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Factors Influencing the Biological Control of *Lantana camara* in Australia and South Africa

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Abstract

The insect species introduced into Australia and South Africa as potential biological control agents of *Lantana camara* (lantana) were reviewed to determine factors that may have contributed to the high proportion of candidates that failed to establish on the plant. Fourteen of the 25 candidates deliberately introduced into Australia and five of the 15 introduced into South Africa have established.

A greater proportion of candidates that were collected from *L. urticifolia* or *L. tiliifolia* established in Australia and South Africa than those collected from other *Lantana* species. DNA studies suggest that *L. urticifolia* and *L. tiliifolia* are more closely related to *L. camara* than other species of *Lantana* and therefore a candidate's natural host may influence its establishment on *L. camara*. Some preference towards different lantana phenotypes has been observed in eight species, while there appeared to be no preference towards phenotypes in three species.

Climate appears to be an influencing factor in the distribution of agents with only two species in Australia and South Africa being found in all lantana regions. The remaining species have distributions ranging from very localised to more widespread. The release methods used and the numbers of individuals released may have contributed to at least five species in Australia and up to eight in South Africa not establishing.

The main factors influencing the establishment of agents on lantana appear to be: (a) the identity of the plant from which the potential agent had been collected; (b) the phenotype of lantana on which it had been released; (c) the climate of the area where it had been released and; (d) the release procedures used. Future research into the biological control of *L. camara* should consider addressing these areas which may result in greater establishment rates of candidates and better control of lantana.

Introduction

Deliberate attempts at the biological control of weeds first began in 1902, when a shipment of 23 insect species were sent from Mexico to Hawaii to control *Lantana camara* L. (Perkins and Swezey 1924). Since then over 100 weed species have been the subject of biocontrol programs, with a total of over 500 species introduced for their control. However, only 64% of organisms introduced have established, with fewer than half of the weeds being under some control (Julien *et al.* 1984). In many instances, there is little substantiated information to explain why many of the weed species are not under control, or why agents have not established.

L. camara is one weed where biological control has not been achieved, despite exten-

sive efforts. It originated from tropical America and was cultivated in glasshouses in Europe for some centuries, prior to its introduction into Australia, South Africa and many other countries in the mid 1800s. *L. camara* hybridises easily with other entities and there are now reportedly over 650 recognised horticultural varieties or phenotypes worldwide (Howard 1969), with 29 occurring in Australia (Smith and Smith 1982) and reportedly up to 40 in South Africa (Graaf 1986).

Thirty-six candidates have been released on lantana in 32 countries, with the resulting control ranging from inadequate to good (Julien and Griffiths 1998). Islands such as Hawaii, Guam and the Solomons have reported good biological control in some areas by a suite of agents while lantana is still a serious problem in Australia, central and South Africa, Asia and many parts of the South Pacific (Neser and Cilliers 1989; Swarbrick *et al.* 1995; Munniapan *et al.* 1996; L. Scott pers. comm.). Only 14 of the 25 species in Australia and five of the 15 species in South Africa that were deliberately introduced have established, with just four of these causing significant damage to the weed in both countries. An additional three species in Australia and six species in South Africa were brought in unintentionally, probably on imported *L. camara* plants.

Four factors have been proposed as critical to the establishment of agents; the plant species from which potential agents were collected, the phenotype of the target weed, the climate where the agents have been released, and the release strategies used (Sands and Harley 1980; Neser and Cilliers 1989; Harley and Forno 1992; Willson 1993). This paper evaluates these factors with respect to the *L. camara* biological control program and suggests methods to overcome them.

The effect of the original host species

The taxonomy of the genus *Lantana* is not fully understood and for many years entomologists surveyed, sampled and collected potential agents from a number of lantana entities in Mexico, the Caribbean and Brazil. However, recent work in Australia, South Africa and the USA has improved the understanding of the *Lantana* genus. Stirton (1977) and R. Sanders (unpubl. data) suggest that *L. camara* is a hybrid species and part of a complex, consisting of several species of lantana, all morphologically similar but with visible variations in flower colour, spininess of the stems and hairiness of the leaves. As a result of hybridisation, there is no naturally occurring lantana species that matches any of the lantana phenotypes occurring in Australia, South Africa or other countries (L. S. Smith unpubl. data).

