any agent should first conduct surveys to determine whether the agent is already present and then conduct additional host specificity studies against their desirable plant species.

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