DNA studies at the Cooperative Research Centre for Tropical Pest Management in Brisbane, together with the findings of R. Sanders (unpubl. data), suggest that the progenitors of *L. camara* may have originated in the Caribbean or Mexico. Seven out of ten agents from Mexico and five out of six agents from the Caribbean have established in Australia, while only one agent from Brazil has established (Table 1). It is interesting though, that the one agent from Brazil that established, *Uroplata girardi* Pic, was collected from *Lantana tiliifolia* Chamisso and is now one of the most damaging agents of *L. camara* in Australia and South Africa (Cilliers and Neser 1991; Swarbrick *et al.* 1995).

In addition, DNA studies showed that *L. camara* phenotypes in Australia, Vanuatu and Fiji have the closest affinity to *Lantana urticifolia* Miller from Mexico, but are also close to *L. tiliifolia* (considered a subspecies of *L. urticifolia* R. Sanders unpubl. data) from Brazil (Scott 1998). There is also a suggestion that the phenotypes of *L. camara* in other countries may have originated from different lantana species, as phenotypes in the

Solomons and Hawaii are quite different to those found in Australia (Scott 1998).

The differences in phenotypes between countries may partly explain why some agents have established in some countries but not others. *Eutreta xanthochaeta* Aldrich and *Strymon bazochii* Godart established in Hawaii, but failed to establish in Australia and South Africa (Table 1), even though Hawaii has fewer lantana phenotypes and a narrower climatic range than Australia or South Africa (Harley 1973).

Of the agents that have *L. urticifolia* or *L. tiliifolia* recorded as their native host, 11 of the 19 species introduced into Australia and 5 of the 12 species introduced into South Africa have established. For some of these agents that did not establish, other factors such as insufficient numbers released may have been contributing. Where potential agents were collected from species other than those above, only one of four species in Australia and neither of the species in South Africa established. For several species, including those unintentionally introduced, the host plant is not known (Table 1).

Effect of phenotype

The possibility that the performance of biological control agents may be influenced by the phenotype of lantana was first mentioned by Haseler (1966). He reported the moth *Neogalea sunia* Guenée showed a preference for the white and pink flowering *L. camara* while another moth, *Salbia haemorrhoidalis* Guenée, was more prevalent on red flowering *L. camara*. Harley (1973) also reported phenotypic preferences, with the tingid *Teleonemia scrupulosa* Stål not performing as well on the common pink *L. camara* as on other phenotypes. Neser and Cilliers (1989) reported that different lantana phenotypes influenced insect performance of a number of agents (eg *T. scrupulosa*) in South Africa in their paper in these Proceedings 10 years ago.

Recent studies at the Alan Fletcher Research Station (AFRS), Australia, and the Plant Protection Research Institute (PPRI), Republic of South Africa, confirm that there are differences in performance of some agents on different lantana phenotypes. Among the candidates that have established, those that failed to establish and those not yet approved for release, six species showed a preference for one or more phenotypes and ten did not show any preference (Table 2). All agents that did not show any preference for particular phenotypes in Australia or South Africa, established. However, only two species, *T. scrupulosa* and *Aconophora compressa* Walker, of the six that showed phenotype preferences, have established.

Conversely, three agents, *Ectaga garcia* Becker, *Charidotis pygmaea* Klug and *Alagoasa parana* Samuelson), that have shown preferences in laboratory trials, with populations dying out on the less preferred phenotypes, have not established in the field (Day *et al.* 1998; Day *et al.* 1999). The sixth species, *Falconia intermedia* Distant has only just been released in South Africa and it is too early to know if establishment will occur (Baars and Neser 1999). The preferences of six agents which are only found in localised areas in Australia, or which did not establish, were not determined (Table 2). A comparison of phenotype preferences of agents in South Africa and in Australia was not possible as the same phenotypes do not necessarily occur in both countries. In addition, the names used for the different phenotypes in the two countries do not necessarily confer with the same name possibly being used for different phenotypes and vice versa.

Ten agents did show any appreciable differences in preference for one phenotype over another. Two hispine beetles, *U. girardi* and *Octotoma scabripennis* Guérin-Meneville are found on all phenotypes, as are the seed fly *Ophiomyia lantanae* Froggatt and the tip

Table 1.
List of agents introduced into Australia and South Africa, the Lantana species from which they were recorded and their biocontrol status in Australia, South Africa and Hawaii.

Family	Species	Country of origin	Lantana Host species	Collected from	Establishment Australia	South Africa	Hawaii
Cerambycidae	*Aerenicopsis championi*	Mexico	u,h	*L. urticifolia*	No	Not Released	No
	Plagiohammus spinipennis	Mexico	h	*L. hirsuta*	Yes	No	Yes
Chrysomelidae	*Alagoasa parana*	Brazil	t,g	*L. tiliifolia*	No	No	Not Released
	Charidotis pygmaea	Brazil	t,f	*L. fucata*	No	No	Not Released
	Octotoma championi	Costa Rica	u,h	unknown	Yes	No	No
	Octotoma scabripennis	Mexico	u	*L. urticifolia*	Yes	Yes	Yes
	Uroplata girardi	Brazil	t	*L. tiliifolia*	Yes	Yes	Yes
	Uroplata lantanae	Brazil	t	*L. tiliifolia*	No	No	Not Released
	Uroplata fulvopustulata	Costa Rica	u	*L. urticifolia*	Yes	No	Not Released
Agromyzidae	*Calycomyza lantanae*	Trinidad	t,g,o	unknown	Yes	Yes	Not Released
	Ophiomyia lantanae[2]	Mexico	t	*L. tiliifolia*	Yes	Yes	Yes
Tephritidae	*Eutreta xanthochaeta*	Mexico	u	*L. urticifolia*	No	No	Yes
Membracidae	*Aconophora compressa*	Mexico	u,h	*L. urticifolia*	Yes	Not Released	Not Released
Miridae	*Falconia intermedia*	Jamaica	u	*L. urticifolia*	Not Released	No	Not Released
Pseudococcidae	*Phenacoccus parvus*[1]	unknown	unknown	unknown	Yes	Yes	Not Released
Tingidae	*Leptobyrsa decora*	Colombia	unknown	unknown	Yes	No	Yes
	Teleonemia elata	Brazil	t,g	unknown	No	No	Not Released
	Teleonemia harleyi	Trinidad	unknown	unknown	Yes	Not Released	Not Released
	Teleonemia prolixa	Brazil	t,g	unknown	No	Not Released	Not Released
	Teleonemia scrupulosa	Mexico	u,h,t,g,o	unknown	Yes	Yes	Yes

Family	Species	Country of origin	Lantana Host species	Collected from	Establishment Australia	South Africa	Hawaii
Gracillariidae	*Cremastobombycia lantanella*[2]	Mexico	u,h,o	unknown	Not Released	Yes	Yes
Lycaenidae	*Strymon bazochii*	Mexico	u	*L.urticifolia*	No	Not Released	Yes
Noctuidae	*Diastema tigris*	Panama	u	*L.urticifolia*	No	Not Released	No
	Hypena laceratalis[1]	Kenya	unknown	unknown	Yes	Yes	Yes
	Neogalea sunia	USA	u,t,g,o	unknown	Yes	No	Yes
	Notioplusia illustrata	Costa Rica	m,s,r	unknown	No	Not Released	Not Released
Oecophoridae	*Ectaga garcia*	Brazil	t,f	*L. fucata*	No	Not Released	Not Released
Pterophoridae	*Lantanophaga pusillidactyla*[1]	Mexico	u,h	unknown	Yes	Yes	Yes
Pyralidae	*Salbia haemorrhoidalis*	Cuba	u,h,t	unknown	Yes	Yes	Yes
Tortricidae	*Epinotia lantana*[2]	Mexico	u	*L.urticifolia*	Yes	Yes	Yes

[1] Agents introduced accidently or were already present in Australia and South Africa
[2] Agents introduced accidently into South Africa
[3] Too early to determine if agent will establish

d=undulata
f=fucata
g=glutinosa
h=hirsuta
m=montevidensis
o=urticoides
r=trifolia
s=hispida
t=tiliifolia
u=urticifolia

Table 2.
The status of agents on the five major groups of Lantana phenotypes in Australia.

Species	Common pink	Red	Australia Pink-edged Red	White	Orange
Aerenicopsis championi	u	u	u	u	u
Plagiohammus spinipennis	u	u	l	u	u
Alagoasa parana	p	acc	acc	pa	pa
Charidotis pygmaea	pa	d	d	pa	d
Octotoma championi	l	u	u	u	l
Octotoma scabripennis	a	a	a	a	a
Uroplata girardi	a	a	a	a	a
Uroplata fulvopustulata	l	u	u	u	u
Calycomyza lantanae	a	a	a	a	a
Ophiomyia lantanae	a	a	a	a	a
Aconophora compressa	d	pa	pa	l	pa
Falconia intermedia	d	acc	acc	acc	acc
Phenacoccus parvus	c	c	c	c	c
Leptobyrsa decora	u	u	u	u	u
Teleonemia harleyi	u	u	u	u	u
Teleonemia scrupulosa	c	c	a	c	u
Hypena strigata	c	c	c	c	c
Neogalea sunia	c	c	c	c	u
Ectaga garcia	pa	acc	acc	pa	pa
Lantanophaga pusillidactyla	a	a	a	a	a
Salbia haemorrhoidalis	u	c	c	u	u
Epinotia lantana	a	a	a	a	a

a=abundant in the field
c=common in the field
l=localised in the field
u=unknown

acc=accept as a host
pa=partial acceptance
d=died out in lab trials

borer, *Epinotia lantana* Busck (Harley 1973; Cilliers and Neser 1991; M. D. Day *et al.* unpubl. data). In addition, all of the agents that were introduced unintentionally, do not show preference for any lantana phenotype (Table 2). Of these, three species (the lantana mealybug, *Phenacoccus parvus* Morrison, the flower feeding moth *Lantanophaga pusillidactyla* Walker and the leaf feeding moth *Hypena laceratalis* Walker), also develop on *Lantana montevidensis* (Sprengler) Briquet in the field.

Effect of climate

Suitable climate has been acknowledged as a major contributing factor to the successful establishment of many biological control agents. Agents from tropical climes are unlikely to perform well when released in subtemperate areas and vice versa (Sands and

Harley 1980). In Australia, *L. camara* is found from Weipa (17°S) to southern NSW (36.5°S), a distance of 3,500 kms. It is also found from coastal regions with >3,000 mm rainfall to inland areas with <700 mm annual rainfall and from sea level up to 1,000 m (Swarbrick *et al.* 1995). In Sub-Saharan Africa, it is found in an equally broad range of climatic conditions, from the Western Cape (34°S) along the southern and eastern coast, through the highveld regions (>1,500m) (Henderson 1995) and northwards to beyond the equator. On Fiji's main island of Viti Levu, *L. camara* is found both in the cooler and wetter eastern and mountainous regions, and in the west which is flat and dry. *L. camara* adapts to climatic conditions by losing its leaves during times of drought or in winter. Consequently, populations of leaf feeding insects are markedly affected and do better in high rainfall areas where lantana maintains its foliage all year round.

Only two agents, *O. lantanae* and *L. pusillidactyla,* are found in almost all *L. camara* areas in Australia and South Africa. Most agents established in Australia and South Africa are found in discrete areas. Climate is considered the principal contributing factor to their distribution, as many areas contain more than one *L. camara* phenotype. *O. scabripennis* prefers cooler wet areas, while *U. girardi* prefers open sunny areas. In South Africa, where both species are found in similar geographic locations, *O. scabripennis* is found on lantana growing under the canopy of forest areas, while *U. girardi* is found around the perimeter where it is more exposed. Cilliers and Neser (1991) suggested that the success of *U. girardi* in South Africa was due to a new strain of *U. girardi* being imported that was more suited to prevailing climatic conditions, whereas a previous strain was ineffective.

T. scrupulosa, is also found in discrete locations, preferring exposed areas subject to full sun over forested areas or those with high humidity (Harley 1973). Furthermore, it has been observed in some areas during the dry months, but it can be virtually non-existent in the same areas during the wet season. Munniappan *et al.* (1996) also reports that *T. scrupulosa* was found mainly in the sites with full sun in Guam.

Other lantana agents only found in discrete locations are the tingid, *Leptobyrsa decora* Drake*,* and the hispine, *Uroplata fulvopustulata* Baly*,* which have established only in tropical far north Queensland. Both of these agents were released in large numbers throughout the lantana areas of the State. The cerambycid *Plagiohammus spinipennis* Thomson, has also been recorded from only one site (central NSW), although it was also released extensively in Queensland and NSW.

Effect of release strategies

The significance of release strategies and how these affect establishment has been recently reported by Grevstad (1996) and Memmott *et al.* (1996). These authors maintain that release strategies should consider the following: an agent's biology, whether or not field cages are necessary, the numbers released, climate and target weed phenotype. A number of establishment failures on *L. camara* were probably a result of inadequate release numbers. We suggest that of the eleven species that have failed to establish in Australia, probably five were due to inadequate numbers released. Inadequate release numbers could also have been the cause for failure of up to eight species to establish in South Africa. In several instances (eg *A. parana* and *Aerenicopsis championi* Bates in Australia and *Octotoma championi* Baly and *U. fulvopustulata* in South Africa), only a small number of adults were released because project funds were cut or laboratory cultures dwindled and the remaining adults were released (Cilliers and Neser 1991).

Discussion

Biological control attempts have been made on *L. camara* longer than on any other weed. However, the plant is still not under adequate control in many countries. The principal factors influencing lantana biocontrol appear to be that the plant is a hybrid species consisting of many phenotypes, originating from two or more species of lantana in tropical America, and that it grows in a wide range of climatic areas.

Recent studies have demonstrated that *L. camara* phenotypes are more closely related to some *Lantana* species than others, and that agents collected from hosts closely related to these phenotypes are more successful in establishing. The value of collecting agents from the same species as opposed to collecting from similar species is contentious. There have been several examples where agents collected from closely related species have brought the target weed under control. *Cactoblastis cactorum* Bergroth was collected from *Opuntia delaetiana* Weber to control *O. stricta* Haworth (Dodd 1940) while *Megacyllene mellyi* Chevrolat was collected from *Baccharis microdonta* de Candolle to control *B. halimifolia* L. (Tomley 1990). In these instances, the agents had a sufficiently broad host range to utilise several species in the same genus, but were specific enough to warrant release in the target country, and successful establishment ensued.

Agents may be collected from species other than the target weed because there are no damaging or specific agents on the target weed. Alternatively, there has been the view that new associations can be more effective. However, many biocontrol practitioners believe that the success of new associations is the exception rather than the rule. A plant may respond to insect attack, not by defence mechanisms but by producing more shoots and vegetative material (Myers *et al.* 1989). Agents should be collected from the target species where possible, as the insect would be better adapted to it. Other plant species may not have all the nutrient requirements that the insect needs to develop, reproduce and build up into large populations. Alternatively, the plant may have a morphology or contain compounds that deters feeding (Corbet 1985).

An example of the importance of collecting from the correct host is *C. pygmaea.* This beetle was introduced into Australia to control *L. camara* and *L. montevidensis* in the early 1990s. It was collected in Brazil from *Lantana fucata* Lindley, a close relative of *L. montevidensis* but it had also been observed on *L. tiliifolia*. The insect did not perform well on *L. camara* and laboratory populations on this plant in Australia died out (Day *et al.* 1999). It was reared in large numbers on *L. montevidensis* but despite over 30,000 adults released over a large number of sites with broad geographic and climatic ranges, the agent did not establish (M.D. Day and T.D. McAndrew unpubl. data). In South Africa, *C. pygmaea* survived on *L. camara* in quarantine but its performance was poorer than when reared on *L. montevidensis* (H. Sparks unpubl. data) and it is unlikely that further field releases will be made.

Priority should be given to collecting potential agents from *L. urticifolia* and if possible, the native host plants of an agent should also be imported into quarantine facilities so that comparative performance trials with the target phenotypes can be conducted. An alternative solution, is to transplant lantana phenotypes into the country of origin and see what agents readily attack them. However, this is probably not feasible due to quarantine restrictions.

The importance of collecting agents from the correct species is supported by the preference shown by agents to some lantana phenotypes. We theorise that if agents have shown preferences for phenotypes within a species, then it is highly likely that they will

show differences in their performance when placed on a different species to that from which they were collected. Blossey and Schat (1997) have also reported the importance of plant phenotypes in the establishment of agents while studying insects attacking purple loosestrife in the USA.

Recent preference and performance tests in Australia and South Africa have resulted in rearing and release methods being modified. *Falconia intermedia* Distant is now performing very well in the laboratory on pink-edged red lantana after trials in South Africa showed this to be the preferred phenotype amongst the phenotypes from Australia exposed to them in South Africa (A. Urban *et al.* unpubl. data). In addition, *Aconophora compressa* Walker is now being reared, released and has established on white lantana in Australia. Previously laboratory populations of both agents were not flourishing when reared on common pink lantana. Sands and Harley (1980) suggested that potential agents should be tested for their ability to build up and maintain populations on a phenotype and not just their ability to complete development on it.

The effect of climate on the establishment and distribution of agents is well documented. *C. cactorum* is controlling *Opuntia* spp. in Queensland, while it does not perform well in southern NSW and Victoria (Hosking *et al.* 1988). Sands and Harley (1980) proposed that agents should be collected from climatic areas similar to those in which agents are likely to be released. They also suggested that the same species should be collected from different climatic areas within their native range.

There are several regions, both in Mexico and Brazil, which are similar to areas of Australia and South Africa, where there are distinct seasons and lantana may yellow or defoliate over the dry winter months. In these areas, insect populations (especially those of leaf feeders) are not necessarily maintained at sufficiently high levels to cause significant damage to the plant. As a result, agents adapted to these various climatic conditions are being targeted. Several species of halticine (including species with root-feeding larvae), which have adults that diapause over winter, two species of cerambycids and several other species that attack lantana stems have been suggested for further study (Winder and Harley 1982; Palmer and Pullen 1995) or are already being studied (Baars and Neser 1999).

The use of CLIMEX (Sutherst *et al.* 1999) has also assisted in matching potential release sites for candidates with those of their native ranges. A number of localities in Queensland and NSW have been identified as possible release sites for *A. compressa*. As a result of releasing in some of these areas, initial colonisation has occurred. However, there are acknowledged limitations with using CLIMEX. Only general areas can be matched because the site used to collect weather data (often an airport) may be quite different from the nearest weed infestations some distance away.

Some candidates which failed to previously establish, possibly due to insufficient numbers released, have been re-imported by both countries. Further releases of *A. parana* and *A. championi* are being conducted in Australia while *E. xanthochaeta* is currently being reared at PPRI with the view to release. Pending the results of these additional releases, the agents may be exchanged between the two countries.

In addition, release programs are being carefully conducted to suit the biology and behaviour of the agents. Grevstad (1996) found significant differences in establishment using mated and unmated adults. When releasing beetles, adults should be held until they had reached maturity and then they can be released without the use of cages. Hispine beetles in both countries have been released and have successfully established using this

method. Moths on the other hand, have short lives and can be difficult to establish. Consequently, field cages should be used initially to hold adults until they mate. Releasing unmated moths may result in dispersion before mating can occur.

For many agents especially those released prior to the 1990s, we cannot accurately determine why they failed to establish. However by careful assessment of each agent both in the field and laboratory, a greater understanding of the factors and processes involved in the relationship of agent and target weed. We are hoping that, with new information such as DNA studies, phenotype testing and climate modelling at our disposal and by addressing the other issues covered in this paper, the establishment rates of agents can increase and lantana could be better controlled biologically. However, we accept that idiosyncrasies of the weed (in that it is not close to any one lantana species), means that finding effective, specific biological control agents suited to all lantana phenotypes in both countries may not be possible.

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